Theoretical Production Ecology: reflections and prospects

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Editorial note

This volume is a compilation of revised versions of the papers presented at the valedictory symposium for Professor C.T. de Wit. It is particularly appropriate that it should appear in the series Simulation Monographs that Professor de Wit himself founded.

The technique of computer simulation plays an important role in the study of complex, ecological systems. Realizing the difficulty of publishing all the details of computer simulation models in scientific journals, Professor de Wit approached Pudoc with the idea of launching a series of monographs so that the results of topical ongoing research could quickly be published.

The Simulation Monographs have now gained an international reputation as the only series solely devoted to simulating agricultural and biological systems and processes. Although at first the authors were Dutch, authors from other countries soon contributed, giving the series a much wider base. The editorial board aims to maintain the standard of the series while knowing that the readership greatly appreciates rapid publication.

One of the most successful Simulation Monographs was *Simulation of Ecological Processes*, written by C.T. de Wit and J. Goudriaan, which first appeared in 1974 and was followed in 1978 by a second, revised edition. A Japanese translation was published in 1977. Another volume in the series, the book by F.W.T. Penning de Vries and H.H. van Laar *Simulation of Plant Growth and Crop Production* (1982) has been translated into Russian and Chinese. To date, three books have been produced as co-editions with Oxford and IBH Publishing Co., four with John Wiley and Sons, and one with the International Rice Research Institute (IRRI).

Through the publication of this book we honour and thank Professor de Wit for the great enthusiasm, support and encouragement he gave to the Simulation Monographs series.

Professor R.A. Feddes
Editor-in-Chief

Preface

This book presents an impression of the field of Theoretical Production Ecology, its development and its position as an interdisciplinary science. Revised versions of the papers presented at the symposium *Theoretical Production Ecology: hindsight and perspectives*, organized on the occasion of Professor de Wit's retirement from Wageningen Agricultural University, are given and his valedictory address is included. The symposium was made possible by funding from Wageningen Agricultural University, the Directorate for Agricultural Research of the Dutch Ministry of Agriculture and Fisheries, and the Royal Netherlands Academy of Arts and Sciences.

The contributors are former students of de Wit, most of whom work at Wageningen Agricultural University and the Centre for Agrobiological Research and scientists from overseas who collaborated with de Wit. The papers have been presented according to the four scientific themes covered by the Department of Theoretical Production Ecology. They give an overview of the major developments during de Wit's inspiring involvement in production ecology, and indicate in which direction these developments may proceed in the years to come. During his scientific career of more than 40 years de Wit made substantial innovative contributions in each of these four fields.

In the theme *Soil and Climate* de Wit's thesis *A Physical Theory on Placement of Fertilizers* (1953) dealt with the influence of fertilizer application method on nutrient uptake and crop yield. He demonstrated that the effect of a given method of fertilizer application (e.g. in bands) could be calculated if the relationship between fertilizer application rate and uptake was known for the case of broadcasting. He also indicated under what conditions placement in bands leads to savings. This work is still relevant nearly 40 years later, as the debate on broadcast fertilization or band fertilization has gained new topicality because of current concern for environmental protection. De Wit's second major contribution to this theme, *Transpiration and Crop Yields* (1958), has become a classic. In this paper he demonstrated that the conventional, but controversial transpiration ratio (the relation between transpiration and dry matter production of crops) is actually a useful and conservative crop characteristic, which is predictably affected by growing conditions. The concept has since been widely used under various conditions, especially in arid and semi-arid areas.

In the second theme, *Crop Growth and Development*, de Wit contributed two classic papers, *On Competition* (1960) and *Photosynthesis of Leaf Canopies* (1965). They mark the beginning of new insight and theories and have had considerable influence on the way agronomic research in these areas has proceeded.

Both papers provide a scientific basis for agronomic studies. In *On Competition* particular solutions of the Lottka–Volterra equations were used to quantitatively describe competition between plants, and a bridge between intra- and inter-specific competition in plants was provided. In *Photosynthesis of Leaf Canopies* de Wit described the principles for the simulation of canopy assimilation from optical, morphological and geometrical characteristics of a crop, incoming radiation and temperature. These papers heralded a new area in agronomy and plant sciences.

De Wit's major contributions to the third theme, *Pests, Diseases and Weeds* has been in the field of weed control. His studies on competition between plants and on no-tillage agriculture have provided a scientific basis for weed science.

In all his work de Wit always has tried to bridge gaps between basic and applied science. This has been especially the case in the fourth theme, *Agricultural Production Systems*. There he succeeded in developing a methodology that allows biotechnical and socio-economic studies to be integrated. Multiple goal optimization techniques have been tailored to the specific needs of agriculturists, thus contributing to the cooperation between socio-economists and agronomists.

In this book, four chapters are devoted to each of the four themes. The 'external' authors illustrate the developments during the last 40 years and highlight de Wit's contribution. In the 'internal' contributions former students of de Wit describe the state of their art and give their views on the prospects in the various fields.

The preparation of the symposium and the editing of the book were easy tasks, as the readiness to contribute was great. A poster session, overviewing the various research projects in the field of Theoretical Production Ecology, was organized by W.A.H. Rossing and W. van der Werf. A summary of the posters is available on request from the Department of Theoretical Production Ecology. Many members of the staff of the Department of Theoretical Production Ecology and of the Centre for Agrobiological Research contributed to the preparation of the symposium and the poster sessions, and to this final publication. The staff of the International Agricultural Centre, where the symposium was held from 17-19 February 1989, were very helpful. It is impossible to mention all individual contributors – but all those who made the 'de Wit' symposium a success are hereby gratefully acknowledged.

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SOIL AND CLIMATE

1 Conservative behaviour in the response of crops to water and light

J.L. Monteith

1.1 Transpiration and crop yields

Transpiration and Crop Yields was the first major monograph that de Wit (1958) published when he returned to Wageningen from Burma. It revealed his skill in using theoretical ideas to reinterpret and illuminate measurements which had been gathering dust for years on the shelves of libraries; and it demonstrated the value of the physicist's approach to the analysis of field experiments in contrast to the statistician's. Physicists analyse systems by looking, in the first instance, for consistency and reproducibility in behaviour. Statisticians often seem more concerned with establishing whether differences and anomalies in behaviour are 'significant' or not!

Clearly, crop ecology has no constants in the physicist's sense but it has yielded a number of useful conservative quantities that have played a major role in the models developed by de Wit, by his Wageningen colleagues and by their many disciples in other parts of the world. I have chosen the subject of transpiration and crop yields partly because it illustrates the principle of conservatism so well, partly because it was expounded to me by Kees de Wit the first time we met in 1959, and partly because the relation between rainfall and crop growth is fundamental to food production in the semi-arid tropics where I now work.

1.2 Hindsight and foresight

Although Woodward (1699) gets credit for the first publication dealing with transpiration and assimilation by plants, J.B. Lawes (1850) was probably first to explore the subject in terms of agricultural production. In a somewhat protracted report to the Horticultural Society of London, he described growing wheat, barley, beans, peas and clover in pots which he weighed regularly to estimate transpiration and eventually harvested to determine production. The gain in dry weight per unit loss of water (a ratio referred to as *C/E* hereafter) differed much less between species than the absolute gain in dry weight. He therefore expressed the hope that '...future experiments may fix a definite relationship between the amount of water given off and that of the non-nitrogenous proximates fixed in the plant...provided their sources were mainly...in the atmosphere'.

The first major investigation of the relation between transpiration and production in arable crops was by scientists working in the Great Plains of the U.S.A. between 1910 and 1930. De Wit made extensive use of measurements by Briggs & Shantz (1914) and by Kiesselbach (1916), an acute observer who laid the foundation for much future research. In addition to demonstrating that C/E was a function of the drying power of the atmosphere as measured with an evaporation pan, Kiesselbach explored the relation between transpiration and leaf temperature, the way in which transpiration by foliage in a stand humidifies the microclimate, the difference in C/E between what we now refer to as C_3 and C_4 species ('approximately double'), and the lack of correlation between leaf anatomy and C/E for sorghum and maize. The final section of his summary is worth quoting because it anticipated by nearly 20 years the major advance made by Penman (1948) in the physics of natural evaporation as well as much subsequent work in the Department of Theoretical Production Ecology at Wageningen Agricultural University.

> Transpiration appears to be a purely physical phenomenon, depending primarily upon the moisture supply in the leaf and the evaporating power of the atmosphere, which is modified in some degree by temperature effects resultant within the leaf from chemical activity, transpiration, and from the absorption of radiant energy.

Penman's own attitude to C/E was ambivalent. A key paper by Penman & Schofield (1951) drew attention to the fact that the rate of carbon assimilation by plants was much smaller than predicted from the assumption that the concentration of CO_2 in intercellular spaces (c_i) was zero. Laboratory measurements demonstrating the conservatism of c_i were still far in the future, so it was perhaps not surprising that Penman & Schofield described C/E as a 'normally useless concept'. They showed foresight in concluding that 'a luxuriant crop grows with a concentration of gaseous CO_2 inside the leaf which in only 10 to 20% less than that in outside air'. In hindsight, they failed to appreciate the finer points of stomatal control of gas exchange when they wrote '...it is obvious that in many assimilation problems all that need be known about stomata is whether they are open or shut'!

De Wit's monograph, the next major publication in this field, and still a standard reference, quotes Penman's conviction that 'there is little value in the concept of "transpiration ratio"'. De Wit demonstrated convincingly that this view was wrong (but was too diplomatic to make the point explicitly!). I never heard Penman admitting that de Wit had persuaded him to change his mind, but the fact remains that his later analysis of irrigation experiments at Woburn and Rothamsted, started in 1951, showed clearly that C/E was conservative and he used this fact to establish a limiting water deficit below which loss of dry matter was proportional to the amount of water lacking for transpiration (Penman, 1970).

De Wit re-examined the role of stomata in determining both transpiration and carbon assimilation, used a Penman-type equation to estimate transpiration and developed a new formula for crop photosynthesis – the origin of much subsequent modelling and experimental work in the Department of Theoretical Production Ecology. However, he was unable to link assimilation and transpiration directly, because so little was then known about the connection between stomatal conductance and c_i. Instead, he reanalysed measurements of dry matter production (or yield) and transpiration for a wide range of species and sites where plants were grown either as groups in containers or as stands in the ground. He showed that in cool, temperate climates, production increased in proportion to transpiration up to a ceiling, whereas in hot climates it was necessary to divide transpiration by pan evaporation to obtain consistent proportionality. This conclusion neatly summarized a bewildering mass of evidence, extracting from it a few simple conservative quantities.

1.3 New perspectives

1.3.1 Single leaf model

In the 30 years following the publication of de Wit's monograph, understanding of how photosynthesis and transpiration are coupled expanded rapidly, stimulated by the development of highly sensitive and stable CO_2 analysers, portable porometers and other convenient equipment that plant physiologists can use either in the laboratory or in the field.

The first major advance was made by Bierhuizen & Slatyer (1965) whose measurements with several common crop species in the laboratory established that photosynthetic rates were approximately proportional to transpiration rates divided by the mean saturation vapour pressure deficit of the ambient air (D_a). Saturation deficit therefore replaced the rate of pan transpiration which de Wit had used as a surrogate for the drying power of air. Rijtema & Endrödi (1970) soon demonstrated that the mean rate at which stands of potato accumulated dry matter was proportional to E/D_a but crop physiologists and agronomists were somewhat slow to grasp the significance and usefulness of this relation. Similar evidence for a number of cereal and legume species has been reviewed by Tanner & Sinclair (1983) and by Monteith (1989).

To explore this line of work, I begin with gaseous exchange by a single leaf and then proceed to a homogeneous canopy treated as a 'big leaf' to avoid the complexities of canopy microclimate which are not relevant at this level of analysis.

For a single leaf,

$$E = \rho_w (e_i - e_a)/(p\, r_s) \qquad \text{Equation 1}$$

where e_i is the partial pressure of water vapour in air within intercellular spaces, usually identified as the saturation vapour pressure at the temperature of mesophyll tissue (Pa); e_a is the partial pressure of water vapour of air in contact with the epidermis: ρ_w is density of water vapour at atmospheric pressure and at the mean temperature of the system (g m^{-3}); p is the atmospheric pressure (Pa); and r_s is the resistance of the epidermis to water vapour diffusion, usually treated as a stomatal component when this is much smaller than the cuticular component (s m^{-1}).

For most types of green leaf, it is legitimate to neglect small differences of temperature that may exist between the mesophyll tissue of a leaf and its epidermis so that $(e_i - e_a)$ can be replaced by the saturation deficit of air in contact with the epidermis (D_e).

The flux of CO_2 assimilated by a leaf, as measured net of photorespiration, can be expressed similarly as

$$N = \rho_c (c_e - c_i)/(p\, r_s') \qquad \text{Equation 2}$$

where c_e is the partial pressure of CO_2 in air at the epidermis of a leaf (Pa); c_i is the partial pressure of CO_2 in the intercellular spaces; ρ_c is the density of CO_2 at atmospheric pressure and at the mean temperature of the system (g m^{-3}); and r_s' is the resistance to the diffusion of CO_2 through the epidermis (s m^{-1}). If the rate of photorespiration is R, the *gross* uptake of CO_2 proceeds at the rate

$$N + R = \rho_c\, c_i/(p\, r_x) \qquad \text{Equation 3}$$

an equation which defines r_x, a carboxylation resistance (Goudriaan et al., 1985). If c_e is set equal to c_i so that N becomes zero, Equation 3 reduces to

$$R = \rho_c\, \Gamma/(p\, r_x) \qquad \text{Equation 3a}$$

where Γ is a minimum intercellular pressure of CO_2, in effect, the decrease in partial pressure across r_x associated with photorespiration. Eliminating N and R from Equations 2 to 3a leads to an equation given by Goudriaan et al. (1985) in the form

$$c_i = f(c_e - \Gamma) + \Gamma \qquad \text{Equation 4}$$

The important ratio

$$f = (c_i - \Gamma)/(c_e - \Gamma) = r_x/(r_x + r_s') \qquad \text{Equation 5}$$

behaves conservatively when the environment of a leaf is changed in a way that affects r_x directly, e.g. through changes of leaf illumination or nutrient status (Goudriaan & van Laar, 1978; Wong et al., 1978) or even through exposure to SO_2 (Kropff, 1987). The implication is that r_s' changes more or less in proportion to r_x, giving values of f which range from around 0.3 for C_4 species to around 0.7 for C_3.

The converse is not generally true: environmental changes with a direct effect on r_s' do not necessarily induce proportional changes in r_x so in this case f is influenced by the state of the environment. The evidence can be summarized by appeal to experiments in which at least two of E, c_i and r_s' were monitored when the saturation deficit of ambient air, D_a, was increased. Two regimes can be distinguished:

- one for small values of D_a up to a limit D_l, often around 1 kPa but extending to 2 kPa in the measurements of Rawson et al. (1977). E increases almost in proportion to D_a implying that r_s is conservative so that c_i and N are also conservative

- and one for values of D_a above D_l, but below some upper limit D_u, usually poorly defined. E becomes almost independent of D_a at a rate determined by the ability of the root system to capture water (see Ackerson & Kreig, 1977, for an example). Consequently, r_s increases almost in proportion to D_a but the fashion for plotting the reciprocal of r_s against D_a (e.g. Bunce, 1985) obscures this fact. In this regime, c_i and N decrease (Sharp & Boyer, 1986; Cooper et al., 1988) implying either that r_x remains constant or that it increases more slowly than r_s. In either case, f decreases as D_a increases.

The conservative nature of f and of Γ, at least when plants have a good water supply or when the water demand is not very large, has major implications for the ratio N/E because Equations 1, 2 and 4 can be combined to give

$$N\,D_a/E = (c_e - \Gamma)\,(1 - f)\,(\rho_c\,r_s)/(\rho_w r_s') \qquad \text{Equation 6}$$

The ratio of densities ρ_c/ρ_w is 2.44 and for molecular diffusion through stomata r_s'/r_s is usually taken as 1.60. The term in square brackets therefore has a constant value of $z = 1.53$.

The quantity $N\,D_a/E$ should therefore be conservative in the absence of stress; with mild stress, it will increase somewhat if f decreases. With severe stress, both f and Γ may increase so that $N\,D_a/E$ decreases.

1.3.2 Canopy (big leaf) model

Following the procedure of Tanner & Sinclair (1983), Equation 6 can be applied to a uniform stand of vegetation rather than a leaf and to rates of dry matter production (C) rather than of net photosynthesis (N). This transformation involves a number of major assumptions but they lead to a conclusion fully consistent with the evidence that $C\,D_a/E$ is conservative in the field.

A major assumption is that Equations 1 to 6 which pertain to a single leaf can be applied to a canopy of leaves of different age and exposed to a range of radiation, temperature and saturation deficit according to the structure of the microclimate and the architecture of the foliage. This simplification, supported both by experiment and by theory (Monteith, 1981), leads to an equation for canopy transpiration analogous to Equation 1, viz.

$$E = \rho_w\,D_0/(p\,r_c) \qquad \text{Equation 7}$$

where r_c is the canopy resistance to the diffusion of water vapour analogous to the stomatal resistance of a single leaf; and D_0 is the saturation deficit of air at the effective level of the vapour source.

(Equation 7 is a link between alternative forms of the Penman equation in which the effective wetness of vegetation is allowed for by introducing either a diffusion resistance r_c or a saturation deficit D_0.)

Extending the analogy between leaf and canopy to carbon dioxide, the net rate of photosynthesis by a canopy can be written as

$$N = \rho_c\,(c_0 - c_{ic})/(p\,r_c') \qquad \text{Equation 8}$$

an equation in which concentrations and fluxes need to be carefully identified. The resistance r_c' is the effective resistance of the canopy for the diffusion of CO_2 through stomata and is therefore the analogue of r_c for water vapour. The concentration of CO_2 at the effective surface of the canopy (c_0) can be found from the concentration at the reference height c_a using the relation

$$c_0 = c_a - (N\, r_a p/\rho_c) \qquad \text{Equation 9}$$

where r_a is the resistance to the diffusion of CO_2 between the reference height and the level of the effective sink for CO_2 within the canopy. Later, this level is assumed to be identical for CO_2, water vapour and heat on the grounds that exchanges of all three entities are dominated by the absorption of radiation. Because the resistances r_c and r_c' both pertain to molecular diffusion through stomata, it is logical to assume that $r_c'/r_c = r_s'/r_s = 1.6$.

The remaining term in Equation 8, c_{ic} is an effective intercellular partial pressure of CO_2 within the 'big leaf' formed by the canopy. This quantity can be estimated when all the other terms in Equation 8 are known, following a procedure often used for single leaves. It is then possible to define a non-dimensional parameter for a canopy with the same physiological significance as f for single leaves, viz.

$$f_c = (c_{ic} - \Gamma)/(c_0 - \Gamma) \qquad \text{Equation 10}$$

The validity of this type of analysis is intuitive because few attempts have been made to establish the conservatism of c_{ic} and f_c experimentally. Values of c_{ic} estimated from profiles of water vapour and carbon dioxide over a field of wheat ranged from about 19 to 25 Pa (Monteith, 1963).

Estimating f_c in the absence of water vapour and CO_2 profiles is possible when the ratio of dry matter production to transpiration is known. To follow this route, it is first necessary to estimate the dry matter equivalent of the net CO_2 flux using factors proposed by Tanner & Sinclair (1983), viz. x_1 is the mean mass of plant material synthesized per unit of CO_2 assimilated, as estimated from the work of Penning de Vries (1975) (see Table 1); x_2 is the fraction of daily integral of N remaining after accounting for maintenance respiration, assumed to be 0.6; and x_3 is the fraction of accumulated dry matter harvested (which usually excludes roots, dead leaves, etc.) assumed to be 0.80.

Then the rate of dry matter production (in g m^{-2} d^{-1}) corresponding to a net photosynthesis rate of N is given by

$$C = x_1\, x_2\, x_3 N \qquad \text{Equation 11}$$

Equations 7, 8, 10 and 11 can now be combined to give

$$C\, D_0/E = z\, x_1\, x_2\, x_3\, (c_0 - \Gamma)\, (1 - f_c) \qquad \text{Equation 12}$$

Two difficulties remain. First, unlike C and E, D_0 cannot be measured directly, but from Equation 7, D_0/E is defined by the value of r_c which can be estimated in a number of ways. Second, Equation 12 is valid for instantaneous rates of photo-

Table 1. Values of $\bar{C}\,\bar{D}_a/\bar{E}$ and e reported for three crop types (Monteith, 1989) and of parameters used in model.

Crop type	Reported values		Assumed values		
	$\bar{C}\,\bar{D}_a/\bar{E}$ (g kg^{-1} kPa)	e (g MJ^{-1})	e (g MJ^{-1})	Γ (Pa)	x_t
C_4 cereals	8.3–9.5	1.2–1.7	1.5	0	0.51
C_3 cereals	2.9–3.1	1.0–1.3	1.2	5	0.51
C_3 legumes*	3.9–4.8	0.6–0.75	1.0	5	0.41

* Excluding groundnut.

synthesis and transpiration, whereas C and E are usually measured as daily mean rates for periods of a week or longer. Because all the terms in the expression $C\,D_0/E$ depend on the diurnal cycle of radiation, they are strongly correlated. It follows that the value of this ratio derived from daily means of its components, i.e. $C\,D_0/E$ will generally differ from the daily mean of instantaneous values $C\,D_0/E$ as Tanner & Sinclair (1983) pointed out.

A simple model for diurnal changes of weather is needed at this stage so that several forms of the ratio dry matter/water can be compared in terms of their dependence on weather and on f_c.

1.3.3 Weather model

Solar radiation S was assumed to be a sine function of time with a maximum of S_m at noon, at phase angle increasing monotonically from 0 at sunrise to π at sunset, and a daylength of 14 h. To find the net radiation R_{ni} received by a canopy if its foliage were at air temperature, the reflection coefficient α was assumed to be 0.2 and the net long-wave loss was taken as $(S_m/900) \times L$ where $L = 100\ \mathrm{W\ m^{-2}}$ was assumed to be the net loss to a cloudless sky from a surface at air temperature. Then the isothermal net radiation at any time is

$$R_{ni} = (1 - \alpha)\,S - (S_m/900)L \qquad \text{Equation 13}$$

The additional long-wave flux associated with the difference between foliage and air temperature was combined with the flux of sensible heat so that a single resistance could be used for heat transfer by turbulence and long-wave radiation (Monteith, 1973). The aerodynamic component of this resistance was assumed to have a value of 30 s m^{-1} characteristic of arable crops.

The air temperature at screen height was also assumed to be sinusoidal with a phase angle increasing from 0 at sunrise to π 18 h later, so that the temperature maximum occurred 2 h after noon. The difference between maximum and minimum temperature was assumed to be proportional to maximum solar radiation and was set at 20 °C for $S_m = 900$ W m^{-2}. Vapour pressure was assumed to be constant during the day so that the saturation vapour pressure deficit was determined by the relative humidity at dawn and the subsequent variation of air temperature.

With the diurnal change of weather specified in this way, corresponding changes in the components of dry matter/water ratios were found as follows.

In rigorous analyses, the relation between gross photosynthetic rate and the irradiance of single leaves is often assumed to be hyperbolic or exponential. As I was primarily concerned with daily totals of dry matter production and radiant energy, I made the simpler assumption that C was proportional to intercepted radiation throughout the day and took ground cover as complete. It was then possible to obtain values of the parameter $e = C/S$ from the literature (see Table 1) so that N could be evaluated as

$$N = e\,S/(x_1\,x_2\,x_3) \qquad \text{Equation 14}$$

The literature contains convincing evidence (e.g. Kiniry et al., 1989) that, at least in the absence of stress, e is not sensitive to differences of environment for a particular species or group of species. Using a linear relation between C and S implies that r_c' will be somewhat overestimated in weak light and underestimated in strong light. The same proportional error then appears in r_c, so when dry matter/water ratios are calculated, resistance errors are partly self-cancelling.

The instantaneous rate of transpiration was estimated from the Penman-Monteith equation as a function of R_n, D_a, air temperature and vapour pressure, and transfer resistances. The canopy resistance for vapour transfer, r_c was evaluated as 1.6 times the CO_2 resistance, found by combining Equations 8, 9 and 10 to give

$$r_c' = (1 - f_c)\,(\rho_c(c_a - \Gamma)/(p\,N) - r_a) \qquad \text{Equation 15}$$

with N found from Equation 14.

D_0/E was evaluated from Equation 7, knowing the value of r_c, and D_a was obtained directly from the weather model.

Changes in the dry matter/water ratio induced by a shortage of water were explored by setting an upper limit, E_m, to the hourly rate of transpiration, conveniently specified as the equivalent flux of latent heat. Using the procedure just described, the diurnal change of E was calculated first, to give the potential rate of transpiration. For hours in which E exceeded E_m, r_c was calculated from an inverse form of the Penman-Monteith equation and the net flux of CO_2 was calculated using $r_c' = 1.6\,r_c$ and leaving the canopy equivalent of r_x unchanged so that f_c decreased as E_m decreased.

1.4 Output from the models

In Figure 1, four ways of calculating the dry matter/water ratio are compared, using daily solar radiation as the independent variable. Ratios are plotted on a

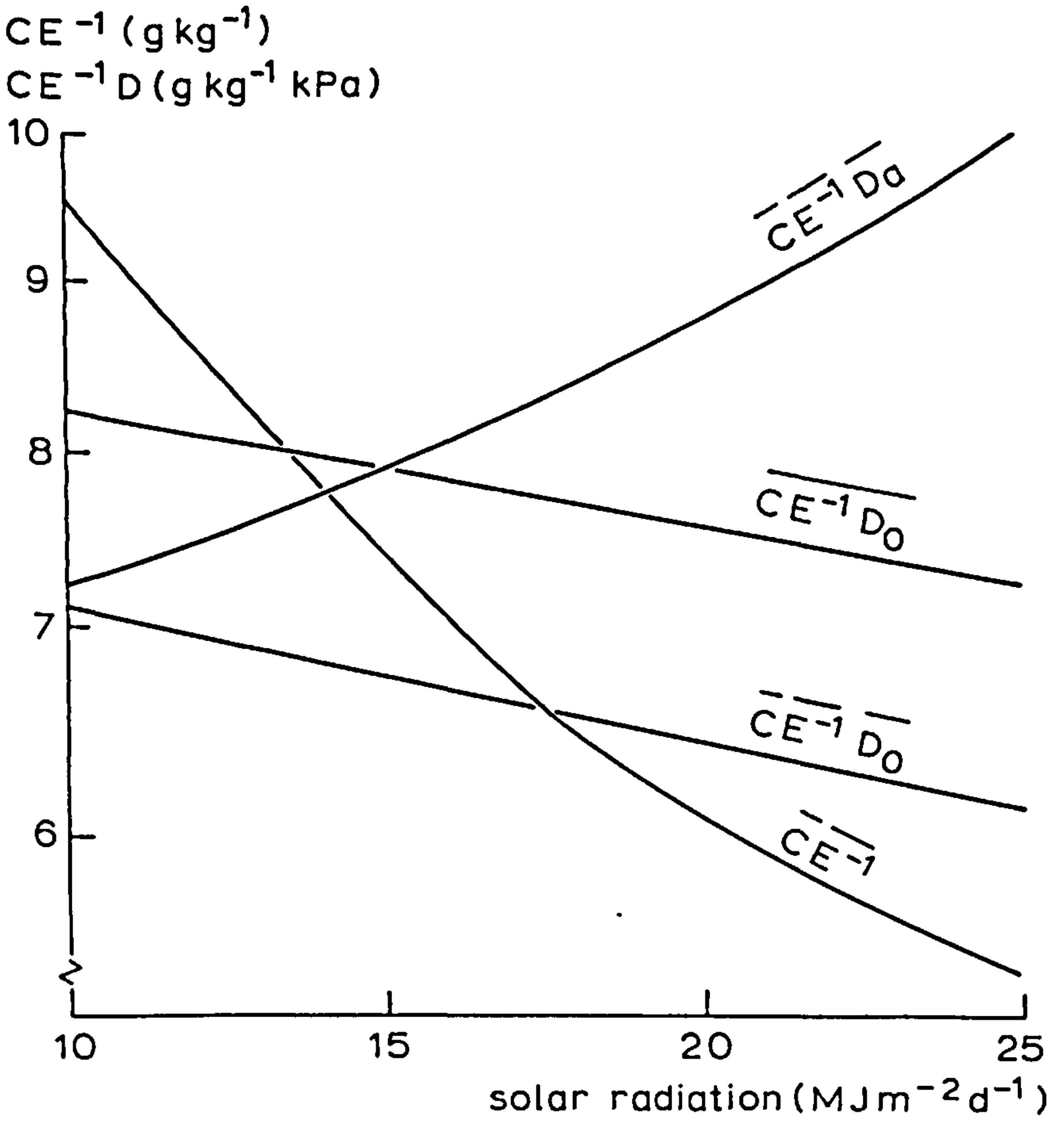

Figure 1. Dependence on daily totals of solar radiation of several parameters which include the ratio of dry matter production to transpiration. Bars indicate mean values of individual components or of products of components over hours of daylight. Physiological parameters were chosen for a C_4 cereal (Table 1) with $f_c = 0.3$. The weather is specified in the text. Mean daytime temperature ranged from 16 °C at 10 MJ m^{-2} to 23 °C at 25 MJ m^{-2}; dawn relative humidity was 80%.

logarithmic scale so that proportional changes can be compared in terms of relative slopes. All ratios are for a C_4 cereal and a time step of one hour was used to estimate daily mean values.

For the range of radiation chosen (10 to 25 MJ m^{-2} d^{-1}) the smallest variation (about 7%) occurs in ratios normalized by the saturation deficit in the canopy, D_0. There would be no variation in the 'theoretical' ratio $\bar{C}\,\bar{D}_0/\bar{E}$ if the concentration of CO_2 in the canopy remained constant, but the microclimatic model allows it to decrease with increasing radiation because of increasing photosynthesis (Equation 9). The ratio obtained from daily mean values of components ($\bar{C}\,\bar{D}_0/\bar{E}$) was somewhat smaller than the mean of hourly values of the ratio ($\overline{C\,D_0/E}$) but depended on radiation in the same way.

A much larger difference appeared when the saturation deficit at a reference height above the canopy, D_a was substituted for D_0. The normalized ratio then increased with radiation and had a range of about 16%. The reason for this increase is that the diurnal cycle of D_a depends on the diurnal variation of temperature imposed by the weather model, whereas the microclimatic model makes D_0 depend both on D_a and on exchanges of sensible and latent heat in the canopy. For the conditions specified, D_a increases more rapidly than D_0 during the first part of the day because the vapour pressure of air at the reference height is assumed to be constant, whereas within the canopy it increases because of transpiration. This effect overrides temperature changes, which usually act in the opposite direction, at least during the morning.

In the real world, however, the lower atmosphere will often be coupled to the underlying surface in such a way that the ratio of D_a/D_0 changes less with radiation (or temperature) than the model predicts, in which case Figure 1 would exaggerate the dependence of $\bar{C}\,\bar{D}_a/\bar{E}$ on weather. Similarly, with small plots, as used by Day et al. (1978) for example, the type of microclimate assumed here (for a horizontally uniform canopy) will not exist and foliage at all heights will be exposed to air with a saturation deficit close to D_a. Here again, the value of $\bar{C}\,\bar{D}_a/\bar{E}$ would exhibit the same weak dependence on radiation (and on temperature) as $\bar{C}\,\bar{D}_0/\bar{E}$. This may be one reason why values of $\bar{C}\,\bar{D}_a/\bar{E}$ reported in the literature are more conservative than might be expected from the evidence of Figure 1.

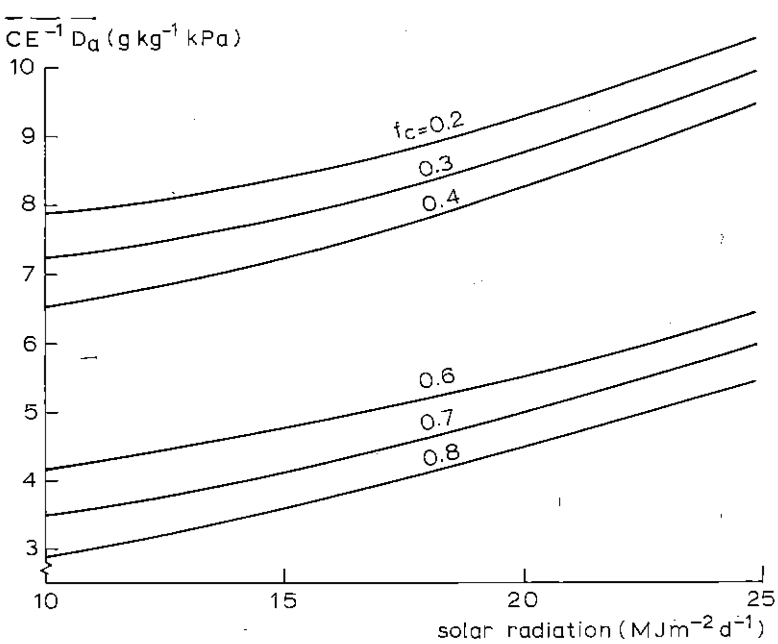

Figure 2. Dependence on daily totals of solar radiation and on f_c of $\bar{C}\,\bar{D}_a/\bar{E}$ for a C_4 ($f_c = 0.2$ to 0.4) and a C_3 species ($f_c = 0.6$ to 0.8). Mean daily temperatures corresponding to a range of 10 to 25 MJ m^{-2} were set at 16–23 °C for C_4 and 13–20 °C for C_3; dawn relative humidity was 80% (C_4) or 90% (C_3).

The value of the straight ratio C/E decreases with increasing radiation (because E depends on saturation deficit as well as on radiation) and has the largest range in Figure 1, about 28%.

Figure 2 shows how the value of $\bar{C}\,\bar{D}_a/\bar{E}$ for both C_4 and C_3 cereals depends on f_c. For sorghum, the mean measured value of the ratio is about 9 g kg^{-1}kPa and for an appropriate range of radiation (20 to 25 MJ m^{-2} d^{-1}); this is consistent with a value of f_c around 0.3, as reported for single leaves of C_4 species. The same value of f_c appears to be valid for maize, which has a somewhat larger value of e (1.75 compared with 1.5 g MJ^{-1} (Kiniry et al., 1989)), offset by a cloudier and slightly cooler environment for which radiation is usually in the range 15 to 20 MJ m^{-2}.

For wheat grown in New Zealand and for barley in the U.K., values of $\bar{C}\,\bar{D}_a/\bar{E}$ close to 3 g kg^{-1} kPa have been reported. Assuming that daily solar radiation was in the range 10 to 15 MJ m^{-2} d^{-1} for most of the growing season, it appears f_c was about 0.8. Although this is somewhat larger than the round number of 0.7 often quoted for C_3 species, it is well inside the range reported in the literature.

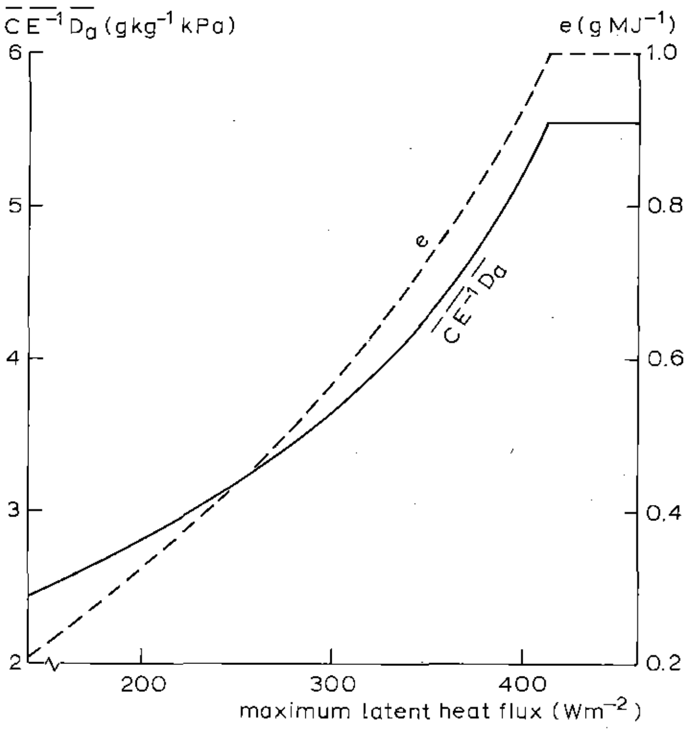

Figure 3. Dependence on maximum latent heat flux λE_m for a C_3 legume, of (e) daily mean value of dry matter per unit of intercepted radiation; and ($C\,D_a/E$) normalized transpiration ratio. Mean temperature 20 °C, radiation 20 MJ m^{-2} d^{-1}, dawn relative humidity 80%.

For C_3 legumes grown in warm climates, values of $\bar{C}\,\bar{D}_a/\bar{E}$ are larger than for C_3 cereals (Table 1), possibly reflecting the influence of higher temperature and radiation as discussed in relation to Figures 1 and 2. Conversely, measurements of e are smaller than for C_3 cereals. To investigate whether an inadequate supply of water could account for this difference, e was assumed to have an upper limit of 1.0 g MJ^{-1} and both e and $\bar{C}\,\bar{D}_a/\bar{E}$ were evaluated as functions of λE_m, the upper limit for latent heat loss during the course of the daily cycle (Figure 3). For the weather chosen, $\bar{C}\,\bar{D}_a/\bar{E}$ decreased with λE_m below 400 W m^{-2}, because stomatal closure reduced C more than E. A value of λE_m in the range 320 to 370 W m^{-2} appears to be consistent with the values of e and $\bar{C}\,\bar{D}_a/\bar{E}$ reported for C_3 legumes (Table 1).

Although precise values of the ratios plotted in Figures 1 to 3 clearly depend on the level of variables chosen for the weather model, the general inferences drawn in this section do not depend critically on the mean values of these levels or on the specific diurnal variations they were assigned.

1.5 Postscript

In this analysis of transpiration and crop production, de Wit was the first to introduce a normalizing factor that took account of the role of atmospheric humidity. This idea was later refined by other workers and notably by his own colleagues in Wageningen whose work has benefited so much from his stimulation and encouragement.

The analysis in this paper goes one step further and is based on several clearly tenuous assumptions. However, it reaches the satisfactory conclusion that the conservative parameter f (ratio of non-stomatal to total physiological resistance to CO_2 diffusion) has similar values for single leaves in the laboratory and for canopies of the same species in the field, treated as a 'big leaf'. It also explores the implications and limitations of using the saturation deficit of air at a reference height as a convenient substitute for the value within foliage.

I am conscious that this tribute to the inspiration and guidance of an old friend lacks the rigour he has always maintained in his own work and within his Department; but at least it demonstrates an important de Wit precept that simulation modelling should be used to relate processes at two levels of organization, in this case, the leaf and the canopy. It also demonstrates that crop models that currently assume a constant value of $C\,D_a/E$ could be made more rigorous by introducing a microclimatic sub-model accounting for vertical gradients of saturation deficit and CO_2 concentration.

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2 Atmospheric CO_2, global carbon fluxes and the biosphere

J. Goudriaan

2.1 Introduction

In the atmosphere carbon occurs mainly as CO_2, in the biosphere mainly as organic compounds, and in the sea mainly as bicarbonate and carbonate ions. The amount of atmospheric carbon is relatively small compared with the amounts of carbon in the biosphere and in the ocean, and therefore the level of atmospheric CO_2 can be expected to be sensitive to changes in the global carbon fluxes. This paper describes a simulation model for the global carbon cycle that was developed to investigate interaction between the carbon pools in the ocean, the biosphere and the atmosphere, particularly how the interaction affects atmospheric CO_2.

The most obvious reason for the rise of atmospheric CO_2 is the burning of fossil fuel, but deforestation is also generally considered to be a significant source of CO_2. However, this source is partly compensated for by regrowth. This paper aims at estimating not only the *gross* but also the *net* release of carbon from the biosphere to the atmosphere.

The terrestrial biosphere, and especially the soil, contains a significant amount of carbon. The quantity of carbon stored depends on a dynamic equilibrium between processes of decomposition and photosynthetic carbon fixation. When atmospheric CO_2 rises, it stimulates leaf photosynthesis, and consequently the dynamic equilibrium can be expected to be shifted towards a larger carbon storage. An important question is to what extent emission of CO_2 to the atmosphere is buffered by biospheric fixation of carbon. Since this storage occurs in reservoirs with vastly different time coefficients, the time pattern of storage is a complex phenomenon.

The carbon pool in the ocean is much larger than the carbon pools in the atmosphere and biosphere combined. Chemical buffering in the ocean stores about 40% of the CO_2 emission, but a much larger percentage could be stored if the emission rate were lower, permitting more time for mixing towards the deep sea.

Although the mechanism for storage of carbon in the ocean is mainly by chemical buffering, there is an important role for the functioning of the marine biosphere. Algae have a short lifetime and so carbon storage in algae themselves is negligible. However, a small portion of their remains sinks to the waters of the deep sea, where it decomposes, causing a considerable carbon flux from the surface waters to the deep sea. As a result of this process, water from the deep sea has a much higher CO_2 pressure than surface water. Algal growth is mostly limited by phosphate, and so eutrophication of the sea can reduce atmospheric CO_2 by increasing the deep sea storage of carbon.

The deep waters of the Atlantic Ocean have lower nutrient and carbonate levels than the deep waters of the Pacific and Indian Oceans. The mixing currents in the Atlantic Ocean are much stronger, and prevent high levels from building up. Ocean currents also have a large effect on atmospheric CO_2, and this may help explain the sudden end of the glacial periods.

The ratios of ^{13}C and ^{14}C to ^{12}C are different in the atmosphere, in ocean water, in fossil carbon and in biomass. These differences and their time patterns are used here for validating the model presented.

2.2 Carbon reservoirs and fluxes

Three major reservoirs of carbon, the atmosphere (700 Gt C), the oceans (39 000 Gt C) and the terrestrial biosphere (2000 Gt C) exchange carbon in the form of CO_2 (Figure 4) (Bolin et al., 1979; Clark, 1982). The photosynthetic activity of the biosphere acts as a powerful driving force for these exchange fluxes.

With industrialization, increasing amounts of carbon from fossil fuels are emitted as CO_2 into the atmosphere, at present at a rate of over 5 Gt C yr^{-1}. At the current rates, about 60% remains in the atmosphere and 40% is absorbed by the oceans, but this partitioning is dependent on the rate of emission itself. A lower rate of emission gives more time for absorption in the ocean. The chemical buffering capacity of the oceans is large enough for about 85% of each unit of CO_2

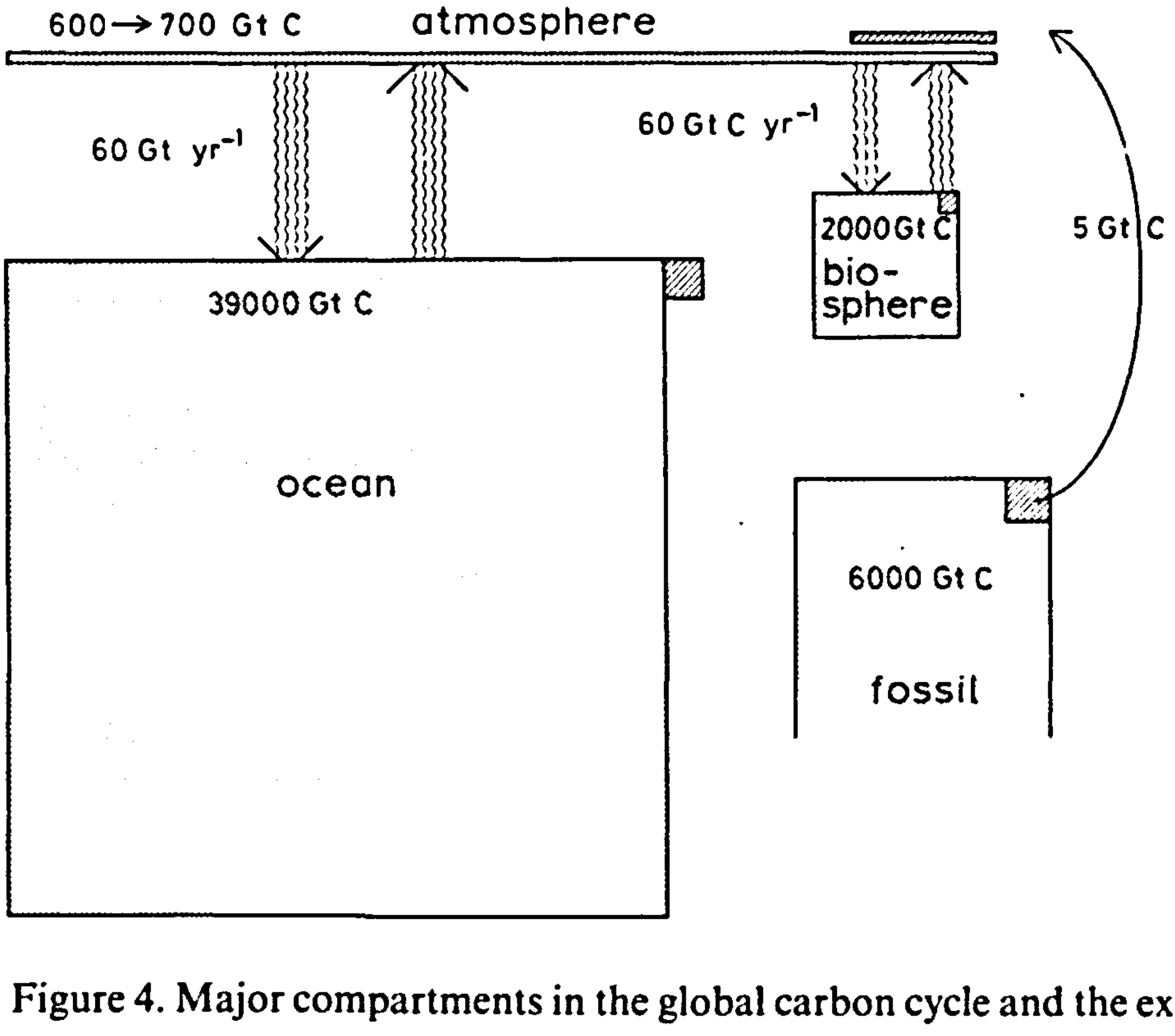

Figure 4. Major compartments in the global carbon cycle and the exchange fluxes between them. The accumulated effect of the fluxes of fossil fuel burning and biomass removal over the last 200 years is indicated by the hatched rectangles.

emitted into the atmosphere to be absorbed eventually, leaving only 15% in the atmosphere. However, mixing in the deep sea is so slow, that hundreds of years will be needed for this absorption capacity to be utilized. Biospheric uptake is not yet included in this calculation.

The surface waters of the oceans are almost in equilibrium with atmospheric CO_2, but the deep waters have a much higher CO_2 pressure (above 1000 μmol mol^{-1}) and a correspondingly higher carbonate and bicarbonate content. This high level is maintained by the sinking of carbon contained in the remains of dead plankton. In the upper layer of the sea photosynthetic activity extracts carbon from the water, and strongly reduces the levels of nutrients such as phosphate. Local upwelling of deep water returns these nutrients and some of the accumulated carbon to the surface layers. The intensity of this circulation flux is estimated to be about 2 to 6 Gt C yr^{-1} (Baes et al., 1985).

The chemical equilibration of ocean water with atmospheric CO_2 is the most important sink of CO_2 released into the atmosphere, either from fossil fuel or from the biosphere. The slope of the graph of carbon in atmospheric CO_2 versus carbon emitted from fossil fuels (Figure 5) can be considered as the fraction remaining in the atmosphere, and it is therefore called the 'airborne fraction'. Because of the chemical nature of buffering of CO_2 in the ocean, this fraction is expected to be fairly stable. Over the period 1960–1980 it had an observed value of 0.576 (Bolin, 1986).

Although the net uptake of carbon by the terrestrial biosphere is modest when

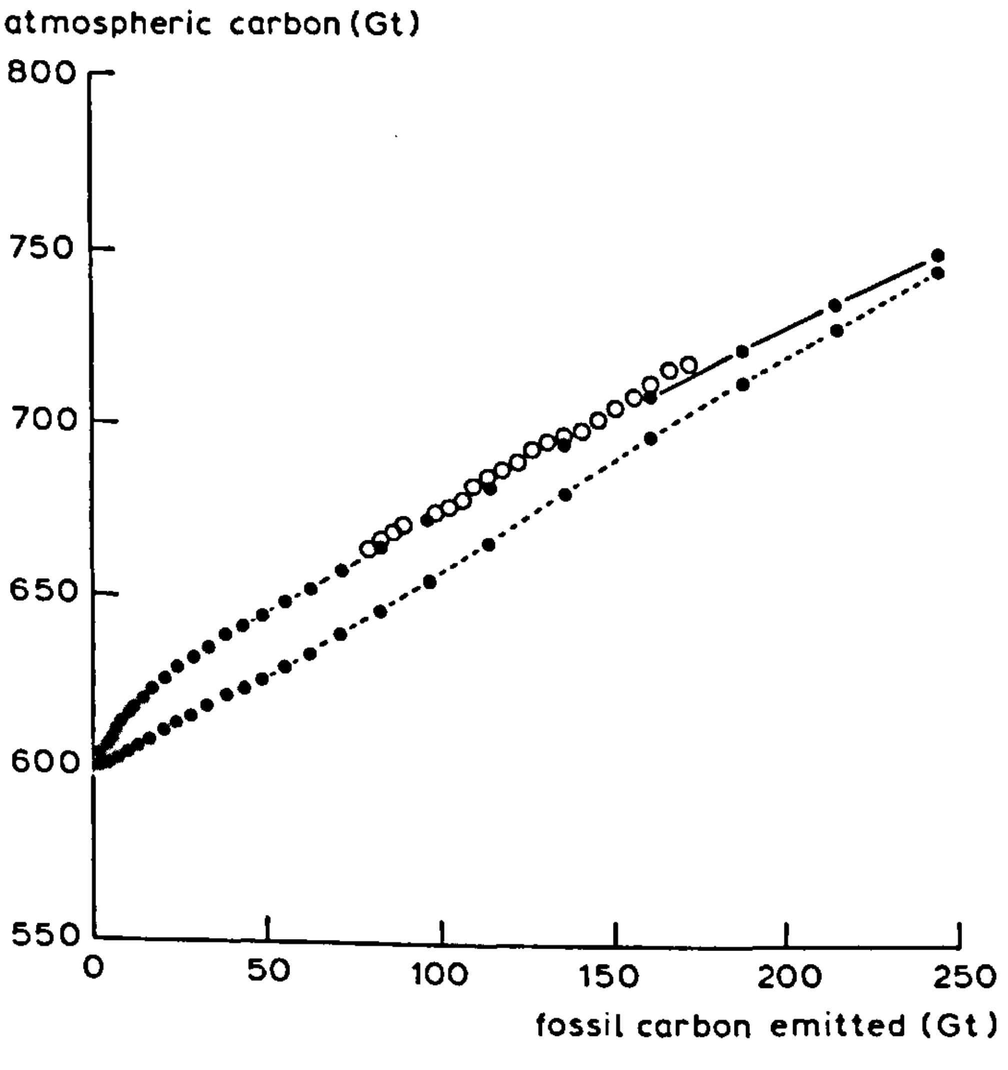

Figure 5. Simulated (every 5 years until 1995, (●)) and measured (annually 1958–1988, (o)) atmospheric carbon versus cumulative emission of carbon from fossil fuels. The simulated results were obtained with (———) and without (- - - -) biospheric exchange.

compared with the ocean, an undisturbed biosphere is potentially able to sequester large amounts of carbon. On the other hand, significant amounts of carbon (mainly in the form of CO_2) can be released from the biosphere when it is disturbed. Reclamation of land for agriculture and for other types of human utilization can cause oxidation of carbon compounds in the soil and of long-lived biomass such as wood. These processes took place on a large scale in the past century. They are still continuing, and are accelerating in the tropics, but at the same time a global stimulus of growth caused by increased atmospheric CO_2 itself is increasingly restoring the terrestrial carbon balance (this study). Regrowth on abandoned land partially compensates for losses of carbon elsewhere. In this study the effect of these processes on the rate at which the level of atmospheric CO_2 is rising, is quantitatively analysed.

The stimulation of net photosynthesis by CO_2 causes an additional buffering of atmospheric CO_2 into the biosphere. The eventual partitioning of carbon over the three reservoirs atmosphere, ocean and terrestrial biosphere will be 0.11 : 0.71 : 0.18, respectively (result of this study), in contrast to the 0.15 : 0.85 : 0.0 mentioned earlier for the situation when the biosphere was ignored.

Over the 200 years until 1980, it is estimated that about 159 Gt C were released by burning of fossil fuel. About 108 Gt C remained in the atmosphere raising the atmospheric partial pressure of CO_2 from 285 to 337 μmol mol^{-1} (Goudriaan & Ketner, 1984). However, the biosphere also released carbon as a result of deforestation and decomposition of organic matter in cultivated soils. Estimates vary from more than 100 Gt C in total (Houghton et al., 1985) to about 39 Gt C (this study). Obviously, to balance the global carbon budget, estimates for ocean uptake over the same period should vary between more than 150 Gt C to 89 Gt C in this study. Whereas the high estimates are hard to reconcile with oceanographic data (Bolin, 1986), my own low estimate is in much better agreement with these observations.

2.3 The terrestrial biosphere

2.3.1 Model components in time and space

Model components in time In this study the biosphere was modelled in the same way as presented in a previous paper by Goudriaan & Ketner (1984). A one-box model is unable to represent the complex dynamic response of the whole system, or to describe the different effects of human disturbance on wood, leaves and soil carbon. Therefore, a cascade of carbon pools (Figure 6), consisting of short-lived (leaves) and long-lived (wood, humus) components was used. Each individual component was treated as a simple first-order box, characterized by its own residence time. The carbon flow to living biomass was driven by net primary productivity (*NPP*), subdivided into flows to leaves, branches, stemwood and roots. The outflows cascade down to litter, humus, and resistant soil carbon. In transition from biomass to humus a considerable fraction of carbon is lost by respiratory processes, and also in transition from humus to resistant soil carbon. In Table 2 the residence time and the fraction of carbon flowing to the next pool are given for each pool of carbon. The complement of this fraction returns to the atmosphere as respiratory CO_2.

For humus and resistant carbon this type of structure can be derived from the work of Kortleven (1963) and of Olsen (1963), who both showed that the response of humus level to litter input is of a first-order character. Schlesinger (1986) reviewed several data sources supporting the contention that the dynamics of humus are first order. He mentioned that considerable losses in soil carbon occurred when virgin land was reclaimed (from an equilibrium of 20 kg C m^{-2}, to a new equilibrium of 15 kg C m^{-2}, to be reached after several decades).

These losses can be well simulated by using a shorter residence time of humus in agricultural soil (20 yr) than in grassland or in forest (50 yr). Resistant carbon (residence time 500 years) which amounts to about 10 kg C m^{-2} is included in total soil carbon, and is much less affected by these land use changes.

Model components in space In an earlier model (Goudriaan & Ketner, 1984) only 6 major types of vegetation ('ecosystems') were distinguished, to represent the major features of the geographical distribution of biotic terrestrial carbon.

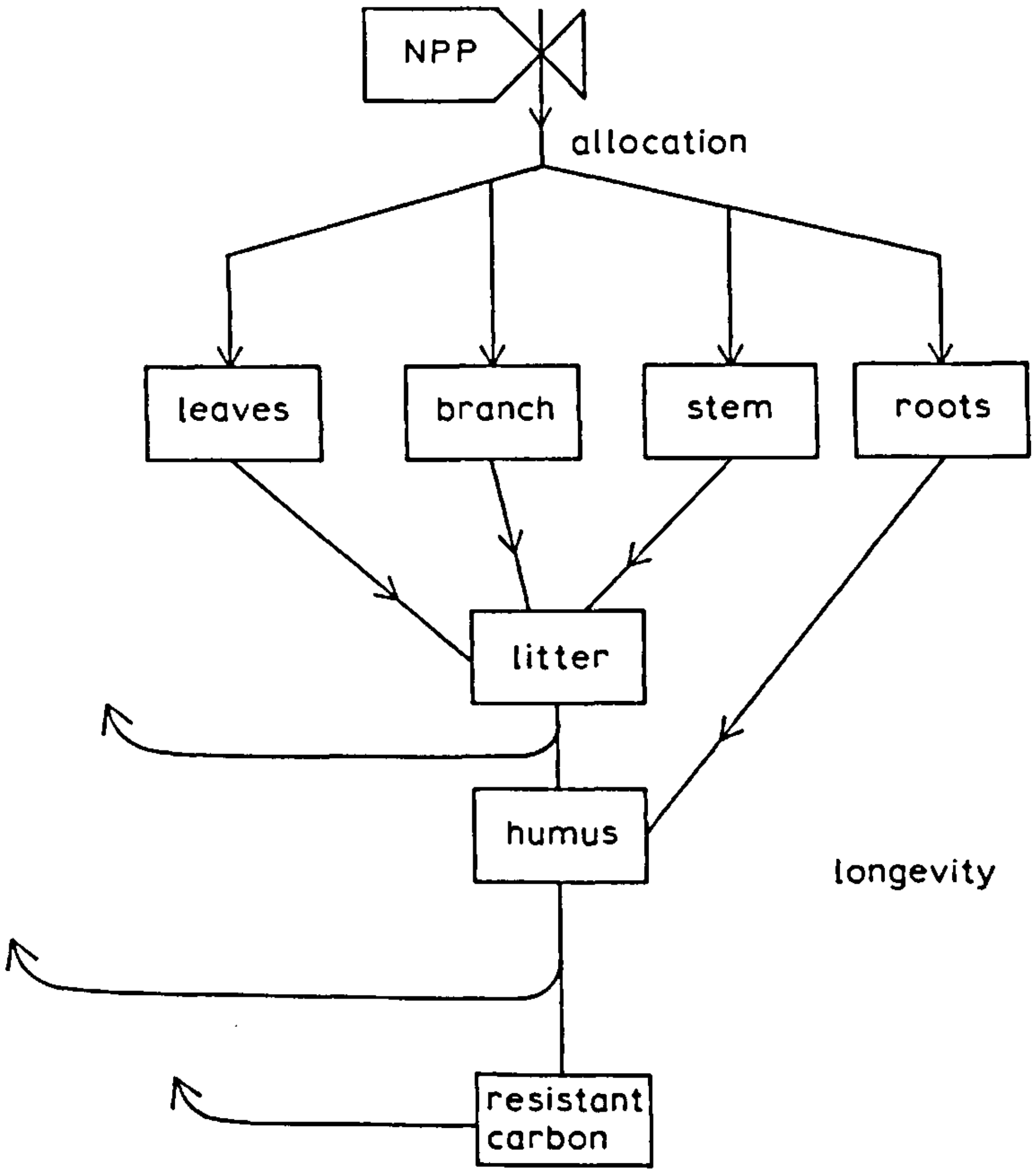

Figure 6. Generalized model structure for an ecosystem. Each box itself is described by first order decay. *NPP*, its allocation, longevities and transitional losses from one box to the next are characteristic ecosystem properties.

Table 2. Characteristics used as model input in this study for the six major vegetation types, based on Ajtay et al. (1979) and on Brown & Lugo (1984).

	Tropical forest	Temperate forest	Grass land	Arable land	Urbanized area	Sparsely vegetated
Net Primary Productivity, per unit land area ($kg\ C\ m^{-2}\ yr^{-1}$)	0.4	0.51	0.57	0.43	0.1	0.07
Fractions of *NPP* partitioned and life spans (or residence times) in yr of living biomass						
leaf	0.3//1	0.3//2	0.6//1	0.8//1	0.3//1	0.5//1
branch	0.2//10	0.2//10	0.//10	0.//10	0.2//10	0.1//10
stem	0.3//50	0.3//50	0.//50	0.//50	0.3//50	0.1//50
root	0.2//1	0.2//10	0.4//1	0.2//1	0.2//1	0.3//2
Residence times (yr) of dead biomass						
litter	1	2	2	2	1	2
humus	10	50	50	20	50	50
resist. carbon	500	500	500	500	500	500
Fraction of litter that becomes humus	0.4	0.6	0.6	0.2	0.5	0.6
Areas (Mha)						
1780	4400	1900	1700	1000	10	3100
1980	3729	1700	1793	1717	176	2992

This low degree of resolution was also used in this study (Table 2). Others (Matthews, 1983; Tucker et al., 1986; Esser, 1987) have worked on a much more refined mapping of vegetation.

The potential distribution of ecosystems on earth is primarily governed by climate. The Holdridge classification scheme (Holdridge, 1967) uses climate variables to map vegetation, and can be exploited for an analysis of the effects of climatic change (Warrick et al., 1986a). Soil carbon can be mapped in the Holdridge diagram (Figure 6.2 in Houghton et al., 1985) which enables the sequestering of carbon in soils caused by a change in climate to be estimated directly. In this study, the potential effect of climate change was not considered.

The combined effect Combination of the driving forces and residence times as presented in Figure 6 and in Table 2, leads to a steady state distribution of surface densities of carbon as presented in Figure 7. In this figure, the width of each bar represents the area of the vegetation type, and the height of each bar the carbon surface density. The high density of soil carbon in temperate forest and in grasslands as compared with agricultural land and tropical forests is noteworthy.

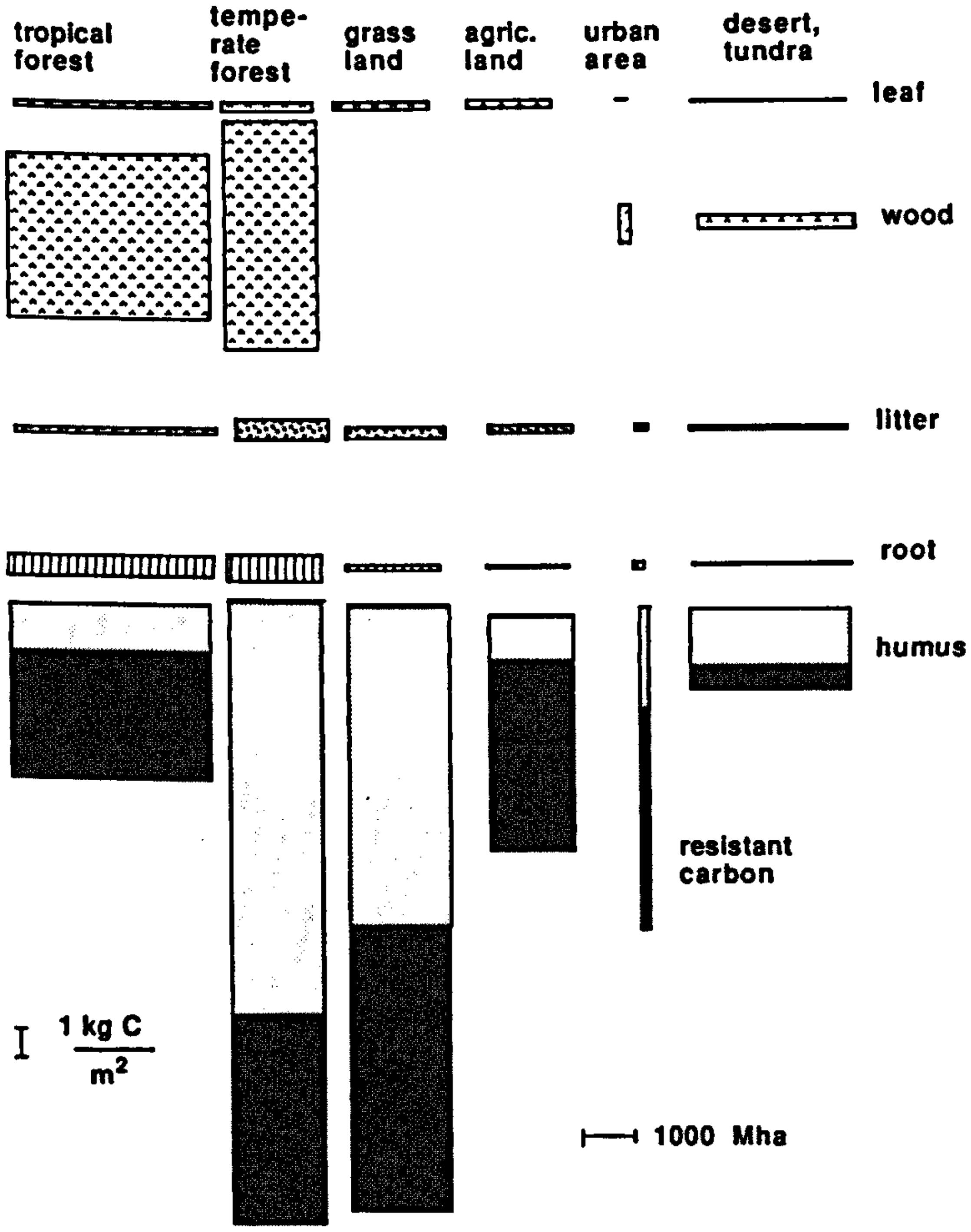

Figure 7. Simulated equilibrium distribution of carbon surface densities (heights of the columns) on the areas of each vegetation type (widths of the columns).

Although leaves in forests receive 30% of the *NPP*, they make up less than 5% of the forest biomass. The density of roots in forests is much higher than in herbaceous ecosystems, because forest roots have a longer residence time.

2.3.2 Human disturbance of vegetation

Houghton (1986) gave a detailed review of the subject of ecosystem disturbance, in which he highlighted the uncertainties of estimates of current carbon contents and of the timing of past carbon releases.

Human activities such as agriculture, logging, pollution and urbanization have strongly altered vegetation and will continue to do so. They are locally clearly visible and tend to obscure the physiological and climatic effects of rising atmospheric CO_2 on vegetation.

A clear distinction must be made between the two reasons for logging. One is to permanently reclaim agricultural land; the other is to remove wood, perhaps with the intention of a temporary agricultural utilization. Both types of disruption can be modelled by a triangular transition matrix that represents the annual area to be transferred from one vegetation type to another.

Disturbance without change of land use For this situation, the local effect of such a disturbance was modelled as a release of most of the aboveground carbon to the atmosphere (burning and decomposition). A small fraction of the biomass, however, becomes longlasting charcoal (5% of leaves, 10% of branches and 20% of stems), and hence is excluded from atmospheric circulation for a long time. This effect reflects the twofold consequence of burning: it not only immediately releases CO_2 into the atmosphere, but it also fixes a small fraction of the carbon of burnt material into the highly inert charcoal pool (Seiler & Crutzen, 1980). Therefore, the repeated burning of forests, agricultural land and savannahs increases the carbon content of soils at the expense of the atmospheric and oceanic reservoirs. In the model, the charcoal was included in the pool of resistant carbon (residence time 500 yr). Simulation showed that without this type of charcoal formation, atmospheric CO_2 would currently be at a level of about 5 μmol mol^{-1} higher and increase 5% faster.

On the time scale of a year, carbon fixation is not greatly reduced after the removal of biomass, because pioneer vegetation will take over. As far as the modelling of carbon is concerned, it does not matter what type of vegetation takes up the carbon from the atmosphere. Several decades are needed, however, to restore carbon pools with long residence times, such as stemwood. Net ecosystem production (*NEP*) after deforestation is typically temporarily positive. After several decades the losses of slowly decaying biomass increase in reservoirs with long residence times (stems in particular) and finally consume almost all production.

An assumed rate of annual burning (800 Mha yr^{-1}) of biomass (mainly litter) on grassland and agricultural land may seem large, since it causes about 5 Gt C per year to be released, the same rate as fossil fuel burning. However, this litter would have decomposed anyway, and for the carbon cycle it matters little whether it is burnt now, or decomposed one year later. So, it is not surprising that the simulated atmospheric CO_2 concentration in 1980 was scarcely affected (6 μmol mol^{-1} lower) when this litter burning was set at zero. Shifting cultivation in tropical forests (15 Mha yr^{-1}) did not have a large effect either: if it did not occur, the simulated atmospheric CO_2 concentration in 1980 was only 1 μmol mol^{-1} lower.

Land reclamation When land use is changed as well, the contents of the soil carbon reservoirs are transferred to the corresponding reservoirs of the new vegetation type, usually agricultural land. The residence time of humus in agricultural land is shorter than in forest soil, resulting in a considerable loss of soil carbon during the subsequent years. For instance, in soils of tropical forests the simulated mean areal density of carbon was 14 kg m^{-2} in contrast with only 8 kg m^{-2} in agricultural land. A rate of transfer of 12 Mha yr^{-1} therefore means that about 0.7 Gt C will eventually be released for each year that this deforestation occurs. This release is not instantaneous but delayed in time. A dynamic simulation model takes such a delay into account, in contrast with simple statistical calculations that assume immediate release.

The rate of land reclamation around the turn of this century was assumed to be faster than in Goudriaan & Ketner (1984), and the current rate was assumed to be lower. This larger emphasis on early reclamation better represents the colonial expansion in that period. The net effect of these land use changes was that during the last 200 years the area of agricultural land rose from 1000 to 1800 Mha (100 Mha = $10^{12}m^2$), mainly at the expense of tropical forests. Temperate forests were also reduced (by 100 Mha), but grassland area increased (by 140 Mha). The assumed present rate of deforestation is about 6 Mha yr^{-1} to agricultural land and another 6 Mha yr^{-1} to grassland.

A straightforward method of estimating biospheric releases is to use the rate of annual land transfer from virgin land to agricultural soil, and to multiply it by the difference between soil carbon content typical for both types of land use. Similarly, the rate of removal of aboveground biomass can also be included. Added to 'calculated soil carbon loss' this rate gives the 'calculated total reclamation losses' in Figure 8. The strong increase in recent times is caused by accelerated deforestation in the tropics.

However, this type of calculation neglects other important components of the global fluxes between atmosphere and biosphere, which can change the net balance considerably. First, deforested land is not only taken into use as arable land but also as grassland, and grassland has a much higher soil carbon content than arable land. Second, the soil carbon is not released instantaneously, but is gradually decomposed over decades. Third, partial humification and charcoal formation reduce the carbon losses by 10 to 20%. Fourth, in other parts of the world land is also reclaimed by irrigation. In such locations soil carbon is increased, not decreased. Fifth, and most important, a global stimulus of *NPP* is likely to occur as a result of the rising level of atmospheric CO_2. This phenomenon will be examined more closely below.

2.3.3 *Terrestrial photosynthesis as affected by CO_2*

The weight fraction of carbon in dry weight of plant material only varies between 40 and 50%, which shows that there must be a close connection between CO_2 assimilation and dry weight gain. Research has shown the importance of environmental factors such as radiation, temperature, water and nutrient supply for primary production (de Wit et al., 1979). Aerial CO_2 itself has been proven to be important as well (Lemon, 1984; Warrick et al., 1986b; Kimball, 1983).

In general, the normal partial pressure of ambient CO_2 of about 300–330 μmol mol^{-1} is suboptimal (Strain & Cure, 1985) for C_3 plants, which form 95% of the biomass. Seasonal dry weight gain is stimulated by increasing ambient CO_2 up to about 1000 μmol mol^{-1} partial pressure. Over a large range of CO_2 (200–1000 μmol mol^{-1}) the response of dry weight gain to CO_2 can be described by a logarithmic response function

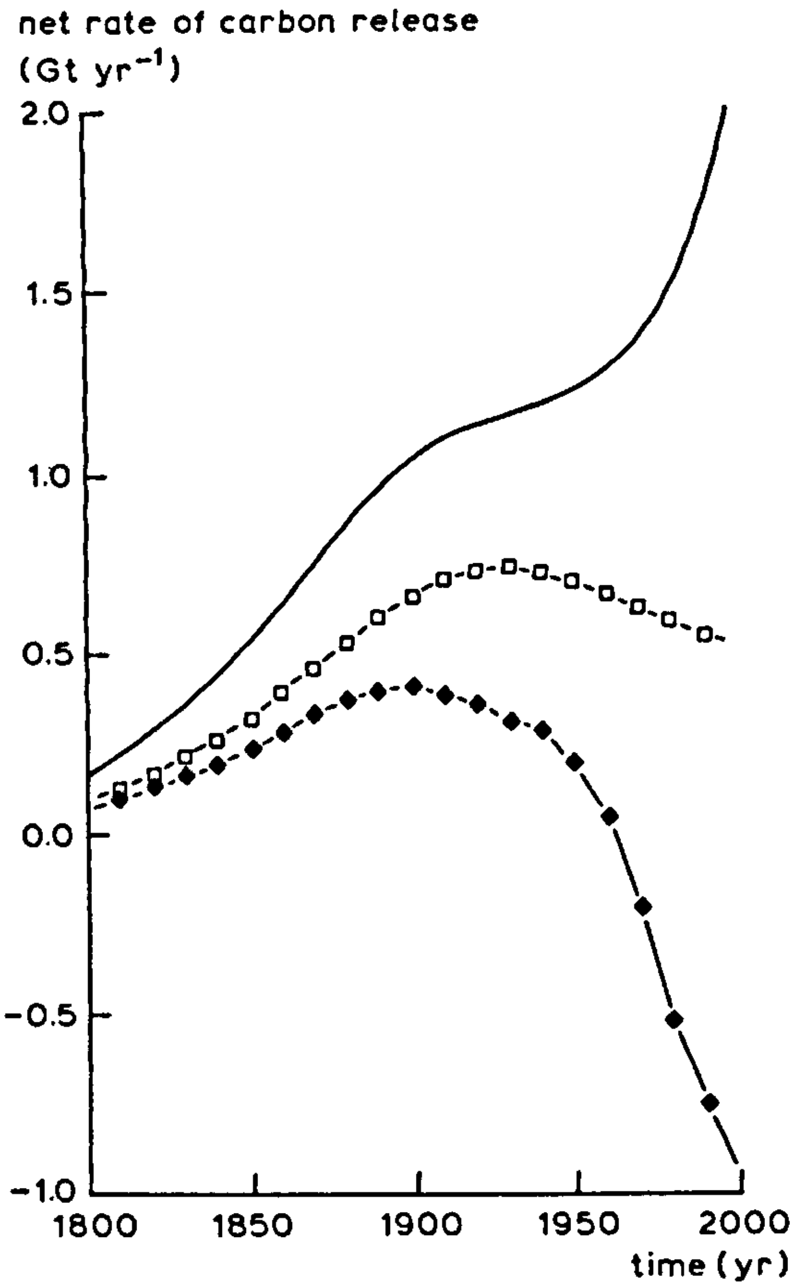

Figure 8. Reclamation losses of carbon from the biosphere to the atmosphere, according to simple statistics, assuming immediate transition to carbon content in the new vegetation type (———). Only those transitions to lower carbon contents are considered. Reclamation losses of carbon from the biosphere to the atmosphere, but including delayed release, charcoal formation, and transitions to vegetation types with higher carbon contents (□). The simulated effect of stimulation by increased CO_2 is also presented (◆).

$$NPP = NPP_0\,(1 + \beta \log(CO2/CO2_0)) \qquad \text{Equation 16}$$

where NPP is the net annual primary production (kg m^{-2} yr^{-1}), and NPP_0 is NPP in the reference situation at 300 µmol mol^{-1}. $CO2$ stands for the CO_2 concentration in the atmosphere expressed in µmol mol^{-1}.

The value of the response factor β is about 0.7 under good conditions for growth (Goudriaan et al., 1985), but declines with increasing nutrient shortage (Goudriaan & de Ruiter, 1983). Under water shortage (Gifford, 1979; Rosenberg, 1981) the growth-stimulating effect of atmospheric CO_2 is not reduced, but may even be enhanced. This interaction with water shortage is caused by partial stomatal closure under increased CO_2. In this situation C_4 plants benefit from increased CO_2 just as much as C_3 plants.

Ideally, the value of β should be determined separately for each type of vegetation, but so far a single value has been used in modelling the global carbon cycle, usually between 0.2 and 0.5. Esser's (1987) equation implies a value of β as high as just above 1. Goudriaan & Ketner (1984) whose model will be used here, adopted 0.5. This relatively high value was chosen to allow for eutrophication as well.

Because of natural heterogeneity, the resulting stimulus of net primary productivity is not directly measurable or visible in terms of biospheric carbon content, but its actual existence can be inferred from what is known from plant physiology. Its global presence makes its effect significant in terms of global carbon flux, as illustrated in Figure 8.

2.3.4 Terrestrial photosynthesis as affected by biomass

The logarithm of the growth rate of a free-standing individual plant is often linearly related to the logarithm of plant size itself: an allometric relationship. This relationship has been used in a number of models as reviewed by Bolin (1986). However, this relationship cannot be used on the scale of a field, let alone on that of an ecosystem. Because of competition between plants, the effect of biomass on growth can therefore better be described in terms of fraction of radiation absorbed by green leaf area (de Wit, 1965; Milthorpe & Moorby, 1979). As a result of the mutual shading of leaves, the fraction of absorbed radiation is soon saturated as leaf area increases. Above a leaf area index (*LAI*) of 3 m^2 (leaf area) m^{-2} (land area), which corresponds to a leaf dry weight of 150 $g\,m^{-2}$ (land area) no further increase of *NPP* can be expected with increasing leaf biomass. Once the soil is covered, positive feedback of biomass on *NPP* is further weakened by increased partitioning of growth to non-photosynthesizing organs such as stems and branches. Therefore, models that use an allometric relationship between *NPP* and biomass on a global scale tend to overestimate the positive feedback of biomass.

Expansion of vegetation onto previously bare land should be explicitly modelled as area growth of vegetation coverage. Such processes were not considered in this study, but it is clear that they might occur as an effect of increasing CO_2.

2.4 The ocean

2.4.1 Layer structure, and two ocean types

Reviews of some of the existing models for carbon exchange between ocean and atmosphere can be found in Björkström (1986), Sarmiento (1986), Broecker & Peng (1982), Baes et al. (1985). As Björkström (1986) pointed out, some of these models have been compartmentalized to such an extent that they need as many as 600 parameters.

The work presented here aims at striking a balance between the needs for high resolution on one hand and for simplicity on the other. As in the model presented by Goudriaan & Ketner (1984), the ocean was compartmentalized into 10 strata, and the top one was further split into three zones: a high latitude zone (after

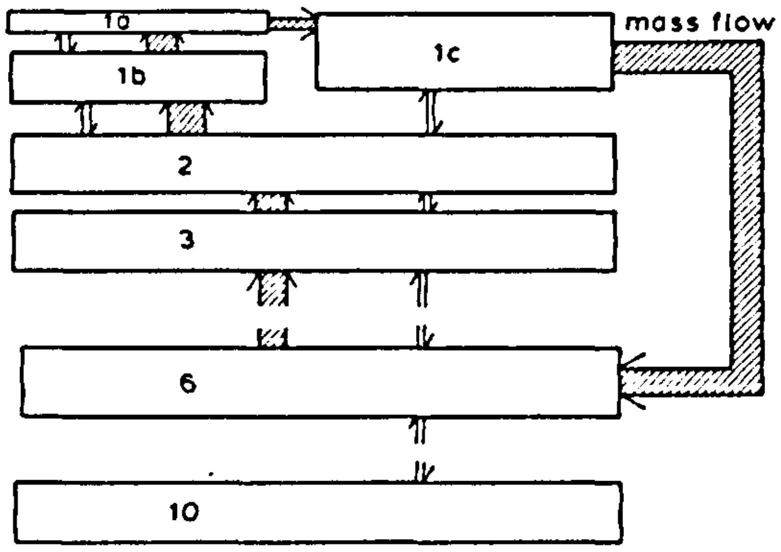

Figure 9. Modelled stratification of the ocean.

Viecelli et al., 1981) and a low latitude zone consisting of two strata (Figure 9). Exchange between adjacent strata was described by a diffusion type equation, with a 'diffusion' coefficient derived from tracer studies ($K = 4000\,m^2\,yr^{-1}$). There was a mass flow (Gordon flow), sinking from the high latitude surface zone, and re-entering the deep sea at a depth between 2000 and 3000 m. This mass flow forced an upwelling into the low latitude surface zone. The circulation was closed by a mass flow from the low to the high latitude surface zone.

In modification of the Goudriaan & Ketner (1984) model, the surface zones of the oceans were considered to be internally well-mixed (K infinite), but a surface conductance of $4\,m\,yr^{-1}$ was modelled for exchange with the atmosphere. The value of this conductance was found by calibration with the rate of decline of the ^{14}C peak after the nuclear tests in the early 1960s (Figure 10). The carbon content of these 4 m of sea water is annually exchanged with the atmosphere, which is equivalent to an exchange rate of about $9\,mol\,C\,m^{-2}\,yr^{-1}$ ($39\,Gt\,C\,yr^{-1}$ globally). However, since the amount of carbon that is needed for chemical equilibration is about 10 times (Revelle factor) less, this same exchange flux involves a 10 times greater depth for chemical equilibration.

In the 1984 model, marine photosynthesis was defined as a fixed driving force. The decomposition of precipitated organic material could account for observed features such as high partial pressure of CO_2 in deep sea water, CO_2 release in the upwelling zone and uptake CO_2 in the high latitude downwelling zone.

In view of large observed differences between the Atlantic Ocean on one hand and the Pacific and Indian Oceans on the other (Baes et al., 1985), the two ocean systems were modelled separately by using the same ocean submodel with adapted characteristics. In the modified model, the two ocean systems differed mainly by their rate of internal turning over of deep and surface water (Gordon flow), which is much higher in the Atlantic than in the Pacific and Indian Oceans ($2\ 10^{15}\,m^3\,yr^{-1}$ versus $0.2\ 10^{15}\,m^3\,yr^{-1}$) (Baes et al., 1985). In glacial periods these oceans may have been more similar (Broecker & Peng, 1982); this was modelled by a reduction of the Atlantic deep mass flow.

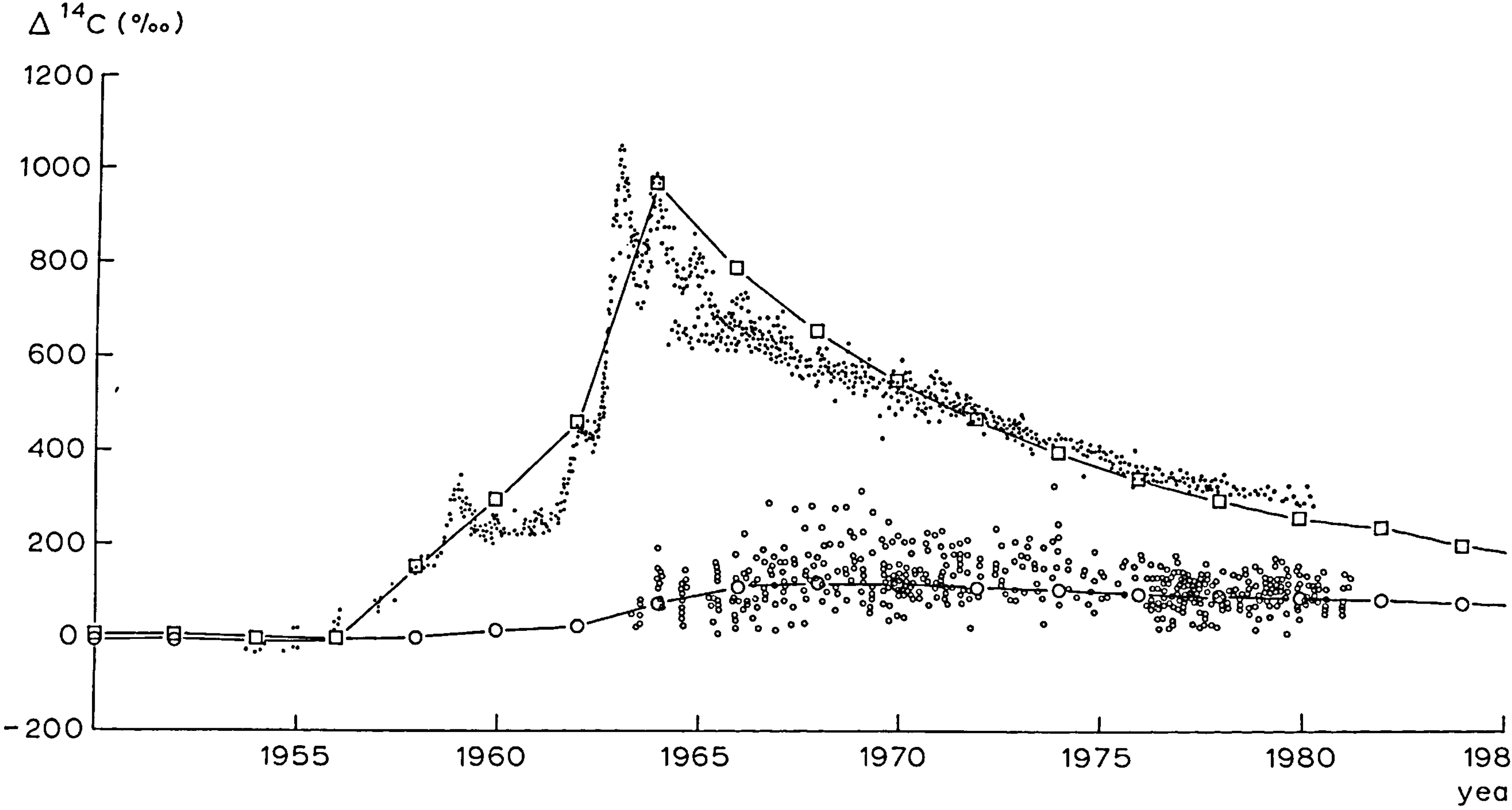

Figure 10. Simulation and observed time courses of $\Delta^{14}C$ in the atmosphere (□) and in the sea surface water at low latitudes (o), for the period around the nuclear tests. The simulation results are presented as an overlay on the data given by Bolin (1986) in his Figure 3.6.

Apart from their obvious connection via atmospheric CO_2, the two ocean systems were connected via a strong circumpolar flow of surface water in the Antarctic Sea, exchanging phosphate, oxygen and total carbon. Some exchange of deep sea water may occur as well, but was not included in the model. At the 45.2‰ isopycnal many characteristics have a steep gradient (GEOSECS data in Broecker & Peng, 1982), which means that there is little exchange between the deep waters of the Antarctic Sea and the oceans.

This modelled connection of both oceans enabled the Pacific Ocean to extract nutrients from the Atlantic Ocean, by a process of skimming the surface water. This combination of primary productivity and exchange of surface water could generate the observed large differences in chemical compositions in both ocean systems. The precipitation of organic material originating from marine photosynthesis was found to be essential in maintaining this difference.

2.4.2 Marine photosynthesis

Since nutrients strongly affect marine photosynthesis, it was necessary to include nutrient transport in the model. Phosphate was treated as the main factor limiting primary productivity. The total amount of ocean phosphate was initialized as an input parameter (92 Gt P, on the basis of Baes et al., 1985), but the distribution of phosphate was established by simulation. The ratio between precipitation of organic material (C) in $g\,m^{-2}\,yr^{-1}$ and phosphate concentration (P) of the upper layer in $g\,m^{-3}$, which had a value of $278\,g\,C\,g^{-1}\,P\,m\,yr^{-1}$, is an important model parameter. This parameterization led to a global downward flux of approximately $3\,Gt\,C\,yr^{-1}$, sinking below 400 m depth. The phosphorus content of organic material, and its oxygen demand upon decomposition were derived from the Redfield equation (Baes et al., 1985), and were $0.024\,g\,P\,g^{-1}\,C$ and $3.47\,g\,O\,g^{-1}\,C$, respectively.

Surface layers received phosphate from the deeper layers by upwelling and by diffusion. The precipitating organic material was allowed to decompose between 400 and 1500 m depth, thereby boosting the levels of phosphate and carbonate and reducing that of oxygen (Figure 11). The profiles generated in this way are similar to observed profiles (Baes et al., 1985). The biological parameters of primary productivity were identical in the two major ocean systems, showing that the difference between these systems is caused by the different characteristics of physical flow.

2.5 The carbon isotopes

The radioactive carbon isotope ^{14}C is absent in fossil fuel, and so the use of fossil fuel leads to a dilution of the ^{14}C concentration in atmosphere, biosphere and ocean. On the other hand, much ^{14}C was produced during the nuclear tests in the 1960s. In the process of photosynthetic carbon uptake there is a slight discrimination in favour of the lighter carbon isotopes in the series ^{12}C, ^{13}C and

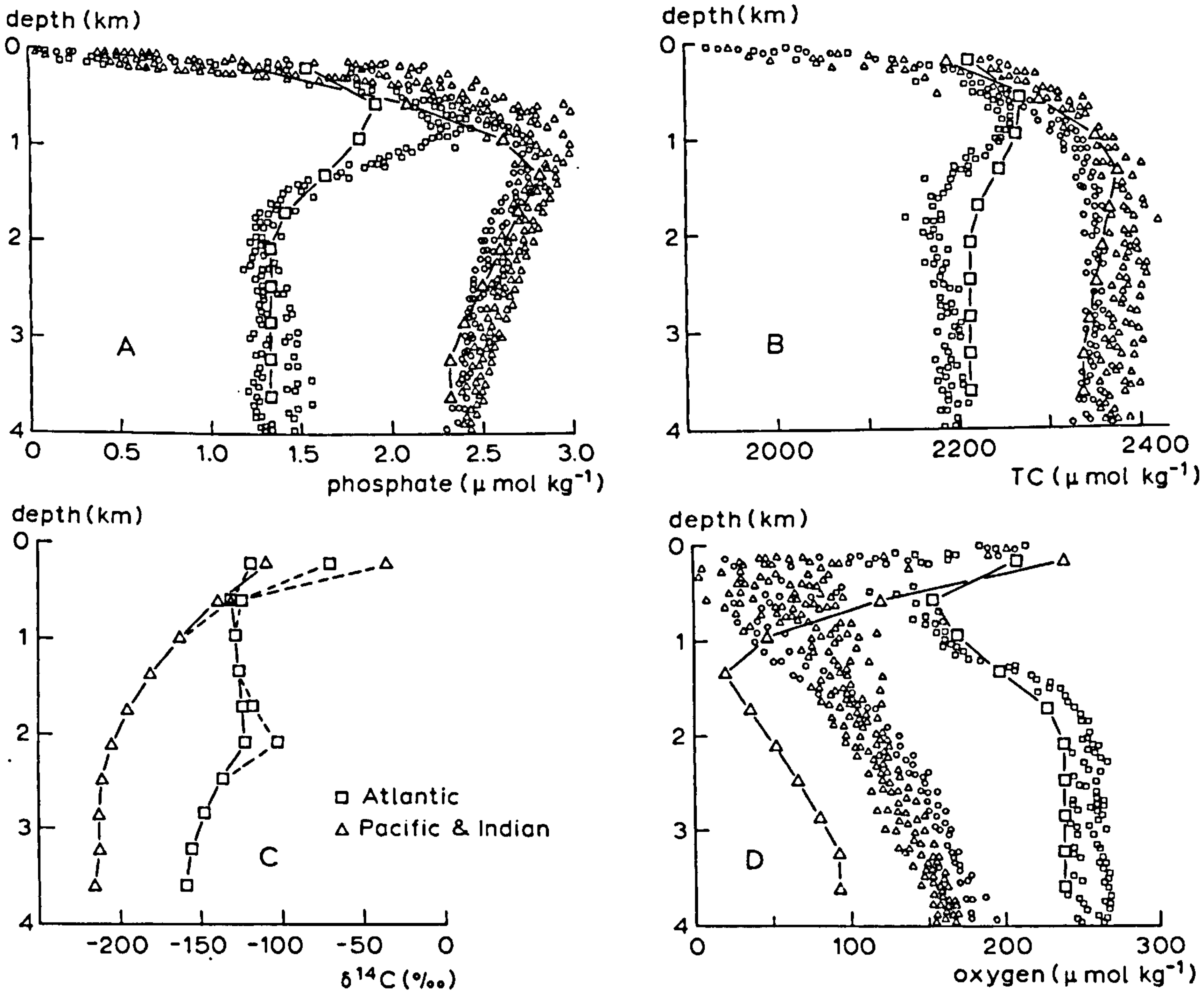

Figure 11. Measured and simulated (symbols connected by solid lines) depth profiles of phosphate (A), of total carbon (B) and of oxygen (D) in the Atlantic and in the Pacific and Indian Oceans. These simulation results are presented as an overlay on Figure 5.6 in Baes et al. (1985). Simulated profiles are given before the nuclear tests and for the year 1972 (broken lines) for $\Delta^{14}C$ (C).

^{14}C. This discrimination is expressed in the isotopic composition of biomass.

In general, discrimination between carbon isotopes offers an additional way of validating model behaviour. For this purpose the exchange of isotopes within the sea was modelled analogously to other passive admixtures. Any mass flow of CO_2 will carry the isotopic composition of the source. Therefore, increasing atmospheric CO_2 leads to increased carbon uptake of all isotopes by the ocean, on account of chemical forces. In this study, as a first order approximation, all isotopes are taken up in proportion to their abundance. However, the primary isotope flux is modified by a second flux component, driven by exchange resulting from difference in isotope ratios in water and air, and by their discrimination upon uptake or release.

The prenuclear equilibrium (Figure 11C) for ^{14}C was found by simulation. The long residence time of water in the deep Pacific shows up in low values of the concentration of ^{14}C. This concentration is expressed by the symbol $\Delta^{14}C$, which stands for 1000 times the relative difference of the ratio $^{14}C/C_{total}$, compared with a standard ratio. In Figure 11C an effect of the nuclear testing period in the 1960s is also visible: a tongue of downwelled water can be seen in the Atlantic Ocean at a depth of about 2000 m.

The assumed discrimination of ^{13}C in photosynthesis (Mook, 1986) caused a correlation between $\Delta^{13}C$ and phosphate practically identical to the observed relationship (see Figure 6–12 in Broecker & Peng, 1982).

The $\Delta^{13}C$ was assumed to be −25‰ for carbon in fossil fuels and −19‰ in photosynthesis, and so the simulated level of atmospheric $\Delta^{13}C$ decreased by 1.47‰ between 1860 and 1980, with a continuing annual rate of decrease of 0.03 in 1980. These figures practically coincide with the data recorded by Freyer (1986) (Figure 12A), but they show a faster rate of decrease than Stuiver (1986) found. For atmospheric $\Delta^{14}C$ a similar, but much stronger decrease (the Suess effect) was simulated, from −23.5‰ in 1860 down to −46‰ in 1950. These model simulations fall in line with the data as given in Stuiver & Quay (1981) and Bolin (1986) (Figure 12B). Using these methods, the accumulated net loss of biospheric carbon between 1860 and 1980, was simulated to be no more than 30 Gt C.

On the basis of direct calculations and of isotope ratios, other researchers have come up with much higher estimates, even exceeding 100 Gt C in total (Bolin, 1986; Houghton et al., 1985). The difficulty with the direct estimates was discussed above (Sections 2.2 and 2.3). The uncertainty range of the isotope-based estimates is also large, because these estimates are based on the difference between the ^{13}C and ^{14}C records. Actual ^{13}C variability in sampled wood is often as large as the signal itself. These high estimates of releases have caused some problem in connection with the actual rate of increase of atmospheric CO_2. The simulation results presented here do not suffer from this problem of 'missing carbon'.

2.6 The importance of model factors

2.6.1 Terrestrial biosphere

Because of the large size of the ocean in comparison with the terrestrial biosphere, the ocean was included when the effect of biospheric parameters was studied. On the other hand the biosphere could have been omitted when studying the first order effects of changes in ocean parameters, but for completeness the ocean was then also included. Unless explicitly mentioned all affects apply to the response of the combined atmosphere–ocean–biosphere system.

Change in vegetated area As a theoretical exercise the effect of the vegetated area increasing by 1000 Mha ($10\ 10^{12}\ m^2$) from bare land to grassland and forest was studied. It is hard to see how such an increase would be possible under steady climatic conditions, but a changing climate could perhaps induce such an in-

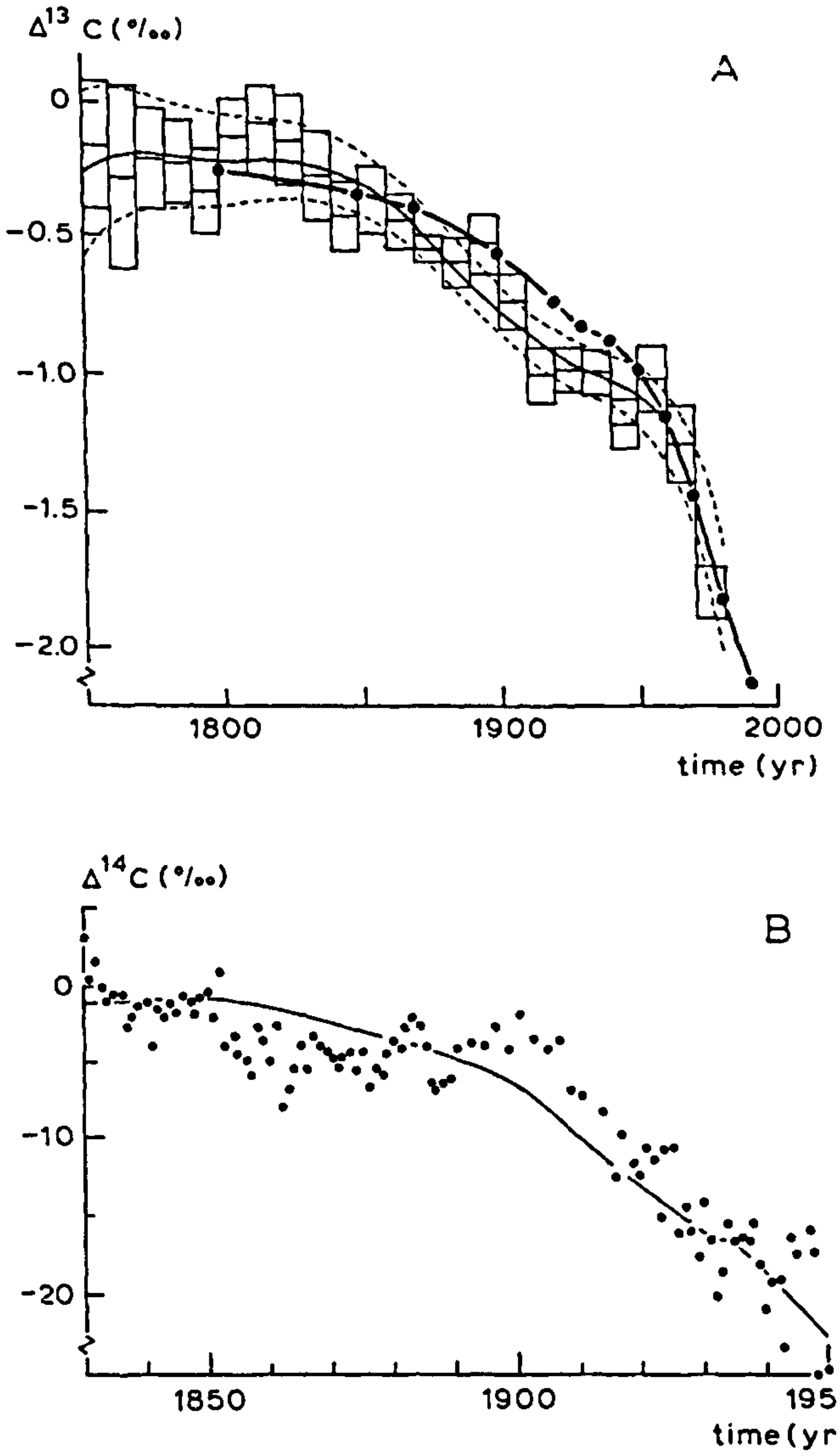

Figure 12. Simulated and measured time courses of carbon isotope ratios. The simulation results are presented as overlays. A: For $\Delta^{13}C$ on the data given by Freyer (1986) in his Figure 7.5. B: For $\Delta^{14}C$ on the data given by Stuiver & Quay (1981). The 'MODEL PREDICTION' of Broecker & Peng (1982) in their Figure 10-23 for the same data and my simulated results practically coincide (solid line).

crease. This increase in vegetated area would cause a carbon sequestering of some 230 Gt C (23 kg C m^{-2}) in the long run. Although such a large amount of carbon is equivalent to about 110 µmol mol^{-1} if extracted instantaneously from the atmosphere, the slowness of growth of stemwood and of accumulation of soil carbon permitted the oceans to gradually release CO_2 in response to the decreased partial pressure of CO_2 in the atmosphere. As a result, atmospheric CO_2 never dropped to more than 25 µmol mol^{-1} below the starting level. It reached an equilibrium after one thousand years, which was only 15 µmol mol^{-1} lower than the initial level.

Change in longevity of soil carbon The longevity of soil carbon (humus and charcoal) is of great importance. When its value was instantaneously doubled, atmospheric CO_2 dropped from 285 to around 220 μmol mol^{-1} within a few decades, and remained at that level. About 1000 Gt C was sequestered in the soil, of which 840 Gt C was extracted from the sea, and 140 Gt C from the atmosphere.

Wetness of climate has a large effect on the amount of soil carbon. Doubling the precipitation/evaporation ratio also practically doubles the soil carbon (Figure 6.2 in Houghton et al., 1985). General Circulation Model (GCM) studies indicate that the hydrological cycle is increased up to 15% when atmospheric CO_2 is doubled, but it is not clear what this means in terms of the precipitation/evaporation ratio in vegetated regions.

Change in CO_2 stimulus of NPP In the control run, β was set at 0.5. In this situation, CO_2, when emitted into the atmosphere, will eventually be redistributed between ocean, biosphere and atmosphere in a ratio of 0.71 : 0.18 : 0.11. If, on the other hand, any effect of atmospheric CO_2 on net primary productivity was assumed to be absent, CO_2 emitted into the atmosphere was redistributed between ocean and atmosphere only in a ratio of 0.85 : 0.15. This redistribution process will take hundreds of years, because of the slowness of mixing in the oceans. On such long time scales the effect of the ocean reservoir is so large that the importance of photosynthetic stimulus by atmospheric CO_2 is only slight.

On a time scale of decades, however, and at the present rate of fossil fuel consumption, a value of 0.5 or of 0.0 for β makes a difference of about 10 years in the rising curve of atmospheric CO_2. This global photosynthetic stimulus slows down the greenhouse effect by about 10 years.

2.6.2 Ocean

Changes in marine photosynthesis In the model, marine primary productivity was linearly linked to phosphate concentration in the surface waters. As a result, two model characteristics dominated the precipitation rate of dead organic matter. First, the phosphate content of organic material (Redfield ratio), since it governs the rate of extraction from surface water, and second, the proportionality factor between precipitation rate and phosphate concentration. When this proportionality factor was doubled, precipitation doubled instantaneously too. However, phosphate was then withdrawn at a doubled rate, and the phosphate concentration in the water dropped. This negative feedback mechanism considerably reduced the eventual effects of the precipitation/phosphate ratio: atmospheric CO_2 dropped by 35 μmol mol^{-1}. A similar mechanism operated when the Redfield ratio was halved: decreased withdrawal of phosphate caused some accumulation of phosphate in the surface layers, thereby stimulating photosynthesis and carbon precipitation to the deep sea: a drop by about 30 μmol mol^{-1}. Only when the Redfield ratio was halved and the precipitation/phosphate ratio was simultaneously doubled, did the phosphate content of the water remain unchanged and a strong change in rate of carbon precipitation could be maintained, resulting in a considerable change of atmospheric CO_2: a drop of 85 μmol mol^{-1}.

Of course, a direct change in the total amount of phosphate in the ocean also had a large effect: about 1 μmol mol^{-1} decline of atmospheric CO_2 for every per cent increase of total ocean phosphate.

Changes in ocean currents Atmospheric CO_2 was remarkably insensitive to the circumpolar flow that connects both ocean systems. If it was decreased from 2 10^{15} m^3 yr^{-1} to 0.1 10^{15} m^3 yr^{-1}, the difference between the ocean systems was largely maintained, and atmospheric CO_2 remained about the same.

A much stronger effect resulted from changes in the mass flow within each ocean system. If the Gordon flow in the Atlantic was reduced from 2 to 1 10^{15} m^3 yr^{-1}, atmospheric CO_2 dropped from 285 to 273 μmol mol^{-1} and a further reduction to 0.2 10^{15} m^3 yr^{-1} resulted in an atmospheric CO_2 of 260 μmol mol^{-1}.

This effect can be explained by decreased upwelling, a lowering of the phosphate concentration in the surface layer of the Atlantic and increase of both phosphate and total carbon in the deep Atlantic. In the Pacific very little changed.

Similarly, if the mass flow in the Pacific was increased from 0.2 10^{15} m^3 yr^{-1} in the control run to 2 10^{15} m^3 yr^{-1}, the atmospheric concentration of CO_2 was increased from 285 up to 334 μmol mol^{-1} in 500 years time. The relaxation time of these changes was about 200 years.

Changing the depth at which the downwelling water of the Atlantic enters the deep sea from 1500 to 3500 m reduced the residence time of the deep water (as indicated by $\Delta^{14}C$) but with little effect for other factors. This lack of importance of the re-entry depth is connected with the completeness of decomposition of precipitated organic material in the upper 1500 m. Below this depth almost no gradient remained.

2.7 Conclusion and discussion

About 60% of the CO_2 currently emitted from the burning of fossil fuel remains in the atmosphere and 40% is absorbed by the oceans. The distribution pattern is strongly dependent on the rate of emission. A lower rate of emission gives more time for absorption in the ocean.

When it is taken into account that net photosynthesis is stimulated by CO_2, the partitioning of carbon over atmosphere, ocean and terrestrial biosphere is shifted from the ratios 0.15 : 0.85 : 0.0 to 0.11 : 0.71 : 0.18, respectively.

Significant amounts of carbon can be released from the biosphere when it is disturbed. Reclamation of land for agriculture and for other types of human utilization can cause oxidation of soil carbon and of long-lived biomass such as wood. In the past century such processes were responsible for the release of large amounts of carbon. At present they tend to be increasingly balanced by a global stimulus of growth resulting from increased atmospheric CO_2 itself. Regrowth on abandoned land also gives a partial compensation.

The role of the biosphere made it difficult to define the airborne fraction of CO_2. If atmospheric increase is related to emission from fossil fuel only, CO_2 uptake by the biosphere is included in the net effect. Since the biosphere does not follow the rules of chemical equilibration, the airborne fraction will be less stable and will also be dependent on human disturbance of the biosphere. For this reason Bolin (1986) introduced the term 'total airborne fraction' which was defined as atmospheric increase divided by the sum of biospheric and fossil fuel emissions. Of course, net biospheric emission of CO_2 should then be used and not the gross emission. When Bolin (1986) criticized the model of Goudriaan & Ketner (1984) for having too low an airborne fraction (0.3), he found this figure by using gross biospheric emission. In fact, when the net result of biomass removal and subsequent regrowth is used, the airborne fraction for the year 1980 in their model was 0.58 and not 0.3.

In this study felling forest for land reclamation for permanent human use was found to be significant, releasing CO_2 at a rate of about 0.5 to 1 Gt C yr^{-1}. On the other hand, this rate of release is more than compensated for by global stimulation of growth by atmospheric CO_2. Model calculations showed that the growth stimulus has caused an additional uptake of about 64 Gt C by the biosphere, reducing atmospheric CO_2 by about 36 Gt C. This increased carbon sequestering is equivalent to 10 years of emission from fossil fuels. However, this additional storage of carbon induced by increased CO_2 is extremely difficult to detect directly by sampling methods in the field, because of the large natural heterogeneity.

The results presented for the time patterns of carbon isotopes give no reason to believe that the *net* accumulated carbon release from the biosphere during the last century has been more than about 30 Gt C. Both the isotopic data and the CO_2 data themselves are consistent with this limited net release of biotic carbon. Even a slight imbalance in the growth of terrestrial ecosystems on a global scale is sufficient to absorb the carbon released by deforestation (Lugo & Brown, 1986). Such an imbalance may result from increasing atmospheric CO_2, as assumed here, but other environmental factors may be involved as well.

A further conclusion along this line is that the terrestrial biosphere, and especially the soil, can store significant amounts of carbon. A 3% increase in carbon content (relative to carbon, not to soil weight) means a carbon sequestering of 50 Gt C.

The ocean is extremely important for the level of atmospheric CO_2. If the rate of upwelling of deep water is increased, more CO_2 will be released and atmospheric CO_2 will rise. This effect is only partly compensated for by a simultaneous increase of marine photosynthesis by the nutrients that are brought to the surface.

During the glacial periods atmospheric CO_2 was much lower than during interglacials, and the vegetated area was presumably much smaller. Although soil carbon may have been higher in the tropics than at present, it seems unlikely that it could have stored the loss of terrestrial carbon in the high latitudes. Climatic wetness stimulates accumulation of soil carbon, but during the glacials climate was probably drier, not wetter. From a physiological point of view the dryness was accentuated by low atmospheric CO_2 which stimulates stomatal opening and transpiration. Dry and CO_2-poor conditions definitely favoured C_4 species, and probably stimulated their evolution. In view of these considerations it is most likely that the terrestrial carbon pool was much smaller during the glacials than between them. The increase of terrestrial biomass at the end of the glacial periods must have created a large sink for CO_2. In addition to going the wrong way, it is hard to see how the terrestrial biosphere could have caused the rapidity of the changes of atmospheric CO_2.

Marine photosynthesis itself can probably not be altered much in its response to the limiting nutrient phosphate. However, it is the precipitated fraction that matters for carbon accumulation in the deep sea. Also, the depth at which decomposition occurs is important. These factors are probably biology-linked and controlled by species composition. One other factor: if release of phosphate upon decomposition of precipitating organic material is accelerated with respect to that of carbon, the remaining material is depleted in phosphate. Such a shift would cause a further decline in atmospheric CO_2.

Ocean circulation, however, must have been the dominant factor. Changes in ocean circulation have a very large and quick effect. The question remains what has initiated the required changes in pattern or magnitude of the circulating flows. The temperature feedback on solubility of CO_2 in sea surface water was found to amplify an externally caused change in atmospheric CO_2 by a factor of 1.5.

According to the ocean part of the model presented here, the differences in nutrient content between the major ocean systems can be sufficiently explained by their vastly different rates of internal water circulation, even if deep sea currents from the Atlantic to the Pacific (Broecker & Peng, 1982) are not considered. These currents will enhance the nutrient-enriched character of the deep Pacific as compared with the waters of the Atlantic.

2.8 Acknowledgments

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3 Nitrogen influence on the physiology of crop yield

T.R. Sinclair

3.1 Introduction

Nitrogen is an essential element in the nucleic acids and proteins that make plant life possible. Nucleic acids allow genetic information to be stored and retrieved, thereby guiding crop growth and development. Proteins are the enzyme catalysts that stimulate and regulate the multitude of biochemical events in living organisms (Novoa & Loomis, 1981). The dependence of growth on these nitrogen-containing compounds indicates that the availability of nitrogen to plants is quantitatively significant for understanding crop productivity.

The importance of the quantitative relation between crop yields and nitrogen is readily demonstrated. De Wit (1972) examined in some detail the historical significance of the use of nitrogen fertilizer on crop yield increases in Western Europe. He estimated that the fertility of the native soils in Western Europe allowed grain yields to be only 750 kg ha^{-1} up through the Early Middle Ages. De Wit concluded that the introduction of practices such as using animal manures and crop rotations increased grain yields to about 2000 kg ha^{-1}. The advent of manufactured nitrogen fertilizers resulted in the dramatic increases in grain yields associated with modern agriculture.

In addition, de Wit & van Heemst (1976) argued that much of the variation in crop yields among regions of the world is associated with the use of fertilizers. In an analysis of mean crop yields of 86 countries they found a linear relationship ($r^2 = 0.822$) between crop yields as consumable protein and the amount of fertilizer used.

To examine the influence of nitrogen fertilizer use on crop yields in the United States, I examined annual production data for maize from 1945 to 1982. In Figure 13 the mean annual yields (Annual Crop Summary, USDA) are plotted against the mean annual amount of nitrogen fertilizer applied to maize (Fertilizer Outlook and Situation, USDA). During this nearly 40-year period both maize yields and nitrogen fertilizer use increased substantially. Even including years when yields were adversely affected by stress (e.g. Southern Corn Leaf Blight in 1970) a close correlation ($r^2 = 0.929$) exists between grain yield and nitrogen application per unit ground area. These data indicate a 29.3 kg ha^{-1} yield increase for each 1.0 kg ha^{-1} of nitrogen applied.

Quantitative descriptions of nitrogen influence in determining crop yields are only now being fully developed. An important part of this understanding is through the use of crop simulation models such as those originating from the Department of Theoretical Production Ecology of Wageningen Agricultural University. A very large number of factors associated with the physiology of

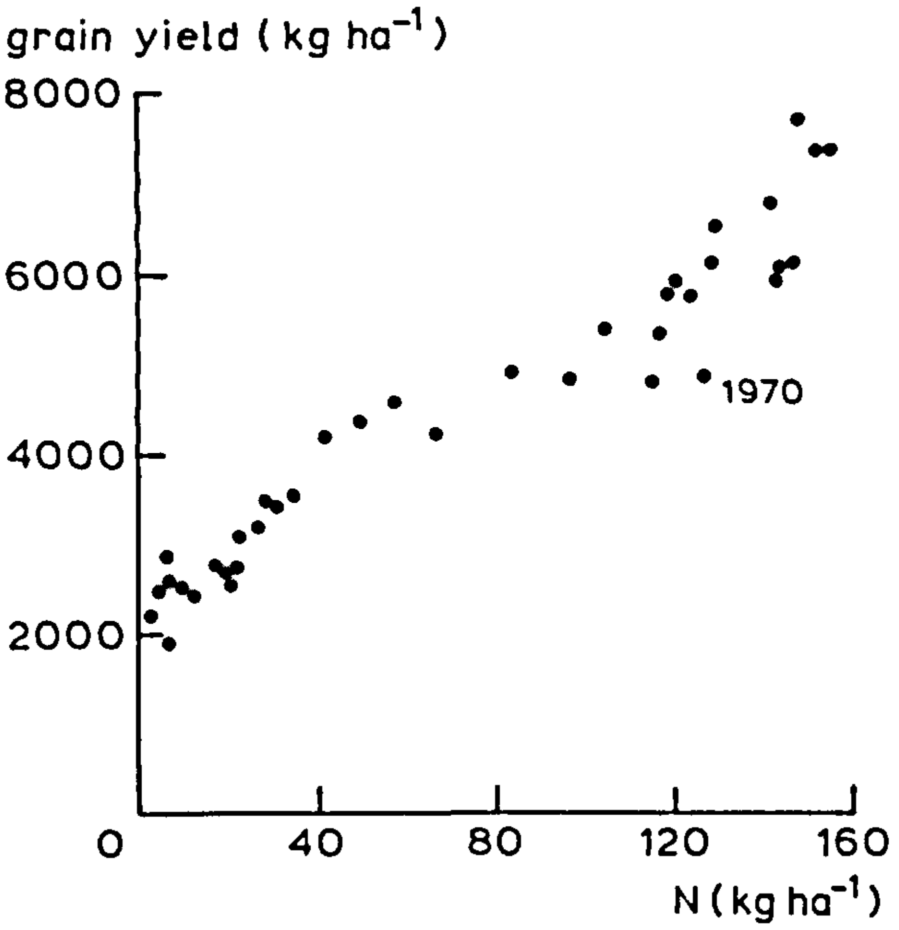

Figure 13. Plot of annual average United States maize yields per hectare versus annual average amount of nitrogen fertilizer applied per hectare for period from 1945 to 1982.

nitrogen use that influence crop yields have been considered and simulated (de Wit et al., 1979; van Keulen, 1982). In this review three key physiological processes sensitive to nitrogen availability will be considered as quantitative determinates of crop yield. Leaf area development, biomass accumulation, and seed growth will each be reviewed for their response to nitrogen and the potential impact of variation in nitrogen availability on overall crop performance. Finally, a brief discussion is included to review simulations that have attempted to evaluate quantitatively the influence of these processes on crop yields.

3.2 Leaf growth

The accumulation of carbon and crop biomass ultimately depends on the interception of solar radiation by leaf canopies and on active photosynthesis by the individual leaves. Therefore, the growth and maintenance of active leaf area is critical for obtaining high crop yields.

An important determinate of leaf area growth is the availability of nitrogen, because the basic composition of leaves requires a minimum nitrogen content. Leaf enzymes, especially those associated with the photosynthetic apparatus, seemingly impose such a minimum nitrogen requirement per unit of leaf mass. Lugg & Sinclair (1981) found that newly formed soya bean leaves contained 50 to 60 mg N g^{-1}. Hanway & Weber (1971) found that the leaves of unfertilized, non-nodulated soya bean plants still contained about 40 mg N g^{-1}. In sorghum, Charles-Edwards et al. (1987) reported that young leaves contained about 50 mg N g^{-1}. The nitrogen content of young wheat leaves was found to be between 40 and 50 mg N g^{-1} (Karlen & Whitney, 1980). All observations indicate that a minimum nitrogen content is required in the development of new leaf area.

Insufficient nitrogen supply to crops results directly in a decrease in final area of individual leaves. Muchow (1988) showed that a decrease in leaf area of the upper leaves of maize and sorghum plants accompanied a decrease in nitrogen fertilization. In wheat, Spiertz & van de Haar (1978) also found that the area of individual leaves changed in proportion to the application of nitrogen fertilizer. Pearman et al. (1977) found an approximately linear increase in wheat crop leaf area as nitrogen fertilizer amounts were increased from 0 to 200 kg ha^{-1}. The growth of leaf area by *Panicum maximum* and *Lolium perenne* was decreased when nitrogen was absent from the growth solutions (Wilson, 1975). In a study of *Amaranthus* (Hunt et al., 1985a) the area of individual leaves was greatly decreased as the nitrate concentrations in the growth solutions decreased. A consistent response among all species is that the leaf area of developing leaves is retarded when nitrogen availability is low.

Surprisingly, the number of leaves produced by plants seems to be relatively insensitive to nitrogen availability. In maize, Lemcoff & Loomis (1986) found that the number of leaves initiated was insensitive to the soil fertility. Similarly, in maize and sorghum Muchow (1988) found that the leaf number was decreased only under the most serious nitrogen deprivation treatments, and this resulted in only a slight decrease in leaf number.

To simulate crop growth when nitrogen availability may be restricted it is important to account for the nitrogen requirement in leaf growth. Insufficient nitrogen to meet the minimum requirements for developing leaf area results in decreased leaf area. For example, in the simulations carried out by Penning de Vries (1982), tissue growth is retarded to achieve the prescribed minimum nitrogen concentration for the tissue when the nitrogen supply is low.

The important consequence of the inhibited leaf area growth resulting from inadequate leaf nitrogen is that the amount of solar radiation intercepted by a leaf canopy is decreased, thereby decreasing the ability of crop canopies to assimilate carbon dioxide.

3.3 Biomass accumulation

Having dealt with how leaf area is grown to intercept solar radiation, I now propose to consider the dependence of photosynthetic activity on leaf nitrogen content. At low irradiances leaf CO_2 assimilation rates are dependent on irradiance, but at high irradiances where light saturates leaf photosynthesis the rates of CO_2 assimilation are dependent on the biochemical activity of the leaves. Since much crop CO_2 assimilation is done by the leaf area exposed to saturated or near-saturated irradiances, the potential biochemical activity of leaves is crucial for quantitatively understanding crop yield capabilities. High correlations are commonly observed between light-saturated leaf CO_2 assimilation rates and photosynthetic enzyme activity (e.g. Massacci et al., 1986; Ford & Shibles, 1988). Since photosynthetic enzymes account for a substantial portion of the leaf nitrogen (Ku et al., 1979), leaf CO_2 assimilation rates and leaf nitrogen content are also highly correlated.

Sinclair & Horie (1989) reviewed reports on the correlation between light-saturated leaf CO_2 assimilation rates and leaf nitrogen content per unit area for soya bean and rice. In these reports they found a range of experimental treatments and germ plasm, but nearly all results showed that the correlation between CO_2 assimilation rate and leaf nitrogen content was high ($r > 0.75$). Further, within each species much of the published data could be represented by a single response function between light-saturated leaf CO_2 assimilation rates and leaf nitrogen contents. The response functions were curvilinear with an approximately linear response at lower leaf nitrogen contents and then approaching a maximum CO_2 rate at higher leaf nitrogen contents (Figure 14). Rice was found to be more efficient than soya bean in nitrogen use, because at all levels of leaf nitrogen the rates of CO_2 assimilation were greater. Sinclair & Horie (1989) also included a function for maize that was similar in shape to the other two crops, but the CO_2 assimilation rates for maize were highest at all leaf nitrogen contents. The comparison of these response functions among species is consistent with the conclusion of Brown & Wilson (1983) that C_4 species are photosynthetically more efficient in the use of nitrogen than are C_3 species.

Functions similar to those in Figure 14 for the response of light-saturated leaf CO_2 assimilation rates to leaf nitrogen contents have been reported in other species. Evans (1983) grew wheat on nutrient solutions of varying nitrate concentrations at differing times of the year. He found light-saturated CO_2 assimilation rates responded to leaf nitrogen contents in a manner nearly identical to the rice response function in Figure 14. Araus & Tapia (1987) performed a similar experiment with a different wheat cultivar and obtained similar results. In *Amaranthus*, Hunt et al. (1985b) also found a close correlation ($R^2 = 0.92$) between

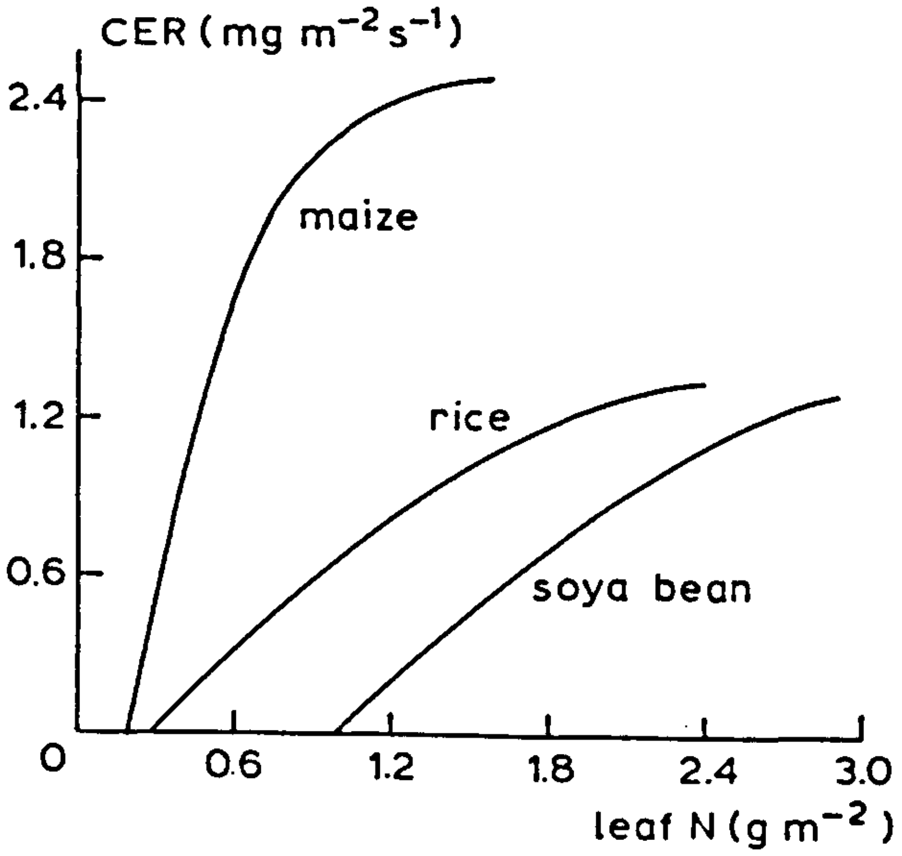

Figure 14. Plot of light-saturated leaf CO_2 exchange rates (*CER*) versus leaf nitrogen content per unit area. Source: Sinclair & Horie, 1989.

light-saturated CO_2 assimilation rate and leaf nitrogen content per unit area.

Since the objective of most simulation efforts is to quantitatively describe crop biomass accumulation, the photosynthetic response characteristics of individual leaves needs to be translated into whole-canopy CO_2 assimilation rates. Fortunately, the method for doing these calculations was derived in the classic work done by de Wit in 1965. De Wit provided the geometrical framework for calculating the radiation interception by leaves and for calculating the irradiance on individual leaf elements throughout the leaf canopy. Using a leaf photosynthetic light-response function, de Wit summed the CO_2 assimilation rates of the individual leaf segments to estimate the CO_2 uptake rate for the entire canopy. Sinclair & Horie (1989) used a greatly simplified version of de Wit's approach to evaluate the consequences of different light-saturated leaf photosynthetic rates and leaf nitrogen contents on canopy CO_2 assimilation rates. To facilitate their calculations, they assumed a uniform leaf nitrogen content throughout the canopy. Sinclair (1989) reviewed the assumed uniform leaf nitrogen distribution and concluded that it only resulted in small errors in the estimates of canopy CO_2 assimilation.

Sinclair & Horie (1989) chose to present the results of their analysis of canopy CO_2 assimilation in terms of a radiation use efficiency. They defined radiation use efficiency as the accumulated crop biomass per unit of intercepted total solar radiation. Monteith (1977) indicated the usefulness of determining radiation use efficiency by showing for many crops that the radiation use efficiency was roughly stable at 1.4 g MJ^{-1}. Sinclair & Horie (1989) calculated radiation use efficiencies from canopy CO_2 assimilation estimates, by accounting for maintenance and growth respiration and by dividing the calculated accumulated crop biomass by intercepted radiation. Similar to the function presented by Monteith (1977), they derived a curvilinear response in radiation use efficiency to light-saturated rates of leaf CO_2 assimilation rates (Figure 15). At the lower leaf CO_2 assimilation rates, the changes in radiation use efficiency were large. However, at greater leaf CO_2 assimilation rates the variation in radiation use efficiency within a species was predicted to be small, as was concluded by Monteith. In these calculations it was predicted for leaf CO_2 assimilation rates commonly observed for crops that the radiation use efficiency of maize is about 1.7 g MJ^{-1}, rice roughly 1.4 g MJ^{-1}, and soya bean approximately 1.2 g MJ^{-1}.

By combining Figures 14 and 15, Sinclair & Horie (1989) plotted radiation use efficiency as a function of leaf nitrogen content (Figure 16). These functions are also curvilinear with approximately linear responses in radiation use efficiency to changes in leaf nitrogen content at lower nitrogen contents. In each species, radiation use efficiency approaches a saturated value as nitrogen content increases. Substantial variation among species in the radiation use efficiency exists at any given leaf nitrogen content. Being a C_4 species, maize has by far the greatest radiation use efficiency at each leaf nitrogen content. Soya bean has the lowest values of radiation use efficiency per unit nitrogen, and rice is intermediate.

There are few experimental studies that allow the predictions of Figure 16 to be tested. Gallagher & Biscoe (1978) found the radiation use efficiency of wheat was

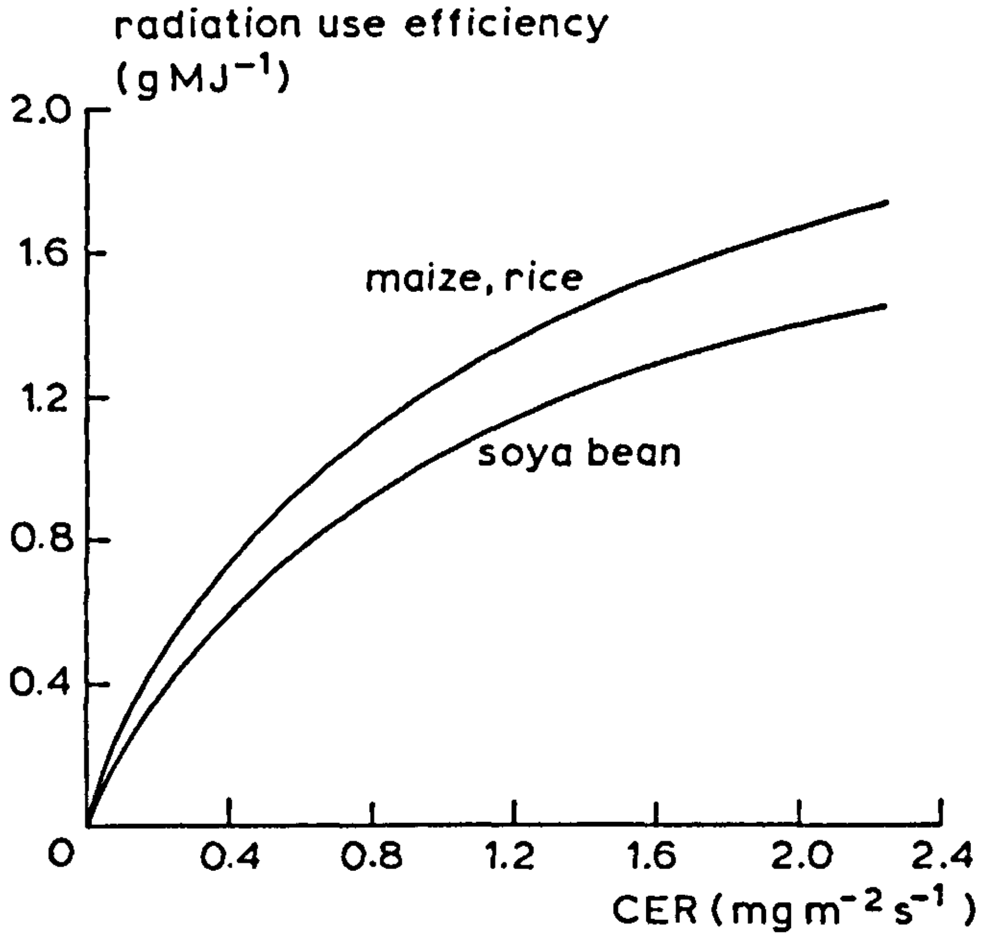

Figure 15. Plot of radiation use efficiency as a function of light-saturated leaf CO_2 exchange rate (*CER*) as derived by Sinclair & Horie (1989).

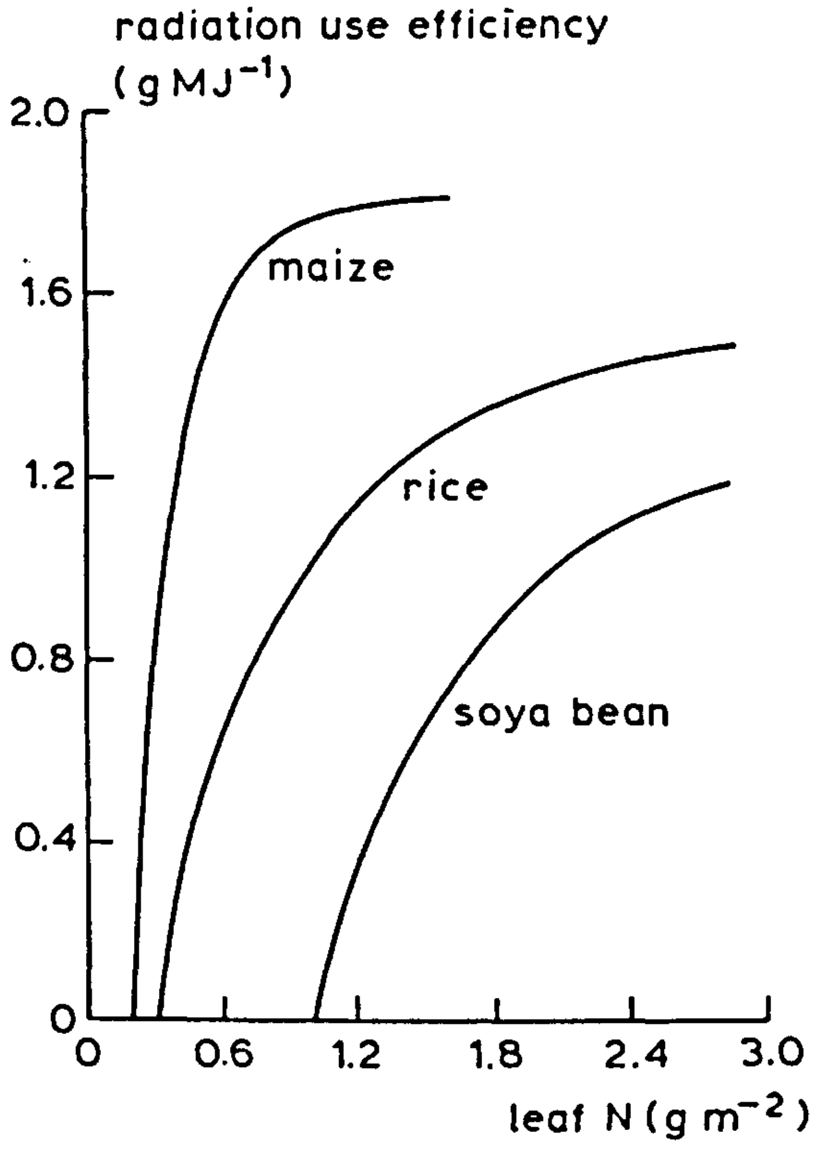

Figure 16. Plot of radiation use efficiency as a function of leaf nitrogen content per unit area as presented by Sinclair & Horie (1989).

increased by about 10 % when their crops were fertilized with nitrogen. Muchow & Davis (1988) reported that in maize and sorghum there is a common linear relationship between increasing radiation use efficiency and leaf nitrogen content. In sorghum, LaFitte & Loomis (1989) also derived a linear relationship between increasing radiation use efficiency and leaf nitrogen content.

The combined effects of nitrogen on developing leaf area and on radiation use efficiency mean that nitrogen availability to the leaves has considerable impact on determining crop biomass accumulation. Retarded leaf area development directly limits the amount of solar radiation that is intercepted and used in photosynthesis. The rate of leaf photosynthesis and, consequently, radiation use efficiency are quantitatively dependent on leaf nitrogen content per unit area.

3.4 Consequences of seed growth

The protein composition of crop seeds often defines their utility to man. For example, the type and amount of protein in various wheats define the commercial uses of the grain produced by specific cultivars. Although the nitrogen fraction in seeds varies among genotypes, this variation is commonly not large. In a study of 121 soya bean cultivars, Spaeth & Sinclair (1983) found the seed nitrogen content was generally between 60 and 70 mg N g^{-1}.

The effect of variation in seed composition among crop species on productivity was analysed by Sinclair & de Wit (1975). As a result of inter-species variation in protein, lipid and carbohydrate content of seeds, a considerable range of seed biomass per unit of photosynthate was predicted. Similarly, variation in the protein content of seeds resulted in a large inter-species range in the nitrogen required per unit of photosynthate used to grow seeds. Sinclair & de Wit (1975) plotted these two variables against each other (Figure 17) and found that the crop species were segregated into four groups. In Figure 17, the cereals are in the lower right quadrant and their seeds are characterized by low protein and lipid content. The upper right quadrant includes species that are high in protein and low in lipid content. The lower left quadrant contains species with high lipid content. In Figure 17, the sole member of the upper left quadrant was soya bean and it is characterized by both high protein and high lipid content. Winged bean (*Psophocarpus tetragonolobus*) was not considered in the comparison of Sinclair & de Wit, but it would join soya bean in the upper left quadrant.

The significance of the analysis by Sinclair & de Wit (1975) was a consideration of the seed nitrogen requirements relative to the potential for nitrogen supply to the crop. They suggested that under good growing conditions a nitrogen supply rate to the crop equivalent to about 20 mg nitrogen per g photosynthate could be sustained for seed growth (dashed horizontal line in Figure 17). To meet the nitrogen requirements for the crops requiring more than 20 mg g^{-1}, they concluded that the plants must commonly translocate nitrogen from the vegetative plant tissue to the growing seeds. During seed growth the amount of nitrogen in the soil usually decreases and the root activity declines, so that the nitrogen supply

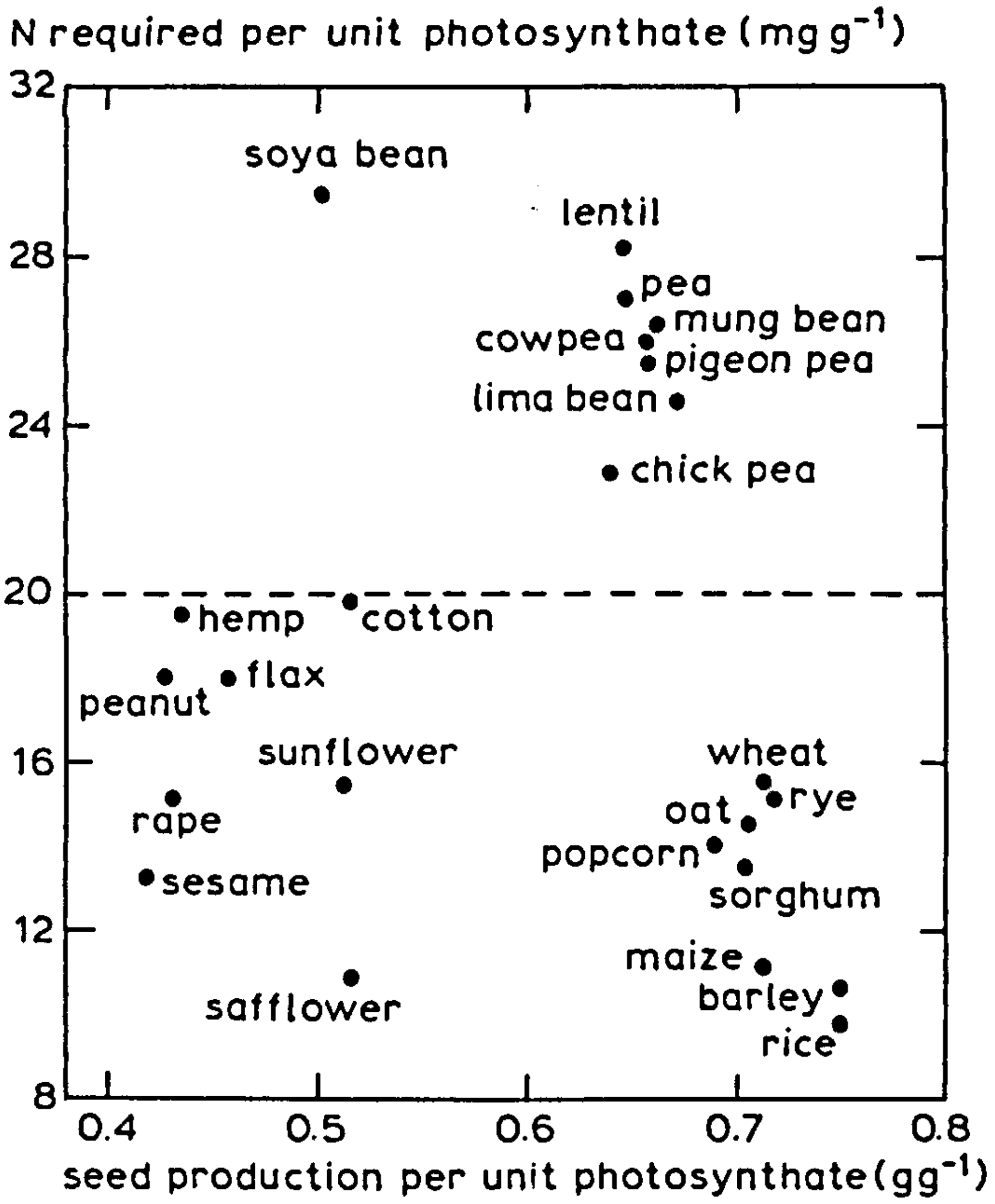

Figure 17. For seed production by various crop species, a plot of the nitrogen required per unit of photosynthate available to the seeds versus the seed biomass produced per unit of photosynthate available to the seeds. Source: Sinclair & de Wit, 1975.

rate for seed growth may be well below 20 mg nitrogen per g photosynthate. Consequently, as the nitrogen supply available to sustain seed growth decreases, all species may eventually translocate nitrogen from vegetative tissue to the growing seeds. Sinclair & de Wit referred to this nitrogen translocation process during seed growth as 'self-destruction', in that the vegetative tissue that is photosynthetically active is destroyed in the process of growing seeds. The self-destruction hypothesis has been the focus of considerable research worldwide.

In general, the self-destruction hypothesis has proven to be very useful in describing the changes observed in crop plants during seed growth. A number of empirical observations have shown that a decline in the nitrogen content of vegetative tissue occurs simultaneously with seed growth and the accumulation of nitrogen by the seeds. As examples, the data of Hanway & Weber (1971) and Spaeth & Sinclair (1983) document the phenomenon in soya bean. In wheat, the decline in leaf and vegetative nitrogen content while seeds are increasing their total nitrogen content has been observed in a number of studies (Karlen & Whitney, 1980; Spiertz & Ellen, 1978; Gregory et al., 1981; Vos, 1985). In maize, evidence of the self-destruction phenomenon is indicated in the data of Swank et al. (1982), Reed et al. (1988) and Wolfe et al. (1988).

An important consequence of the self-destruction hypothesis is that translocation of nitrogen from leaves can result both in a loss of photosynthetically active leaf area and in a decrease in leaf CO_2 assimilation rates (Figure 15). Sinclair & de Wit (1976) analysed the potential effect of the self-destruction phenomenon on soya bean in a simulation study. A conceptually simple model was used, in that leaves generated photosynthate for seed growth and nitrogen was freely supplied to the seeds to synthesize the requisite seed protein. The nitrogen required for growing seeds and which could not be obtained from the rhizosphere was translocated from vegetative tissue, including leaves. Translocation of nitrogen from leaves was simulated to result in a loss of crop leaf area. The simulations were terminated when equality was reached between the constant rhizosphere nitrogen supply rate and the declining seed requirement rate.

The simulation results obtained by Sinclair & de Wit (1976) and shown in Figure 18 illustrate the types of response generated by the model. Photosynthetically active leaf area index was simulated to decrease during seed growth and, depending on the rhizosphere nitrogen supply rate, the simulations reached the termination point after between 22 and 40 days. Seed yields in this example were calculated to range from 2550 to 5180 kg ha^{-1}. These types of calculations indicated the critical nature of the variables that define the seeds' nitrogen requirement and the rhizosphere nitrogen supply rate. Low nitrogen supply rates placed great demands on translocated nitrogen and severely limited the capacity of leaves to generate photosynthate.

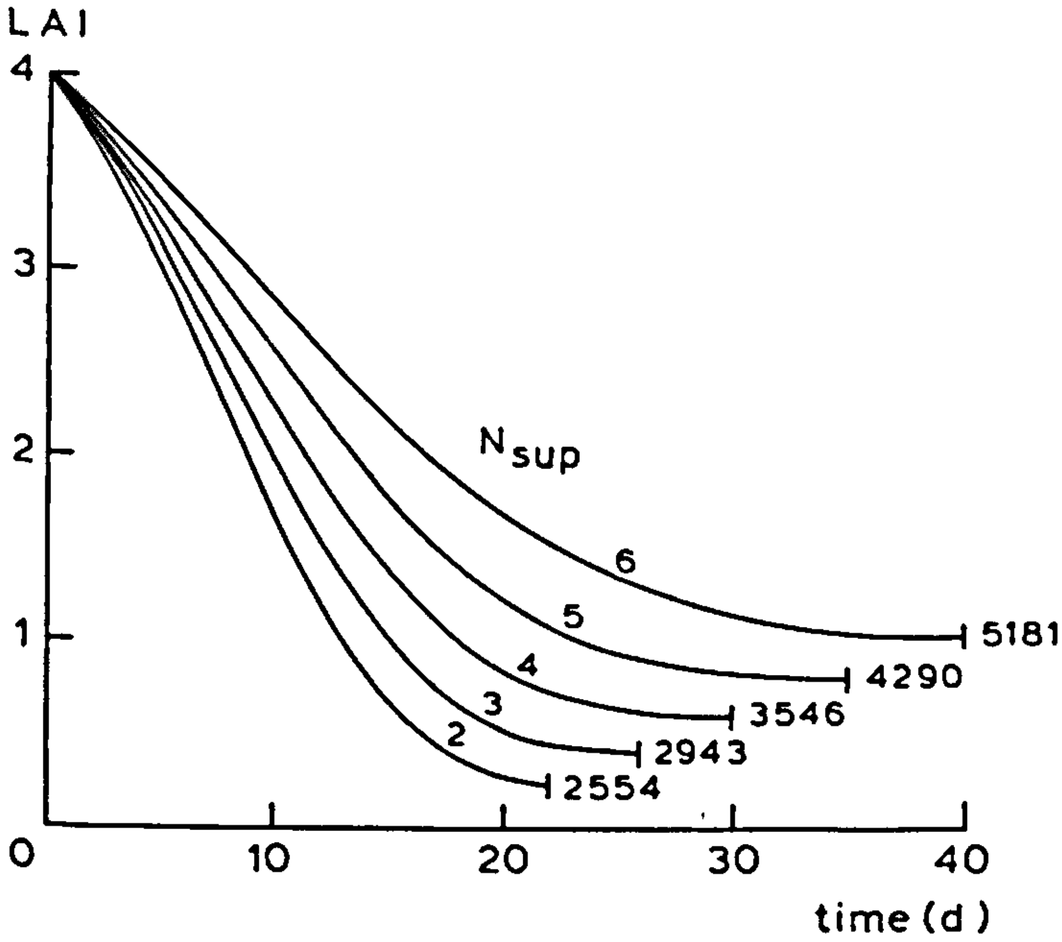

Figure 18. Simulated leaf area indices (*LAI*) resulting from a simulation of the self-destruction phenomenon in soya bean crops with differing rates of nitrogen input (N_{sup}, kg ha^{-1} d^{-1}). Final seed yields (kg ha^{-1}) are presented in lower, right-hand portion of the figure. Source: Sinclair & de Wit, 1976.

3.5 Nitrogen in crop models

Considerable effort has gone into accounting for the influences of nitrogen on crop growth in simulation models, including the work of the Theoretical Production Ecology group. For example, van Keulen (1982) has incorporated considerable complexity in the PAPRAN model to account for the influence of nitrogen on pasture growth. In his model, insufficient nitrogen results in both decreased growth of various tissues and decreased dry matter accumulation.

I have been interested in developing simple models for grain crops that allow an evaluation of climate modifications on productivity. Consistent with PAPRAN and the prior discussions in this chapter, in these simple models an insufficient supply rate of nitrogen retards leaf area development and decreases radiation use efficiency through decreased leaf nitrogen content (Sinclair, 1986). During seed growth, nitrogen translocation from vegetative tissues including leaves is allowed, to meet the nitrogen requirements of the developing seeds.

An important problem in developing simple models is the calculation of the rhizosphere nitrogen supply rate. In a simple soya bean model (Sinclair, 1986) the amount of nitrogen obtained directly from the soil is assumed to be small and it is given as an input variable. The major source of nitrogen for legume crops is commonly symbiotic nitrogen fixation rates. In my modelling efforts nitrogen fixation rates are computed daily and are based on the vegetative biomass and soil moisture content. From experimental evidence, it is assumed the potential nitrogen fixation rate is linearly dependent on vegetative biomass (e.g. Denison et al., 1985). Consequently, potential fixation rates increase with vegetative biomass through the initial stages of seed growth, and then the nitrogen fixation rates decline. Symbiotic nitrogen fixation rates were experimentally found to be especially sensitive to soil dehydration (Sinclair, 1986). A unique function altering nitrogen fixation in response to changing soil moisture content was included. This function helps to express the sensitivity of legume crops to soil dehydration (Sinclair et al., 1988).

This simple model accounting for carbon and nitrogen input to the soya bean crop has been found to satisfactorily mimic the growth of crops (Muchow & Sinclair, 1986). Additionally, the simple model has been used to analyse the growth and yield differences among several grain legumes (Sinclair et al., 1987). The same model structure, with only a few alterations of coefficients, was used for soya bean, cowpea, and black gram. The one substantive variant in the model among the three species was in the nitrogen supply to the crops during seed growth. Consistent with experimental evidence, cowpea and black gram had no symbiotic nitrogen fixation after flowering. This adjustment in nitrogen fixation activity allowed the simple model to work well for all three species (Table 3). Of particular interest was the calculation of potential crop yields for cowpea and black gram for the hypothetical circumstance where symbiotic nitrogen fixation might be sustained after flowering. In each species sustained nitrogen fixation rates were simulated to extend the duration of seed fill, increase total accumulated

Table 3. Observed and simulated seed and biomass yields for cowpea, black gram and soya bean at Lawes, Australia in 1981.

	Seed g m^{-2}	Biomass
Cowpea		
observed	198	609
simulated without N_2, fixation after flowering	198	641
simulated with N_2, fixation after flowering	510	964
Black gram		
observed	233	713
simulated without N_2, fixation after flowering	230	727
simulated with N_2, fixation after flowering	405	917
Soya bean		
observed	301	635
simulated	301	569

biomass, and increase seed yield (Table 3). Although these simulations of prolonged nitrogen fixation by cowpea and black gram are almost certainly unrealistic, they highlight the possible consequences of altered nitrogen fixation rates in these legumes.

3.6 Summing up

Research in the last 25 years by C.T. de Wit, the Department of Theoretical Production Ecology at Wageningen Agricultural University, and others has made great strides in quantitatively elucidating crop production. An important component of this progress has been an understanding of the influence of nitrogen on the physiology of crop yield. The basic components of how nitrogen affects yield-producing processes have been defined. Nitrogen is known to be an essential element of the nucleic acids and proteins that allow plants to grow and survive. Since nitrogen is essential in these abundant molecules, most plant tissues invariably require minimum amounts of nitrogen to grow. One major consequence of a lack of nitrogen in plants is that the growth of leaf area can be quantitatively depressed. This is especially significant for crops, because light interception is thereby decreased, resulting in less accumulated crop biomass. Leaf nitrogen also directly influences leaf photosynthetic rates, so that the radiation use efficiency of the crop canopy is also altered.

Whereas seed growth also requires minimum nitrogen contents, seeds commonly sustain their growth during periods of low nitrogen availability by acquiring nitrogen through translocation from vegetative tissue. The transference of nitrogen from vegetative tissue to the seeds led to the proposal of the self-destruction hypothesis. The phenomenon of self-destruction is now well established, even though important physiological questions concerning mechanisms and regulation are unresolved.

Experimental and simulation evidence all point to a central role of nitrogen in influencing grain crop yields. Adequate nitrogen supplies are required to obtain unrestricted leaf area growth and high radiation use efficiencies. Simulation results (e.g. Muchow & Sinclair, 1986) clearly indicate that yield potential of crops is intimately associated with the nitrogen input to the crop. Sustaining nitrogen supplies during seed growth is an important challenge for achieving these calculated yield potentials. Quantitative analyses of crop growth have been substantially improved by understanding the nitrogen influence on the physiology of crop yield.

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4 On scale problems in modelling: an example from soil ecology

P.A. Leffelaar

4.1 Introduction

Agricultural research aims to increase our understanding of systems and to reveal manipulable characteristics at the farm scale, so that management practices can be improved. Because agricultural systems are too complex to understand as a whole, subsystems (e.g. soil, plant, microclimate) and subprocesses (e.g. transport processes, photosynthesis, energy balance) are distinguished (Figure 19) and studied (systems analysis) with the ultimate objective of interconnecting the resulting knowledge and of returning to the farm scale (systems synthesis). Subsystems and subprocesses usually operate on much smaller spatial and temporal scales than the total system: they represent a different level of organization than the farm level.

For example, crops in the Netherlands usually have a fairly homogeneous appearance on a hectare scale, indicating the integrative power of the root–soil system with respect to space and the homogenizing effect of soil tillage and fertilization. For the crop growth process the characteristic time in which a substantial change in amount of biomass occurs, i.e. the time coefficient, is of the order of a week. Soil oxygen concentration, however, which may have a pronounced influence on crop growth (Drew, 1983), is known to vary substantially at a

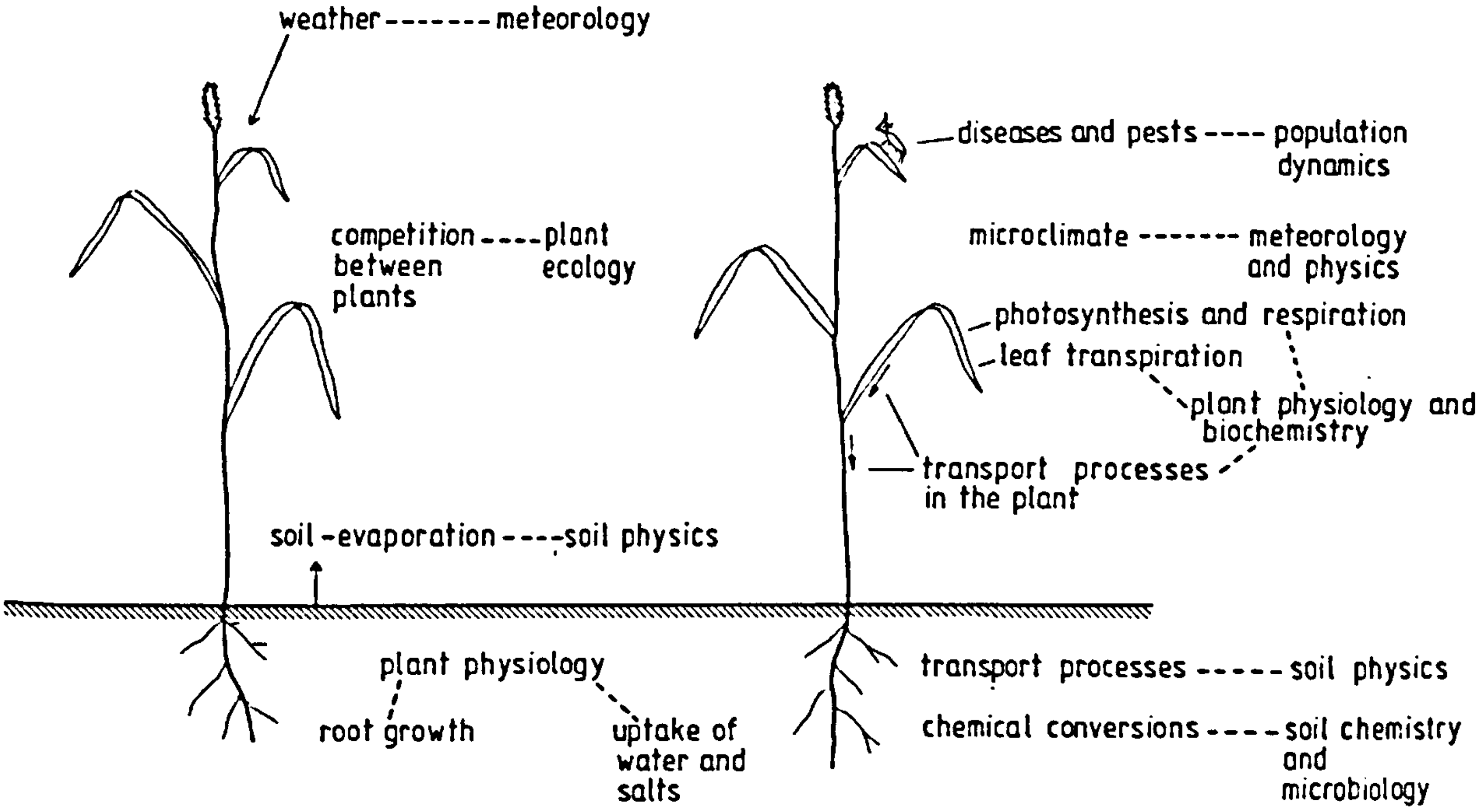

Figure 19. A crop system and some subsystems and processes that may be distinguished for its study (Source: de Wit, 1982b).

millimetre scale in the soil, i.e. at the root scale. Oxygen distribution quickly reacts to events such as rain or ploughing: its time coefficient is less than hours.

Such different levels of organization confront us with a general problem of applying the systems analysis and synthesis approach to complex systems, namely how many levels of organization can or should be bridged to combine an optimal causal insight in the system with the possibility of returning to the desired level of organization? In other words: to what level of detail should problems be analysed and studied to move forward in research without losing contact with the highest level of organization that should ultimately be reached? A factor that complicates the problem is that models remain simplified representations of reality. Different models of the same system may thus be developed and a puzzling question is: are there rules on how a system should be represented? De Wit (1968; 1970) was probably the first to focus attention on these problems from an agricultural point of view.

The general importance of the problem is beyond dispute, since each researcher is faced with it in each new modelling study. The scale problem and related questions cannot be answered simply. Instead, they should be discussed and each study means that new compromises need to be found. The following aspects need to be coherently considered, to clarify the problem of scale:

- objective of the study
- level of organization or scale of processes
- availability of theories
- possibility of clearly defining subsystems
- possibility of validating the model of a system
- possibility of returning to the field level of organization in the systems synthesis phase.

In this paper some aspects of these problems of modelling and related questions will be explored, using the soil ecology process of aeration and denitrification as illustration.

4.2 Objective of the study

The objective of a study is the first determinant of what level of organization will be studied. For example, the objective of a soil ecology study I carried out on aeration and denitrification* (Leffelaar, 1986; 1988) was to integrate knowledge about the major processes that cause and affect denitrification in unsaturated soil, by modelling and experimentation. This objective indicates that an explanatory simulation model interconnecting different spatial and temporal scales of organization was aimed at: the overall spatial scale is in the order of one to ten centimetres which is the level of soil aggregates, whereas the oxygen concen-

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* Denitrification denotes the process of nitrate reduction to molecular nitrogen under anaerobic conditions by heterotrophic microbes via the intermediates nitrite and nitrous oxide, resulting in losses of (fertilizer) nitrogen from the soil.

tration varies from 21 to 0% within a few millimetres when soil is water-saturated. The time coefficients for the biological processes of respiration and denitrification, for water flow and for gas diffusion flows, range from about 24 h to 60 s. Causal relationships were sought, rather than a direct answer to how much nitrogen was lost from soil per hectare.

If the latter had been the objective, it would have been better and faster to measure these gaseous losses directly in the field. Such experimental results would, however, apply uniquely to the site of the measurement and would not be general: there would be hardly any possibility of extrapolating the results. In causal studies, generality is contained in the model structure, as expressed by the differential equations and the feedbacks, whereas specificity is introduced by the parameters.

4.3 Level of organization or scale of processes

The level of organization or the scale on which a process occurs is another determinant of how that process should be studied. For example, microbes have a typical dimension of one μm^3 and they work on the pore scale in soil. Their numbers amount to 10^7 to 10^9 per g soil (Alexander, 1977). Because of these large numbers, one might at first sight expect a homogeneous distribution of microbes over the available soil surface area. This is not the case, however: the degree of occupation of soil surface area by microbes is about 0.1–0.2% and, moreover, the microbes form unevenly distributed colonies (Woldendorp, 1981). The scale at which microbes work suggests that they can best be studied at the level of the cell or colony. Combining the resulting data with the uneven distribution of the microbes could than give average respiration and denitrification data for a macroscopic part of the soil, e.g. thin soil layer. The objective of the aeration/denitrification study mentioned earlier, only demanded a measure for the consumption of oxygen at this higher scale of organization to calculate the degree of anaerobiosis, and for the consumption of nitrate and other intermediate electron acceptors. Therefore, it did not seem necessary to study the cell level in combination with the distribution of microbes over the soil surface area to obtain these bulk parameters. Instead, the objective of the study together with the level of organization of the biological processes led to the decision to model growth of biomass in relation to the availability of electron acceptors and organic matter for a thin soil layer. In this layer the underlying cell level and the effect of an uneven distribution of the microbes over the soil surface area are summarized in parameters such as an effective growth yield (kg of biomass-carbon kg^{-1} of organic matter-carbon) and an effective relative growth rate (μ, d^{-1}) that resulted from more detailed models (van Verseveld et al., 1977).

The process level of water flow in soil was chosen at the level of soil as a porous system, rather than at the pore level. Darcy's law gives a macroscopic description of soil water movement. Although this description of soil water movement is often considered to be based on first principles, Darcy's equation was found empirically and the relationships between hydraulic conductivity and water content ($K-\theta$) and between the soil moisture tension and water content ($\Psi-\theta$) must be determined anew for each soil. Such characteristics thus integrate geometrial information on the pore system, the interactions among the clay platelets and water, and the macrostructure of the soil in the flow behaviour of water.

In both the description of the biological processes and the water flow process, the parameters (i.e. growth yield, μ, $K-\theta$ and $\Psi-\theta$) lump a number of aspects: they represent some kind of average. At present, measurements in soil can only be performed at this level, however, and in the light of the objective of the study it did not seem worth the trouble to detail the theories any further. These experimental aspects will be discussed further in Section 4.6.

4.4 Availability of theories

Agricultural simulation models integrate theories developed in various disciplines, particularly biology, physics and chemistry. Each separate theory, whether well-founded or merely a series of hypotheses, is based on a number of assumptions and is developed for a particular system. Often, the system considered is homogeneous, e.g. diffusion of gases in a continuum, or bacterial growth in a well-stirred continuous culture. The potential success of a theory when applied in the modeller's system can only be judged if the assumptions underlying the theory are thoroughly understood.

For example, models of soil respiration and denitrification require a description of diffusion of gases such as oxygen, carbon dioxide, nitrous oxide and molecular nitrogen in a porous medium, because among other things these gases determine the environmental constraints of these biological processes. Diffusion of gases is usually described by Fick's law, which assumes that transport of a gas is given by minus the product of its concentration gradient and a diffusion coefficient. This implies that each gas moves independently of the other gases. This last assumption needs further consideration. Diffusion is the process by which matter is transported from one part of a system to another as a result of random motions of molecules that have individual speeds of the order of 100 m s^{-1} (Marrero & Mason, 1972). The average displacement velocities of the gas, however, are much less: about 0.01 m s^{-1}. This large difference in velocities is caused by the collisions of molecules. Hence, diffusive fluxes of different gases in a mixture are coupled and the assumption of independent gas fluxes in Fick's law is just a rough approach to the diffusion process.

The rigorous gas kinetic theory, developed by Maxwell and Stefan (Hirschfelder et al., 1964), includes the coupling of gas diffusion fluxes. An interesting phenomenon that can be predicted very well with this theory is that when water evaporates from a water surface through a column of oxygen and molecular nitrogen, the latter gases are stagnant in the steady state situation, although they show concentration gradients (Toor, 1957; Leffelaar, 1987). If Fick's law is used to predict fluxes from such concentration profiles, nonsense is produced: the order of magnitude of the calculated oxygen flux is similar to respiration measurements in the field (Leffelaar, 1987). The understanding of the assumptions of a theory is thus very important for proper modelling as well as for the correct interpretation of measurements.

Because the equations of Maxwell-Stefan and Fick are both available to describe gas movement, one has to choose between these models. If results for a specific system do not differ more than some preset fraction, there is no doubt that the simplest model should be preferred. The results of the Maxwell-Stefan and Fick equations for gas diffusion in soil were compared by Leffelaar (1987; 1988). For other process descriptions it is necessary to compare different theories before a proper choice can be made. Though necessary, this is sometimes, unfortunately, impracticable.

4.5 Possibility of clearly defining subsystems

To study a system and to develop models for it, the system must be clearly defined with respect to its environment. For this, boundaries should be chosen to isolate the system from its environment. Although system isolation may perhaps be approximated in the laboratory, it would certainly kill all field research if it were demanded for the field, because interactions between the system and its environment will always exist. Therefore, instead of trying to isolate a system, one should choose its boundaries in such a way, that it is possible to quantify the flows that result from the interactions or feedbacks between the system and its environment by taking measurements at these boundaries. Since measuring is expensive, the number of measurements at the boundaries should be minimized and the boundaries should be chosen so that the outside world may affect the system, but that the system hardly affects the environment. 'To achieve this, it may be necessary to choose a system that is larger than necessary for the original purpose', de Wit (1982a). It is an art to judge whether at a chosen boundary the flows that may result from the interactions or feedbacks from the system on the environment and vice versa are absent, or sufficiently small to be neglected, or whether these flows can be easily quantified by measurements. Only when flows that result from feedbacks are absent, negligible or measurable, can systems be reduced in size and can subsystems be studied separately. We may distinguish between geometrical or physical system boundaries and process boundaries.

In the case of the aeration/denitrification study, thanks to a specially designed laboratory respirometer system, in which homogeneous, cylindrical, soil aggregates can be studied (Leffelaar, 1986), it was possible to choose a geometrical boundary that isolated the system. Thus, an experimental reality was created that had the advantage of enabling a simulation model to be developed for the same geometry. The experimental system thus precluded any speculation about form of the aggregates and contact areas between aggregates as they occur in the field from the discussion about the comparison of the experimental and theoretical results of the aeration/denitrification study: the comparison of results could therefore focus on the causal relationships affecting denitrification, as intended (Leffelaar, 1988). The disadvantage of such a laboratory system may be the difficulty of comparing the results with the field scale, but this was not the objective of the study.

The processes, each with their approximate time coefficients, that can be distinguished in the denitrifying system are biological respiration and denitrification, and the transports of water, solutes and gases, as depicted in Figure 20. Each of these processes is complex and involves different disciplines. Hence, one would like to first study each process separately before it is possibly integrated into a larger model, and again we are confronted with the problem of how boundaries should be chosen, but now at the process level. For process boundaries, the same rule applies as for system boundaries: flows that result from feedback mechanisms should be absent, negligible or measurable. Therefore, we should first examine if interactions between the processes mentioned exist. By way of illustration two such examinations follow below, one with regard to gas and water transports and one with respect to the environment and microorganisms.

4.5.1 Feedback mechanisms of water content on gas transport

The amount of water in soil affects the cross sectional area that is available for transport processes via the gas-filled pore space and the gas continuity of pores. Water also affects the length of the path (tortuosity) that is to be travelled by a substance, both for the water phase and the gas phase. The change of water content directly influences the transport of gases, because the total gas pressure increases at the site where water content increases. Permanent pressure differences are unlikely to exist at short distances apart, though, because a change in water

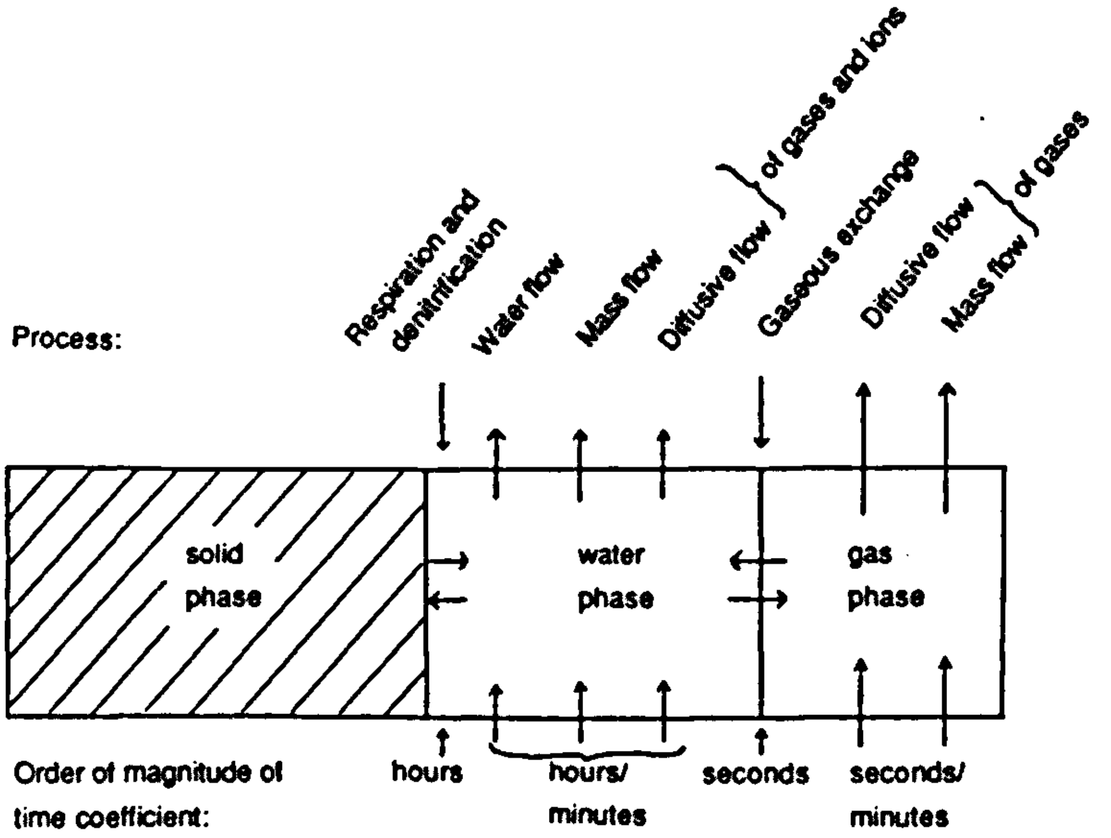

Figure 20. Processes distinguished in one soil layer of the aeration/denitrification model, with their approximate time coefficients.

content causes a countercurrent of gas: thus mass flow and mixing occur and the total gas pressure usually does not change. Besides, each gas has a different solubility in water. Thus, if gas composition changes, the total gas pressure changes, which also induces a mass flow of gas. At the same time, dissolved gases are carried along with the water, and gas diffusion takes place through the water phase and the gas phase.

Since the flows of matter that result from these feedback mechanisms are neither negligible nor measurable (at present), an accurate description of gas transport in soil is only possible when soil water movement is taken into account. Still, the gas flow model can be tested for the situation of water being stagnant or in the extreme condition of a dry soil (Leffelaar, 1987), but it is clear that in this situation not all feedbacks are included and certain interactions could be overlooked.

4.5.2 Feedback mechanisms of the soil environment on microorganisms

Soil water content affects the concentrations of substrates and electron acceptors as experienced by the microorganisms in soil. It is expected that these concentrations, rather than the corresponding amounts, affect microbial growth and maintenance. Water further affects the possibilities for transport (by diffusion, mass flow and hydrodynamic dispersion) of dissolved substrates, of electron acceptors and of microorganisms – if these are not attached to soil particles. At higher water contents microorganisms may be (more) mobile, which enhances their chance of survival. At low water contents microgradients of substrates around colonies may develop and microorganisms might not obtain enough food. Furthermore, soil water potential may affect the activity of microorganisms (Griffin, 1981). This implies that both soil water content and soil water tension are needed to elucidate problems of soil biology such as denitrification. If gaseous electron acceptors have a low solubility in water, fewer electron acceptors are available for the microorganisms, if one assumes that microorganisms live in the soil water phase. Finally, soil pores form niches for microorganisms, protecting them from predators. These feedback mechanisms of environmental conditions on soil microorganisms are neither negligible nor measurable at present, so that isolating microorganisms from their soil environment with the aim of studying them separately, gives results that are not applicable to the real soil. As in the case of the gas model, it is possible to test the respiration/denitrification model under the condition that water, substrates, electron acceptors and microorganisms are homogeneously distributed in the soil, e.g. by working with a very thin soil layer in which it may be supposed that gradients and thus transport processes are absent (Leffelaar & Wessel, 1988). It is not possible, however, to exclude the influence of soil water tension and gaseous solubility on the biological processes that occur in the thin soil layer.

Both for the gas model and for the aeration/denitrification model the proposed study of the simplified system is only meaningful if the simplified system behaves similar to the system as a whole.

The existence of many feedback mechanisms between microorganisms on the one hand and the environment on the other hand, means that biological and physical processes in the soil need to be studied in conjunction with each other. Similarly, soil biology parameters must be determined in the environment in which they should apply, not only because of the feedbacks mentioned, but also because organisms adapt themselves to a new environment. One such soil-biology parameter, whose value when measured in soil differs significantly from its value measured in pure cultures, is the half saturation value in the Monod equation. This parameter was found to be higher in soil than in pure culture studies (Firestone, 1982), apparently because some kind of mass transfer is involved (Shieh, 1979), e.g. diffusion on a microscale. The feedback mechanisms mentioned were partly discovered by combining the different submodels of the processes mentioned into a large simulation model (Leffelaar, 1988). Thus, the coupling of the processes and the explicit documentation of the (theoretical) interactions brought soil ecology research a step forward. In fact, the coupling action is the only new element in the application of biological and physical knowledge to solve the aeration/denitrification problem: Fick's law was reported in 1855, based on the analogy with the description of heat flow by Fourier (1822), Darcy's law was discovered in 1856 for saturated soil (but in 1931 Richards concluded that Darcy's law could also be applied to unsaturated water flow), Maxwell and Stefan presented their gas kinetic theories in 1867 and 1871/1872, respectively, and Monod's equation was launched in 1942, based on work by Michaelis and Menten (1913).

4.6 Possibility of validating the model of a system

Sometimes models need not be validated if they are based on well accepted (usually previously validated) theories and if they are exclusively applied to a type of system similar to the one for which the theory was developed. Models of ecological systems will, however, always need validation, not only at the level of the integrated model but also at the explanatory level, i.e. the submodels and processes. There are at least two reasons for this.

Firstly, results on the explainable level may compare very favourably with experimental data, whereas the underlying processes are not well simulated. This is demonstrated in Figures 21 and 22. Figure 21 shows the experimental and simulated time courses of the oxygen pressures in the centre and 4 cm from the centre of the experimental aggregate in the aeration/denitrification study, and the increase of nitrous oxide and molecular nitrogen in the chamber that contains the aggregate. The oxygen pressure curves show satisfactory agreement with the experimental findings. Simulated losses of nitrous oxide and molecular nitrogen lag behind the experimental curves, but the qualitative resemblance is reasonable. Figure 22 shows the distribution of nitrate in the experiment and in the simulation: these distributions are almost mirror images! Hence, the combined study of

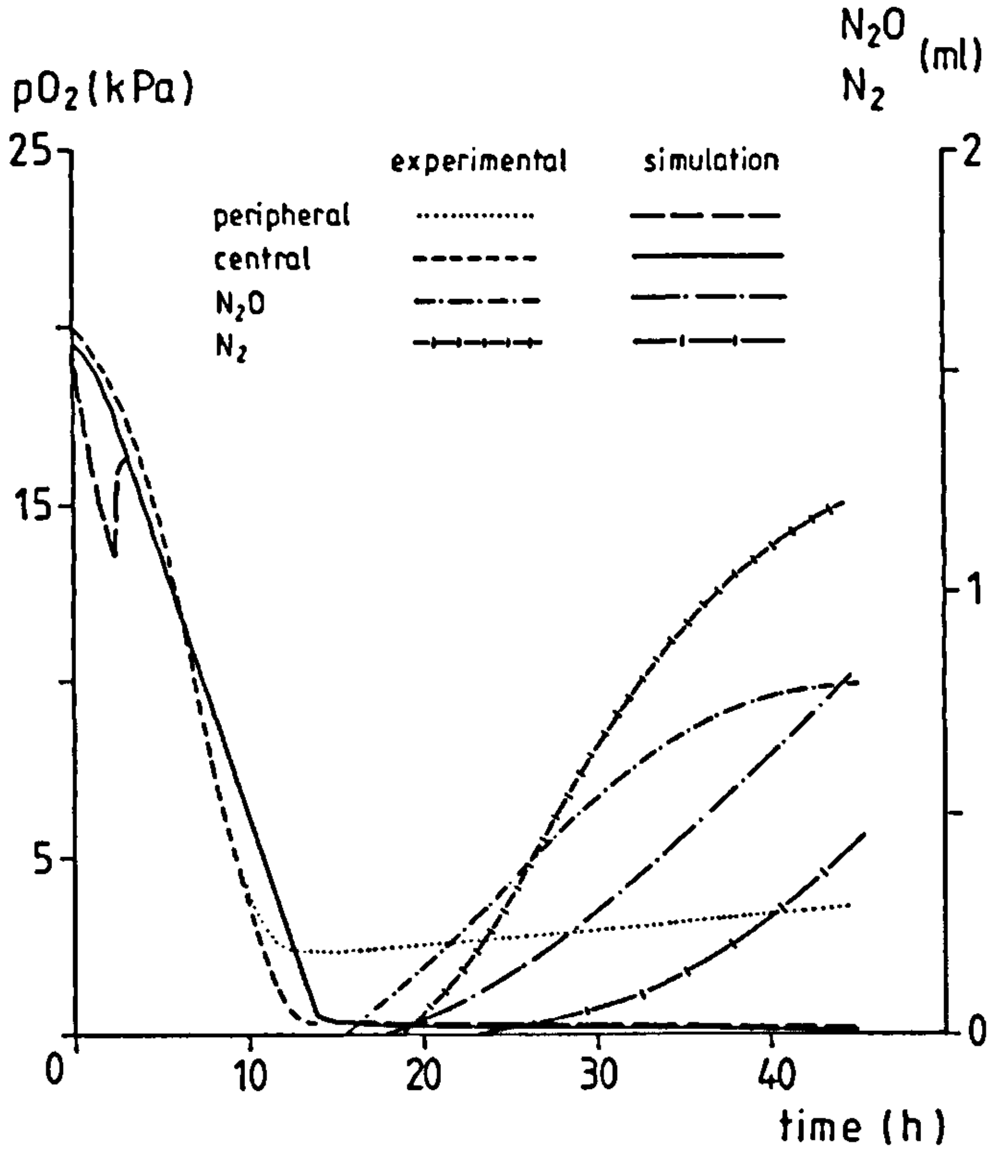

Figure 21. Simulated and experimental oxygen pressure (left *y* axis) in centre and 4 cm from centre (peripheral) of soil aggregate and volumes of nitrous oxide and molecular nitrogen in chamber that contains the aggregate (right *y* axis) as a function of time (Source: Leffelaar, 1988).

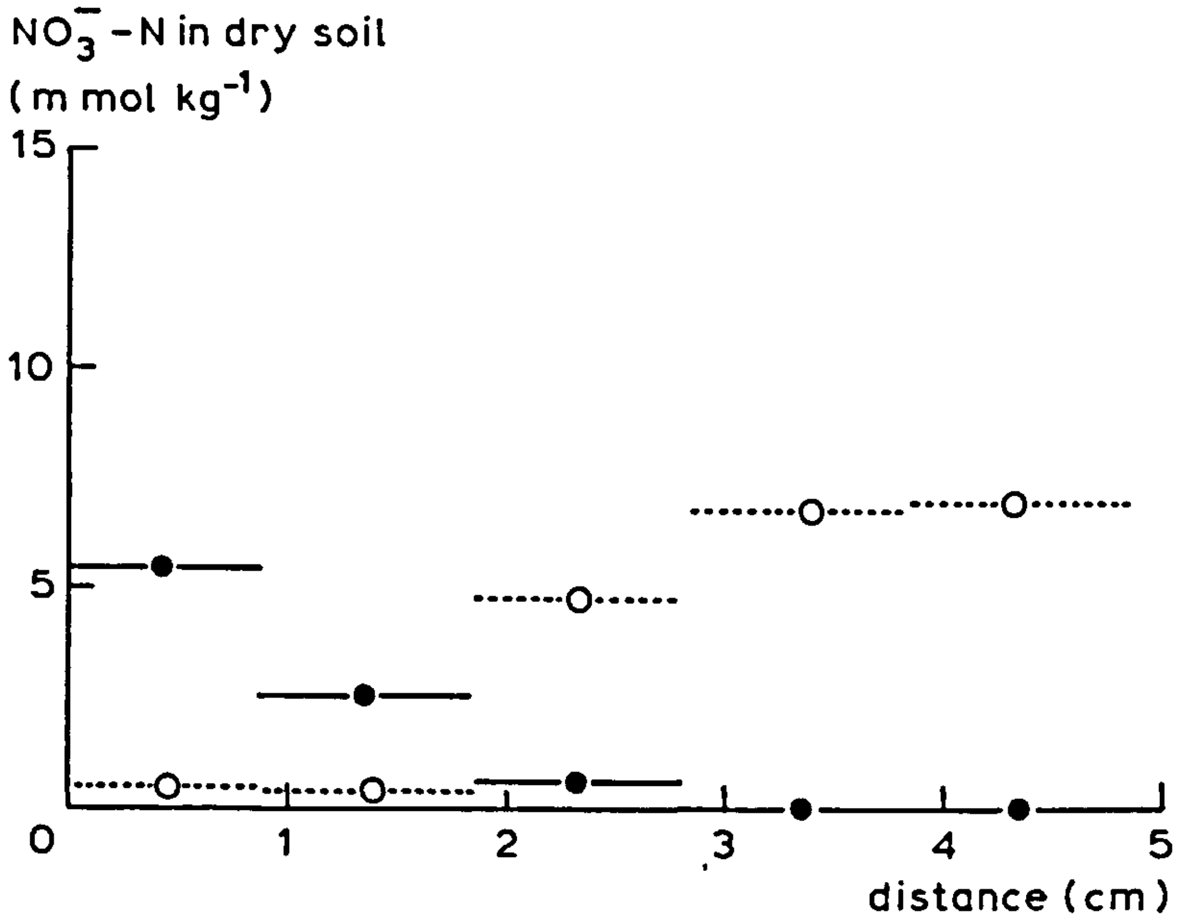

Figure 22. Simulated (——●——) and experimental (---o---) distributions of nitrate in a cylindrical soil aggregate (centre at 4.9 cm) after 45 hours (Source: Leffelaar, 1988).

experiment and simulation reveals that parts of the processes are not correctly described, implying that a hypothesis is not valid, or that some of the measurements may be suspect. Further study is then needed.

The second reason to validate models at the explainable level and at the explanatory level is that the quality of biological and physical models is usuallly not the same, because biological processes are more complex than physical processes. The description of the biological processes of respiration and denitrification on the basis of growth, first order rate constants, yield factors, maintenance coefficients, and so on, was founded on many more assumptions than the description of water flow (Leffelaar & Wessel, 1988). The quality of models is thus reflected by the number of assumptions or 'non-binding opinions' (de Wit, 1970) underlying the rate equations: more assumptions mean more possibilities of introducing inaccuracies, and less quality of the model description. Nevertheless, models of different quality need to be coupled, simply because problems that contain aspects that are known to various degrees of detail must be solved; ecological research would be seriously hampered if models of similar quality had to be developed first.

As indicated above, the physical model for water flow is less complicated than the model for the biological process. On the one hand, this is because empirical relationships between the hydraulic conductivity and water content and between the matric suction and water content are used in Darcian water flow models (see Section 4.3). On the other hand, it is assumed that the soil is homogeneous and rigid: cracks, aggregates or other structures are absent and no swelling or shrinking occurs.

Model validation implies that the modelled state variables can be measured as a function of time. The more detailed the model description, the more difficult the measurements that need to be performed (see Section 4.7). For example, microorganisms in the soil pores will experience a certain oxygen pressure and water tension. Although a polarographic oxygen electrode that might be used to monitor the oxygen pressure in soil may have a diameter as small as 0.5 mm, this is still very large compared with the pore diameter of about 0.03 mm at field capacity. When the reaction of microorganisms to moisture tension is to be evaluated, it is only possible to measure on the 'tensiometer scale' having a surface area in the order of cm^2. Both the oxygen sensor and the tensiometer thus seriously disturb the environment in which the processes take place and, moreover, they yield integrated results over space. Such average experimental results, which include the feedbacks mentioned before, apply at a higher level of organization than the cell level where the process of respiration actually occurs. In view of these experimental restrictions, it seems most appropriate to model such a process at the same level of detail as it can be measured. This means that average parameters are used to characterize the respiring soil organisms, and that it is assumed that this is permissible because the process considered is distributed fairly homogeneously throughout the soil and that the process will show a linear dependence on these average parameters. Field measurements, however, usually show a large variability. When models are parameterized with average parameters, one should therefore not be surprised about deviations from reality. In fact, the calculations should be performed with a number of point-measured parameters under the assumption of homogeneity and thereafter the field average should be calculated, using the additional information on how the parameters are distributed over the field (de Wit & van Keulen, 1987). A sound description of soil heterogeneity is thus needed, and in this respect, the work of Rappoldt (1990) is promising.

4.7 Possibility of returning to the field level of organization in the systems synthesis phase

Suppose detailed validated models are available that describe a number of different processes of a subsystem and that explain system behaviour satisfactorily. To proceed to the field level would imply that a gap of several orders of magnitude must be bridged both for the spatial scale, i.e. from centimetres to hectometres and for the time scale, i.e. from days to seasons, and this comes on top of the range of orders of magnitude that is already incorporated in the detailed submodels. Is such an extension possible in principle and is it necessary?

4.7.1 The possibility of proceeding from detailed models and/or submodels to the field scale

Models need to be initialized and parameterized and submodels need to be coupled. Models usually contain negative feedback mechanisms that result in stable equilibria after some time. For models of natural systems, where one is often interested in the behaviour of the model after a perturbation of the equilibrium situation, equilibria should be independent of the initial conditions. Therefore, initialization need not be very accurate, but the experiments with the model should begin after a simulation period that is sufficiently long to allow the model to reach such an equilibrium (which is mostly dynamic).

In production systems, however, one is interested in the time course of the state variables from a start position to the equilibrium (which is mostly static); for instance, crop growth ending in crop maturity. Because different initializations will give different time courses towards equilibrium, the initialization of models describing production systems must be done with care. Furthermore, when a system can reach different states of equilibrium, which state is reached will depend on the initial conditions. This may happen in the competition of crops and weeds for light (Spitters & Aerts, 1983). To initialize a model, the values of all the state variables should be determined within a short time span in which they do not change materially (de Wit, 1982a). This might present practical problems if a number of levels of organization with their concomitant time coefficients were bridged within one model.

Model parameterization for the models of natural systems and of production systems should always be done with care, because the parameter values largely determine model behaviour.

When coupling models, the relative magnitude and the (experimental) uncertainty of states and rates should be reconsidered, to assess whether model coupling will yield a reasonable integrated model. Suppose that two separate models exist, one for grass and one for earthworms. Both models calculate the dynamics of the amount of carbon in the grass and in the earthworms. In each model the state variable of the amount of carbon is important, but will this also be true if these models are combined? To judge this, let us first compare the state variables, i.e. the amounts of carbon. If the amounts of carbon are, for instance, 99 for the grass and 1 for the earthworms, one would consider neglecting the latter in a combination model.

A second consideration when judging the meaningfulness of model coupling is to compare the rates of change of the carbon states or carbon turnover rates, which, when combined with the values of the carbon state variables also give information about the related characteristic times or time coefficients of the models. If the carbon turnover in the earthworms was very high compared with the carbon turnover of the grass, one would like to take the earthworms into account in the combination model. The accuracy of determination of the carbon state of the earthworms could be much lower than for the grass, however, because of difficulties in collecting worms. This could create unacceptably large differences in accuracy of initialization in the combination model. Pool size, turnover rate and accuracy of determination of state variables and related parameters should be considered when knowledge is to be integrated in combination models.

It is probable that for a given system there is an optimum number of state variables or processes that should be included in a model. This is illustrated in Figure 23, where the number of state variables or processes in a model is given on the x axis and the approximation of reality on the y axis. Adding processes before the optimum is reached will improve the model's applicability, because systems reality is better approximated. Systems reality will never be reached, however, because de Wit's statement from 1970 that 'we know only bits and pieces of nature around us' remains valid. Taking more processes into account than the optimum number would give problems of initialization, parameterization and accuracy, but moreover, the researcher might lose his overview of the problem he wanted to clarify. Above the optimum number of processes one would like to consider the model as a system, to subsequently simplify or model it.

Unfortunately, it does not seem possible to determine the optimum number of processes in a model as depicted in Figure 23; finding the optimum remains an art. Also, the number of different orders of magnitude in level of organization that can be bridged at this optimum is still unresolved.

These general problems with respect to initialization, parameterization, coupling of models and finding an optimum of processes to be included in explanatory models would, when solved in terms of general operative rules, considerably advance research in soil ecology, even without building the models, but until

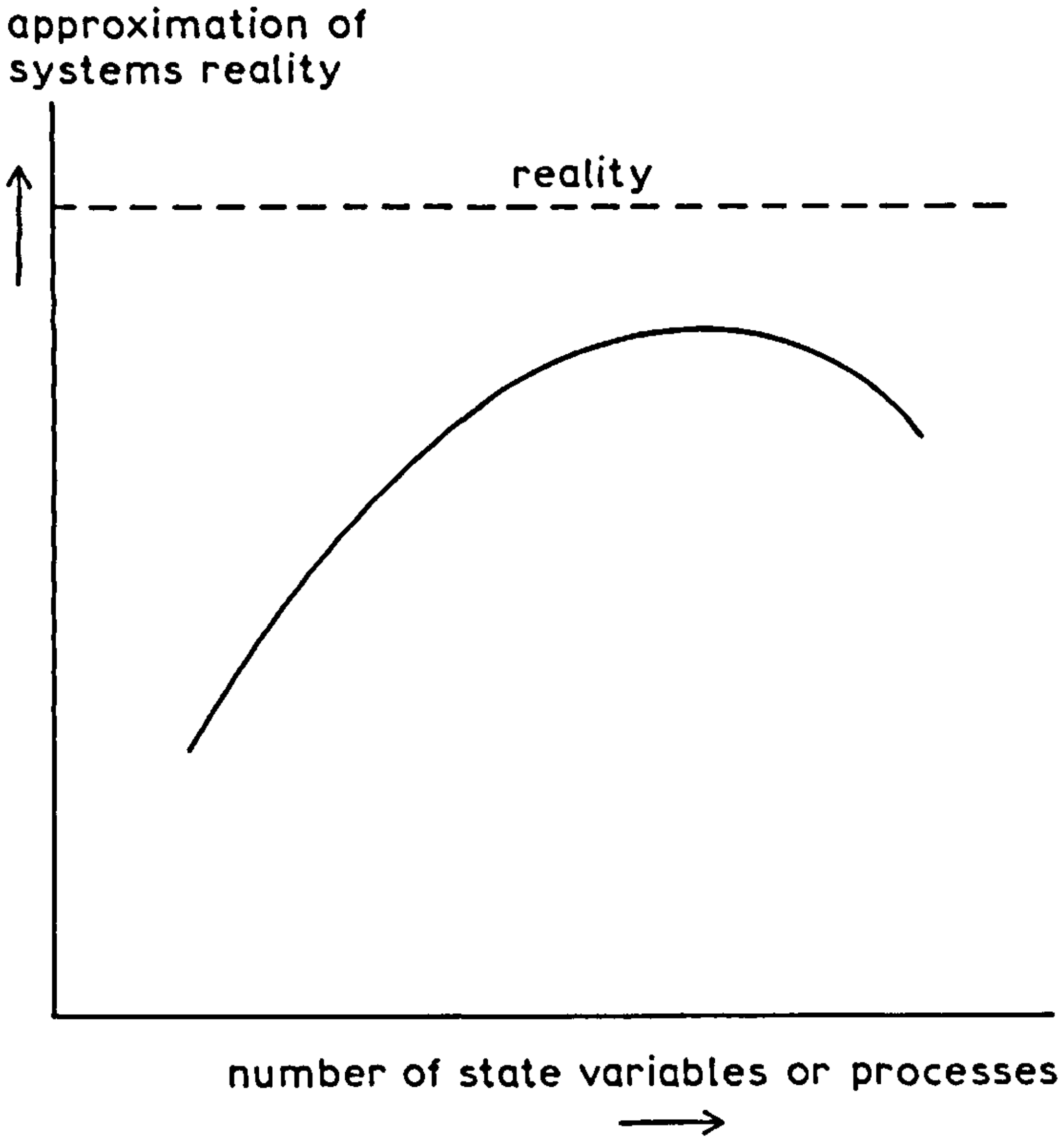

Figure 23. Qualitative relationship between the number of state variables or processes included in a model and the approximation of systems reality.

that time common sense, experience and trial and error must be practised.

4.7.2 *The necessity to proceed from detailed models and/or submodels to the field scale*

Sometimes it may be possible to proceed from the detailed level of organization directly to the integrated level, when concepts of thinking from small-scale studies happen to apply to the larger field scale. Then, manageable characteristics are directly derived from the small-scale study, and applied at the field scale. For example, the aeration/denitrification processes occur in a similar cause and effect relationship in the field as in the small-scale experimental and model studies. Therefore, it would not be unlikely that conclusions from the detailed study could be directly applied to the field. Indeed, nitrogen losses in the laboratory experiments (Leffelaar, 1988) were of similar magnitude to those reported by Rolston et al. (1976; 1978) and Colbourn & Dowdell (1984) for the field.

Another striking example of the direct use of a small-scale process to the field scale is the process of photosynthesis, which occurs at the chloroplast level with characteristic length and time scales of 1 μm and 10 ms (van Kooten, 1988). The process at the chloroplast level is directly responsible for the crop production process, and explanatory crop growth models start with a description of photosynthesis (de Wit, 1965).

When conclusions applying to the field level can be drawn from more detailed work, the level of integration in the detailed study is already sufficiently high. In other words: it may be that the field scale of say 100 by 100 m is not the smallest unit that contains all different subsystems and subprocesses with respect to the aeration/denitrification process. A square metre or even less might be sufficient.

4.8 Concluding remarks

The modelling of systems is an admission that we cannot understand systems fully and as a whole. The systems analysis and synthesis approach can be exploited best if this admission is translated into real simplifications, rather than by trying to split up an ecosystem into all its composing subsystems, with the purpose of modelling each subsystem and of interconnecting all submodels. This implies that no general purpose models can be built (de Wit, 1970).

It is very likely that the better a system is understood, the more simply it can be represented in a model (Cole et al., 1983), because the major state variables and feedback mechanisms are known.

Coupling of processes and submodels that influence each other will advance ecological research because:

- the coupling assumptions need to be formulated explicitly
- the coupling will expose shortcomings in our knowledge
- by including more processes in a model, it may be concluded from sensitivity analysis that it is not strictly necessary to incorporate some of these processes to get a better understanding of the system. In the coupling process different scientific disciplines will meet.

Agricultural models need to be validated or tested with respect to each different process modelled (if possible), since the overall model results may be good because of compensating negative feedback mechanisms, whereas intermediate results are not well described.

To determine if a soil organism or a process can be studied separately from its environment, with the purpose of using the results subsequently in the system from which it was separated, the possible feedback mechanisms should be listed and judged beforehand.

We still cannot say much in general about the number of subsequent levels of organization that can or should be bridged in a model. If a model involves time coefficients of different orders of magnitude, a stiff-equation problem exists. This may give rise to excessive number crunching. De Wit (1982b) stated that this should be avoided in simulation programs for digital computers by restricting the number of levels of organization that are incorporated in one simulation model. Present-day computers are very fast, however, and this number crunching should no longer be the prime reason for restricting the number of levels of organization. Rather, a possible restriction should be judged in terms of whether including another level of organization would sufficiently increase causal insight in the system and, if so, whether no problems with the initialization and parameterization are expected. To this end a pragmatic method of trial-and-error must be applied.

Research should aim to discover laws that integrate detail to acceptable levels (de Wit, 1968). Models can be very helpful in this process: they can be used to investigate if model results can be summarized in a single number or in simple equations (Penning de Vries et al., 1974; Goudriaan, 1977).

Most natural systems are heterogeneous, implying that average parameters do not often characterize the system. For example, there is no average aeration status of soil when anaerobiosis and aerobiosis coexist. In such cases it is more informative to measure with a certain strategy, rather than to perform measurements at random.

Modelling remains largely based on common sense and experience. Modelling thus remains an art, rather than a science. A unique art, though, with strong practical and theoretical possibilities and results.

4.9 Acknowledgments

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PLANT GROWTH AND DEVELOPMENT

5 Assimilation, allocation, explanation, extrapolation

L.T. Evans

5.1 Introduction

After an initial preoccupation with soil water and nutrients, de Wit turned to the estimation of transpiration and then of potential photosynthesis by crops. This led him on various occasions to estimate the potential yield of crops in different environments, from the viewpoint of an unabashed optimist. Thus, de Wit et al. (1979) conclude that the crux of the world food 'problem is not so much yield potential as the economic and social constraints on the rate of increase of food production'.

For the world as a whole I tend to agree with them, but particularly for those areas where crop yields are already high we need a far better understanding of the opportunities for raising yield potential further, despite the discouraging effect of present surpluses on the support for such research.

In this chapter I shall focus on only two of the many processes that may limit the yield potential of crops, namely the assimilation of CO_2 and the allocation of assimilates among competing organs of the plant. These are both crucial to any simulation of crop growth and yield and they form a pointed contrast in that although we understand assimilation far more thoroughly than allocation, it has nevertheless been changes in the latter rather than the former that have contributed to past improvements in yield potential.

5.2 Assimilation

In their review of the physiological potential of crop production de Wit et al. (1979) conclude that 'plant breeding has not resulted in any increase in potential growth rate, in spite of the relatively large variations in maximum leaf assimilation rates observed...'. Some plant breeders, such as K.J. Frey, believe that crop growth rates (*CGR*) can be increased by the introduction of alien genes, but their growth rates have usually been measured over the whole life cycle of the crop and their results are confounded with varietal differences in crop duration, and possibly also in height. In several comparisons of old and new varieties of wheat, rice and other crops there has been no evidence so far of improvement in maximum *CGR*.

The relatively few varietal comparisons made of photosynthetic rates from closed crop canopies also suggest that the superiority of higher-yielding varieties is usually apparent only towards the end of the growing season, i.e. in the duration of photosynthesis rather than in its maximum rate. This is particularly clear in the work of Wells et al. (1982) with 16 varieties of soya bean from four maturity groups, in which the decline in canopy photosynthesis was found to occur five or more days later in the highest-yielding variety of each maturity group than in the lowest one. These varieties were the same as those used by Bhagsari et al. (1977) for a comparison of the CO_2 exchange rates (*CER*) of individual leaves; correlation of these leaf rates with the canopy rates over two intervals in 1975 gave coefficients of only 0.30 and 0.15.

Comparisons between old and new varieties, and with their wild progenitors, for many forage and crop plants, have only rarely revealed a positive correlation between maximum *CER* and yield potential. Far more frequently the correlations have been negative (*cf.* Elmore, 1980; Eagles & Wilson, 1982) and in wheat, rice, sorghum, pearl and barnyard millets, sugar cane, soya bean, cotton, brassica, sunflower and cassava the highest *CER*s recorded have been for the wild relatives, not the advanced cultivars. Moreover, selection for high *CER* has resulted in decreased yield in several crops and pasture plants.

We are, therefore, confronted with a significant paradox. Increases in photosynthetic rate associated with higher irradiance or CO_2 levels generally result in higher yield, yet selection for greater *CER* appears to have the opposite effect. We need to resolve this paradox if selection for higher *CER* is to contribute to increased yield potential in the future.

Of the various counter-intuitive effects at work, the most potent is the frequently found negative relation between *CER* and leaf size. This was striking in our early work with wheat (Evans & Dunstone, 1970), and has since been found in many other crop plants (*cf.* Bhagsari & Brown, 1986). Its explanation is largely in terms of what has been called 'the dilution effect', that larger leaves have fewer pigments and photosynthetic enzymes per unit area, and therefore a lower maximum *CER*. Bunce (1989) argues that the lower *CER* of larger leaves is also due to the greater likelihood of their developing in the shade of others. The lower surface/volume ratio of larger cells for gas exchange may also contribute.

Granted these trade-offs between leaf size and *CER*, why should larger leaves have been selected in the course of crop improvement? In most of the cases where there is a negative relation between leaf area and *CER*, yield has been positively related to the former. When both leaf area and *CER* are varied in one genotype, e.g. by daylength in *Poa pratensis* (Heide et al., 1985), the gain from greater area for the interception of light outweighs the fall in *CER*, and this is likely to be significant in the early stages of crop growth. But once the canopy is closed, one might expect smaller-leaved varieties with higher *CER* to have the advantage. Indeed, as more fertilizers and better crop protection lead to still faster crop development and early canopy closure, we may well find that a more positive relation between *CER* and yield begins to emerge or, alternatively, that there is a more pronounced ontogenetic shift from larger leaves with low *CER* during early growth to smaller ones with high *CER* once the canopy is closed. Constraining this shift, however, would be any allometric relation between leaf size and fruit or grain size, such as we found in wheat (Evans & Dunstone, 1970).

Thus, the apparently obvious route to higher yields through selection for higher *CER*, which emerged from several early models as more likely to enhance potential photosynthesis than changes in light interception, may need help from simulation of the trade-offs associated with the relation between *CER* and leaf size. Other trade-offs may also be involved, such as those between maximum *CER* on the one hand and the duration of photosynthetic activity or its tolerance of adverse conditions on the other.

As in the work of Wells et al. (1982) with soya bean varieties, so also with other crops such as wheat, rice, maize, cowpeas, sugar beet and cassava, the most noticeable change in photosynthesis with crop improvement has been in the duration of activity. Maize breeders, for example, have achieved increased 'stay green'. One result of this is, of course, that varietal rankings for *CER* made late in crop development may correlate positively with yield, even though maximum *CER*s correlate negatively.

For no crop, do we yet know whether the greater duration of photosynthetic activity is due to direct selection for leaf longevity or to the effects of more prolonged demand for assimilates as a result of selection for more prolonged grain growth. Nor do we know what limits there are to the increase in leaf longevity, or the trade-offs involved. Sinclair & de Wit's (1975; 1976) hypothesis of self-destruction suggests that photosynthesis is cut short in high-protein, high-yielding grain legume crops because of the remobilization of amino acids out of the leaves to the grain. Whether protein storage is driven by the rate of photosynthesis, as their model assumes, remains an open question, but the consequence they deduce of a shorter photosynthetic life when the *CER* is higher illustrates one of the possible trade-offs of selection for high *CER* rather than high yield.

5.3 Allocation

Despite the complications we have just been considering, crop photosynthesis has been simulated reasonably effectively on the basis of physical principles of mass transfer, and respiration on the basis of a distinction between synthesis and maintenance components. But when we come to the allocation of the net photosynthate, explanatory models give way to empirical ones. As de Wit & Penning de Vries (1985) admit: 'By far the weakest feature of these production models is the simulation of assimilate partitioning among organs...'. Yet this is the very area where plant breeders have made their most striking progress.

Van Dobben (1962) was the first to point out, with reference to wheat varieties used in the Netherlands from 1902 to 1961, that only the proportion allocated to the grain, not the total dry matter, had increased. This proportion, now called the harvest index, is 15–20% in many of the wild progenitors of the cereals, and since van Dobben's time it has continued to rise from 40 % to more than 50 %. Wheat varieties in England have followed a similar trend (Austin et al., 1980; 1989), as have rice varieties in the Philippines (Evans et al., 1984), barley, oats and some pulse crops. We have estimated that, in wheat, the harvest index could probably be raised to at least 62 %, so there is scope for further progress, but that limit is likely to be reached within 40 years. In the meantime, and not only for the purposes of simulation, we need a better understanding of the processes involved in the rise in harvest index and in the partitioning of assimilates.

5.3.1 Sources of the rise in harvest index

When there is no change in biomass and crop duration, greater yield can be achieved only through reduced investment in other organs. And this in turn may be achieved only at the expense of adaptation to stress or by the provision of better agronomic support for the crop.

In recent years the most striking trend for many crops has been the reduction in height by the introduction of major dwarfing genes, made necessary by the use of heavier dressings of nitrogenous fertilizers, and made possible by the effective control of weeds with herbicides. The reductions in stem height have been accompanied by parallel reductions in stem weight, as in wheat (Bush & Evans, 1988). Thus, substantial savings of assimilate are freed for investment in the grain but only after adjustment of the genetic background to ensure their diversion to grain growth rather than to additional tillering or root growth. In some cases the gain in grain yield has been approximately equal to the reduction in straw weight (e.g. Austin et al., 1980), which might suggest a direct reallocation from stem to ear growth, but in others the gain in yield may exceed the reduction in straw weight, as with dwarf maize at CIMMYT (Centro Internacional de Mejoramiento de Maiz y Trigo, Mexico) (Fischer & Palmer, 1983). Despite quite intensive investigations of the effects of the Rht dwarfing genes in wheat, it is still not entirely clear how the savings from stem growth are used to enhance grain yield. Partly this is because the magnitude of the savings varies with both genotype and environment. For example, dwarfing commonly leads to the development of more ears in spring wheats but to larger ears in winter wheats. Sugar concentrations in either the ear or the stem are no higher in the dwarfs either during ear development or at anthesis (Fischer & Stockman, 1986; Bush & Evans, 1988). In fact, total stem sugars are lower in the dwarfs. Thus, the savings from stem growth are not stored to support later grain growth but are presumably used immediately to promote greater ear development, which is ultimately expressed in greater yield in ways that appear to depend greatly on the relative timing of ear, stem and tiller growth. We are far short of understanding even this dominant component of yield enhancement and the rise in harvest index over the last 20–30 years.

Of the other components let me simply assert, on the basis of a comprehensive review, that there is little evidence that the investment in root systems has been reduced as yield potential has been raised, although there have been shifts in the spatial and temporal patterns of root development. Likewise, there is little evidence of reduced investment in reserves with crop improvement, although I anticipate such a change, at least in varieties adapted to a high level of agronomic support. On the other hand, there does seem to have been selection for reduced tillering or branching in many crops, resulting in a higher proportion of fertile tillers and a higher harvest index.

Another trend that has helped to raise the harvest index, especially in tropical crops, and that is also dependent on agronomic improvement, is the shortening of the life cycle, or at least of the length of the vegetative phase relative to the reproductive one. More time was required in earlier agricultural systems, e.g. for rice growing in the tropics, for the crop to accumulate enough N and other nutrients to yield well. With fertilizers and better weed and pest control, the juvenile stage can be shortened, reproductive development accelerated and fewer leaves formed, contributing to a rise in harvest index, as is apparent in rice (Tanaka et al., 1966). Longer leaf life, especially in the later stages of the life cycle, could also enhance the harvest index. Selection for it would be dependent on better agronomic support during the storage phase of the crop, and would enhance yield only when paralleled by selection for a greater duration of storage. In temperate zone crops this may also require selection for somewhat earlier flowering, as has occurred with British winter wheats (Austin et al., 1989), whereas grain drying of maize has permitted selection for greater duration of grain growth without change in flowering time (Cavalieri & Smith, 1985).

Clearly, the rise in harvest index in modern varieties is far more subtle and complex than a simple reallocation of assimilates from one organ to another, and any changes by selection are highly dependent on the level of agronomic support for the crop.

5.3.2 Some principles governing allocation

Allocation and partitioning are fashionable words in research grant proposals, and are used in a wide range of contexts: between organs of a plant, between leaf area growth and higher *CER*, between photosynthetic assimilation and respiratory loss, between sugar and starch formation, between carbohydrates and other compounds, etc. All are relevant to the yield of crops, but here we focus on allocation at the level of organs. Even with this restriction, at least several factors appear to be involved.

Functional equilibria The balance between root and shoot growth, characteristic for particular conditions and stages, has long been known. Brouwer (1962) referred to and explained it in terms of functional equilibria, the growth of each organ being dependent on the supply of essentials from the other. As such, the partitioning of growth between root and shoot as influenced by water and nutrient supply, evaporative demand and photosynthesis can be simulated (de Wit & Penning de Vries, 1983). Such functional equilibria may be quite robust, as Robbens & Pharr (1988) have shown for cucumbers grown in a range of pot sizes. However, the equilibrium between root and shoot growth changes as the crop grows, and may differ substantially between genotypes, as shown by selection in sugar beet (Snyder & Carlson, 1978) or comparison of isogenic lines in wheat (Bush & Evans, 1988). Although such comparisons have not ruled out the existence of a common functional equilibrium in all genotypes as determined directly by the supplies of water, nutrients and assimilates, it seems likely that other mechanisms, possibly hormonal or enzymatic, which regulate these supplies are also involved, as Lambers (1983) suggests. And it is these that are presumably modified by plant breeding although not taken into account in 'crop growth models without hormones' (de Wit & Penning de Vries, 1983).

Spillover effects These reflect a hierarchy in the allocation process such that certain functions are not supported until other, presumably more essential ones, are satisfied. Tillering appears to be such a function, being severely restricted under adverse conditions and progressively more abundant at higher levels of water, nutrients and irradiance. The extent and timing of tiller development in grasses and cereals is presumably related to the level of photosynthate, and can be so modelled, but how the response hierarchy is determined, and by which pools and where, is not known. Here again, although it is possible to simulate the influence of environment on the extent of tillering without invoking the action of hormones, we know that auxin, for one, has a major controlling influence on apical dominance. We also know that there are strong genetic controls on tillering, and that these have played an important part in the enhancement of yield potential. An extreme case is 'Gigas' wheat, in which the total suppression of tillering at cool temperatures is combined with the ability of the main stem ear to set more and larger grains than usual (Atsmon et al., 1986).

Such variation is the stuff of plant improvement, and we need to understand the interplay between assimilate levels and hormone status before we can confidently differentiate spillover effects from functional equilibria and the other processes influencing allocation.

Vascular resistance The allocation of assimilates is strongly influenced by such geometric factors as the relative sizes of competing sinks and their relative distance from, and vascular connection to, the various sources. The advantage of being close to the source was emphasized by Brouwer & de Wit (1969) and is a significant element in the explanation of functional equilibria. We have examined the effect of relative distance from the source in experiments with wheat ears, in which two spikelets compete for ^{14}C-labelled assimilates from a single source (Cook & Evans, 1983). In this case, which involved competition between organs of similar type and stage, the share of labelled assimilates fell as the square of their relative distance from the source.

Such a relation could be modelled in terms of resistance to transport in the phloem, as suggested by Thornley (1972). However, the resistance is likely to vary greatly with the vascular connections. In our experiments, for example, the vascular resistance across the ear was 10–30 times greater than that over a similar distance on the same side of the ear. Improved vascular connections are likely to have been an indirect outcome of crop improvement, and are evident in the more direct pathway from the leaf to the ear in modern wheat varieties as compared with their wild progenitors (Evans & Dunstone, 1970). Thus, variations in vascular connections could have a pronounced effect on assimilate allocation patterns.

Sink size The other geometric factor we examined was the relative size of the competing sinks, by varying the number of grains in each spikelet. Here we found a striking example of the Matthew effect: 'unto them that hath shall be given' (Matthew 25:29). The larger the sink, the greater its share of current assimilate, which varied approximately as the square of the relative size of two competing spikelets. The more grains, up to five, within a spikelet – the total number of grains for the two spikelets being fixed at six – the more ^{14}C-activity there was in each grain, presumably reflecting a steeper concentration gradient to the spikelet with more grains. The 'condensation' of many small inflorescences into one large one during the domestication and improvement of crops such as sunflower and maize could reflect the advantage of large storage organs in competition with other parts of the plant. This is especially so when the storage organs are more distant from the source, as shown in our wheat experiments.

Hormonal effects These tend to be invoked when all else fails, so we should bear in mind the example of the wheat grain that can grow at a constant rate in spite of profound changes in its content of cytokinins, gibberellins and auxins (Wheeler, 1972) and also in abscisic acid (King, 1976). However, although functional equilibria may account for slow progressive changes in allocation, they do not account for the rapid shifts associated with reproductive development. The sink size effect, on the other hand, could quickly lead to an unbalanced distribution and development, and other initiating and controlling mechanisms are needed. In fact, the various endogenous hormones are known to influence photosynthesis, phloem loading, the translocation process and phloem unloading, as well as the activity of growing tissue, so there are many ways in which the allocation of assimilates could be influenced by hormones.

Consider the shoot apex. It is a minutely small sink, rather distal from the sources of assimilates and nutrients, and poorly vascularized. The geometric factors affecting allocation could soon lead to its demise without the intervention of other, possibly hormonal, mechanisms. The vegetative shoot apex in *Lolium* has extraordinarily high contents of both gibberellins and abscisic acid, and is probably high in auxins and cytokinins as well. The changes in its content of sugars, and even of phosphorus, can be quite dynamic, suggesting that factors other than those already listed control allocation to it.

Consider also the early stages of reproductive development. Functional equilibria, spillovers and geometrical factors cannot account for the sequential initiation and differentiation of inflorescence, flowers and fruits and the rapid shifts in allocation patterns which these entail. Almost certainly, hormonal controls are involved, but they may not be reflected in changes in total content. Conjugation, transport, and localization of the hormones may change or, alternatively, the reception of and sensitivity to the hormone, as in the case of the Rht dwarfs in wheat to gibberellic acid. Environmental conditions such as daylength modify these, as may plant breeding.

Models without hormones have proved their value in some contexts, but given the centrality of changes in allocation for crop improvement, they will not suffice as a guide to the further enhancement of yield potential.

5.4 Explanation

De Wit has always insisted that crop growth models should, as far as possible, be explanatory models, built on our understanding and trying to extend it. With crop photosynthesis that is possible, but not, as we have just seen, for the allocation process. Given our article of faith that understanding is the surest way to impact, the fact that plant breeders have greatly modified allocation which we do not understand, but not assimilation which we do, is cause for chagrin. By way of explanation I would suggest that in the case of assimilation we are trying to improve on prolonged and intense natural selection, which will not be easy, whereas the enhancement of allocation to the organs which we harvest is in response to selection pressures different from those in nature and is conducted in quite different environments.

As with the rest of biology, however, much of the data in the crop sciences can be looked at in several ways. Brouwer & de Wit (1969) admitted: 'it is opinion that is really simulated'. In most crop growth models the driving force is assumed to be the supply of assimilate, as it may well be in many cases. In some conditions such as low temperature, high irradiance or even incipient water stress, however, the capacity to initiate or expand leaves or other organs may be the primary limitation to growth, and feedback inhibition of photosynthesis may occur, and may indeed be quite common (Sage & Sharkey, 1987). Not only may photosynthesis be reduced below its potential level when assimilates accumulate, but respiration may be enhanced via the cyanide-resistant pathway (Lambers, 1983) so that net assimilation may be as much determined by growth as vice versa. Although Sinclair & de Wit (1976) assume that photosynthetic rate drives the rate of protein storage in seeds and therefore the remobilization of amino acids from leaves and the rate of senescence in high protein pulse crops, these latter processes may be under independent genetic control. Indeed, with processes of such significance to survival and productivity, multiple interactions and controls are bound to be involved.

5.5 Extrapolation

At the Třeboň conference de Wit (1970) commented that '...the model may be adjusted such that a better agreement is obtained...However, it is a disastrous way of working because the model degenerates then from an explanatory model (to) a demonstrative model which cannot be used anymore for extrapolation...'. Even without that capacity for extrapolation, simulation models can be valuable as a form of review and by bringing several levels of biological analysis together. But de Wit has emphasized extrapolation partly as a way of testing the validity of models, and partly as a means to organized thinking about the future and about the possible. Remembering his comment about opinions being modelled, it may be a case of 'optimism in, optimism out' in his studies of future populations and agricultural development. And it may well be that global optimists do more harm than global pessimists. Their infectious optimism can generate complacency, and they are not as readily proved wrong as the pessimists have been on the subject of world food supplies. But de Wit's optimism has been tempered by his comprehensive and realistic approach to the improvement of agriculture.

In that context, one consequence of what I said earlier should be emphasized, namely the mutual dependence of genetic and agronomic improvement. The genetic improvement of crop yield over the last 50 years has been impressive, and has often been the Trojan horse for improved agronomy and agricultural development. So it is sometimes viewed by policy-makers as the prime mover that should be able to achieve advances in adverse environments as well as in favourable ones, a belief fostered by claims for the superiority of some new varieties across all environments.

We have seen, however, that the improvement in yield potential has largely resulted from shifts in the allocation of assimilates, and that these have been dependent on greater agronomic support for the crop, so that stems may be shortened, tillering reduces, life cycles abbreviated and leaf senescence delayed. As higher levels of inputs are used, and more efficient formulations and application procedures devised, there is a continuing reciprocation between breeding and agronomy. As in evolution, with each innovation there is greater scope for synergistic interactions, and it is these that have kept both Malthus and the asymptote for crop yields at bay. These interactions deserve more recognition by policy-makers, more acknowledgment by plant breeders, and more attention from crop modellers. We have neglected them unwittingly. Now we should consider them more wittingly.

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6 Can crop models contain economic factors?

F.W.T. Penning de Vries

6.1 Introduction

Crop simulation is currently in the limelight: papers on modelling studies proliferate, conferences on agronomy and crop physiology devote significant sections to models, and simulation is the vehicle for extrapolation in impact studies. The reasons for this attention are easy to identify: models are getting better, more environmental data are becoming available, computers abound, and the number of scientists trained in systems-thinking is increasing.

The scientists who model crops are enthusiastic about this development, but prudent research leaders ask: can crop models contain economic factors? I will address this question in two ways: by extrapolating the evolution of crop models of de Wit's school, and by examining the nature of crops. I shall then consider how crop models can support decision-making and, finally, whether economic models should include crop models.

The socio-economic conditions in poor countries are often unfavourable for agricultural production. How socio-economic factors can be integrated with crop modelling studies is therefore a particularly relevant question to justify crop modelling in developing countries (e.g. Randhawa & Venkateswarlu, 1990).

Whereas models provide insight and information that can be used to improve management, they do not change things by themselves: something still has to be done. A relevant question, therefore, is whether crop models can provide information that can improve decision-making in regions where socio-economic constraints are dominant. The answer is 'yes': crop modelling can support farming indirectly by being a source from which guidelines, diagrams, and extension service advice can be derived, and by enabling explicit alternatives for agricultural development to be drawn up.

For the purpose of this chapter, I define a crop model as a dynamic model to simulate the behaviour of an agricultural crop, including soil and pests if necessary, and will restrict myself to arable crops. The crop environment consists of weather conditions, soil conditions and pest levels when these are not part of the model, and of crop management expressed as the choice of crop, planting date and physical inputs. A crop model has a narrower focus than a cropping systems model. I will use the term 'crop model' for models that are adequately evaluated and documented. Yet, it may be emphasized that careful testing and evaluation remain essential when models are applied to new situations.

6.2 Evolution of crop modelling

Crop modelling has been evolved in various parts of the world by several groups of researchers; I choose de Wit's school for illustration. One of the first dynamic crop simulators was developed by de Wit and co-workers (de Wit et al., 1970). The ELementary CROp Simulator contained a detailed canopy photosynthesis section, an elementary component on organ growth rates with the shoot-root equilibrium concept, and preliminary ideas about crop respiration. Improving the basic descriptions of processes in ELCROS led to the comprehensive BAsic CROp Simulator (de Wit et al., 1978). ELCROS, and BACROS to a smaller extent, contain little of traditional plant physiology, but are quantitive, whole-crop physiology models. Both models have their roots in sciences basic to crop physiology, as is shown by the field of the professional journals in which de Wit and his colleagues have published: biology, plant physiology, agrometeorology, agronomy, theoretical biology, ecology, soil physics, optics. To ensure scientific integrity and robustness, the 'explanatory' approach to crop modelling was followed: the nature and regulating mechanisms of basic processes are analysed, quantified and modelled (de Wit, 1982). The open structure of such models allows interactions with other disciplines.

A research project in a semi-arid region was the testing ground for coupling an ELCROS-type model to a water balance model by a root–water uptake interface (van Keulen, 1975). Crop physiology and soil physics have since been combined fruitfully in models in many studies, such as in the semi-arid (Stroosnijder, 1982) and semi-humid tropics (Penning de Vries et al., 1989).

Modelling nutrient dynamics in soils and crops started later. It developed more slowly, since the biological and soil chemical processes involved are difficult to measure and because soils are heterogeneous in complex manners. The 'three quadrant figure', a static model relating crop yield to applied and to absorbed nitrogen (de Wit, 1953; van Keulen, 1982), is still an important practical link between crop models and soil fertility. Comprehensive dynamic models were published recently on aspects of the dynamics of nutrients in soil and crop (van Keulen & Seligman, 1987; Leffelaar, 1987; de Willigen & van Noordwijk, 1987). It is expected that summary models will be derived from them in the near future for application on a wider scale.

Micrometeorology was associated with crop modelling from the outset, as evident in de Wit's early work (1958; 1965), which aimed at thoroughly understanding the transport processes involved (Goudriaan, 1977) so that canopy photosynthesis and transpiration could be simulated in a dynamic fashion. In addition, the insight obtained in stomatal regulation (Goudriaan & van Laar, 1978) is now used when simulating the impact of high ambient CO_2 levels (Goudriaan, 1986) and of air pollution (Kropff, 1987).

Interactions with the disciplines mentioned earlier benefited from the increase in physiological detail in models. Linking crop modelling with crop protection sciences benefits particularly from summarized comprehensive models, such as

SUCROS (van Keulen et al., 1982; Spitters et al., 1989). Deriving relations between infestation level and crop damage with such combination models appears to be effective (Rabbinge et al., 1989), and I expect many more such studies to be performed.

De Wit's baseline 'no experimentation without evaluation' and opportunities to apply crop modelling in developing countries provided a strong push towards the interaction of sciences and modelling (van Keulen et al., 1982; Penning de Vries & Djitèye, 1982; Alberda, 1984). Interactions also developed with other disciplines, including plant ecology (Spitters & Aerts, 1983), grassland management (Lantinga, 1985) and forestry (Mohren, 1987).

This glance at an evolution in two decades of crop simulation by de Wit, his collegues, students and visiting scientists demonstrates clearly that crop modelling interacts with an increasing number of disciplines. Is it a matter of time until crop models include socio-economics?

6.3 Crop modelling and economics

The number of disciplines associated with crop modelling is increasing, but concluding from that by extrapolation that 'economics' and 'sociology' are next on the list is not valid. Extrapolation does not recognize that crop-related modelling in the disciplines mentioned looks at crops in homogeneous fields where key processes have time coefficients in the order of hours to days. An economic system, such as an arable farm, deals with crops at significantly larger temporal and spatial scales: a farm may consist of several fields with different crops, and whereas interactions between farmers and crops occur only a few times during the season, they span periods of many years. Farmers cannot and should not be included in crop models as state variables. Why?

At any given moment, the rate of growth of a crop depends exclusively on the condition of the crop and on its physical, chemical and biological environment. Crops respond to concentrations of soil nutrients and to weather conditions, and pests reduce growth. But it matters not what process causes these environmental conditions to be at a particular level, or who controls them. (For instance, whether urea is expensive or not does not affect the crop response to it, and whether weeds are eliminated by women or chemicals does not matter either. There is a marginal and indirect effect, at the most, such as that on the availability of the applied nitrogen: more careful placement if expensive, and on damage to crop plants: less in handweeding.) Sociological and economic factors never interact directly with plant growth. Sowing, transplanting, thinning and harvesting, it may be argued, are activities by which farmers affect the crop directly. These activities are boundary conditions or prescribed rules in crop models, rather than dynamic, interactive processes. Hence: economic and sociological factors are no real part of crop models.

Moreover, crop models *should not* prescribe the behaviour of farmers. Prescription would take away their freedom to choose between alternatives, the development of which is one of the challenges to crop modelling. Modelling farmers would defeat the purpose of the exercise.

If crop models cannot include socio-economic factors, what relevance can be attributed to crop models (outside the area of agricultural research itself)?

6.4 Crop modelling and decision support

Farmers use a range of information for management: about the farm (soils, labour, equipment), about the state of the crops, the climate, soil fertility and pest problems, availability of irrigation water and fertilizer, about prices and markets (Figure 24), and for all these factors they consider both values and anticipated future values (PAGV, 1987). Some factors are fairly constant (land area available, land quality, machinery, crop characteristics), whereas others are variable (weather, pest level, future prices). Crop modelling can provide some of the information required for efficient farm management in the short and long run, and is particularly powerful with regard to variable factors. In the following paragraphs I shall show how crop modelling and socio-economics can interact to support farm management and agricultural development.

Decisions in farm management can be categorized as 'operational', 'tactical' and 'strategic'. Each of the categories relates to groups of processes with impacts over relatively similar scales of time and space. Operational decisions on arable farms relate to choices during a cropping season, e.g. about irrigation dates, intensity of fertilization, timing of insecticide spraying. Tactical decisions relate to choices made once per cropping season, such as species planted, date of sowing, yield targets. Strategic decisions have impacts during subsequent cropping seasons, such as those on investments in machinery, on improving fields and infrastructure, on education and training (Table 4).

6.4.1 Tactical decisions

Before the season starts, the farmer makes a production plan. He considers the available land, capital, tools and labour, seed stocks, climate and prices, and then decides on crops to be planted, how many hectares to plant, target yields, input levels and loans.

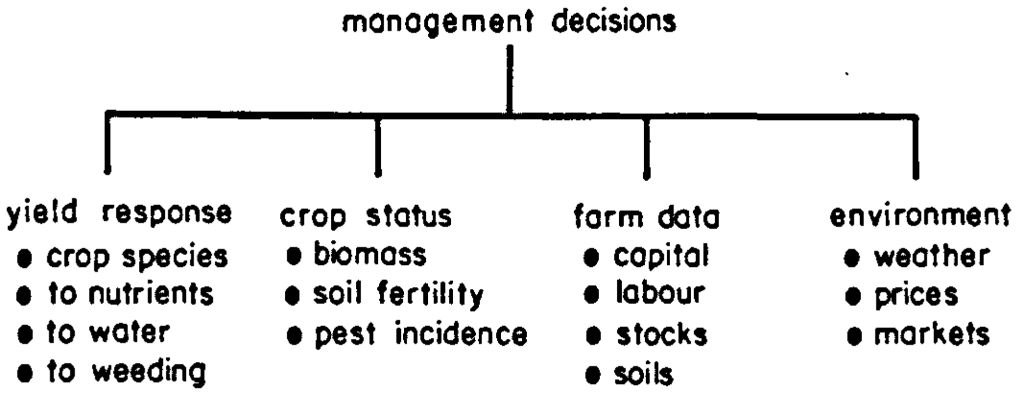

Figure 24. Types of information used for decision-making on farms.

Table 4. Levels of decision on arable farms.

	Impact on crop growth lasts	Typical decision
Operational	1–25 days	Weeding date
Tactical	5–50 weeks	Species sown
Strategic	0.5–10 years	Land improvement

How does crop modelling support tactical decisions? Modellers can generate guidelines in the form of rules, equations, tables, charts or maps, for aspects such as potential yield related to planting date, periods with increased risk of drought, and economic thresholds for pesticide application. Guidelines can be presented to farmers in various ways: as an aid to identify the crops that, on average, provide the highest yields, to set financially optimal target yields, and to calculate levels and timing of fertilizer and irrigation that correspond with the targets. Explicit and quantitative guidelines should be helpful when new opportunities arise (new crop types, irrigation facilities) or conditions deteriorate (lower prices, decreasing pest resistance) and farmers cannot rely on experience when making tactical decisions. This applies to developing countries where agriculture is evolving rapidly.

Using guidelines may be called 'indirect' support for decision-making. The guidelines are based on average weather, soil and crop data. Simulation for specific locations and situations may be called 'direct support'. This is still restricted to experimental stations, but it is moving towards intensively managed farms (Challa, Chapter 8). A few examples of support by modelling for tactical decision-making illustrate my point.

The first example relates to risk. Simulation of sorghum yields as a function of rainfall, soil type, crop duration and crop management provided charts of expected yield levels for first and second plantings at specific locations and sowing dates (Huda & Virmani, 1987). Long series of historical weather data were used, so that variability could be quantified as probabilities of attaining certain yield levels with specific planting dates. Guidelines can help farmers to consider risk in tactical decisions.

The second example is a survey of potentials for soya bean production, a new crop in the Philippines. A crop model was adapted to and evaluated for soya bean in rice-based cropping systems (Penning de Vries et al., 1990). It simulates yields for four situations: rainfed and irrigated upland, rainfed lowland and saturated soil moisture culture (Lawn et al., 1986). By simulating year-round monthly sowing for sequences of 20 years with different weather patterns, the relations between yield level and sowing date that have a 75%, 50% and 25% chance of being exceeded are established (Figure 25). Analysis of cost (labour, inputs, land) and benefits (harvested pods, increased soil nitrogen) gives the potential net profit (Figure 26). Even when rice remains the first crop planted, there is a window of

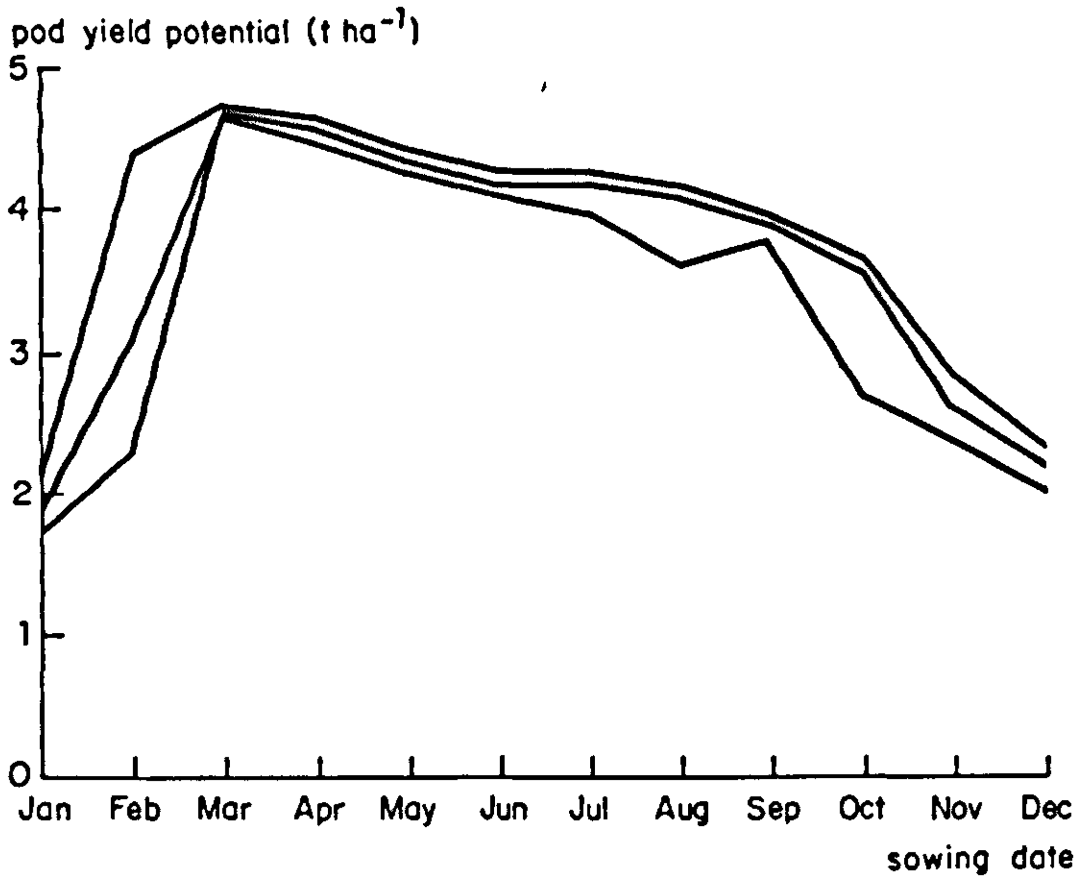

Figure 25. The simulated potential yield of soya bean on rainfed upland in Baguio, the Philippines, as a function of sowing date. The lines represent yield levels with a 25% (upper line), 50% (middle line) and 75% (lower line) chance in any year of being exceeded. The seasonality is due to temperature and precipitation fluctuations. Source: Penning de Vries et al., 1990.

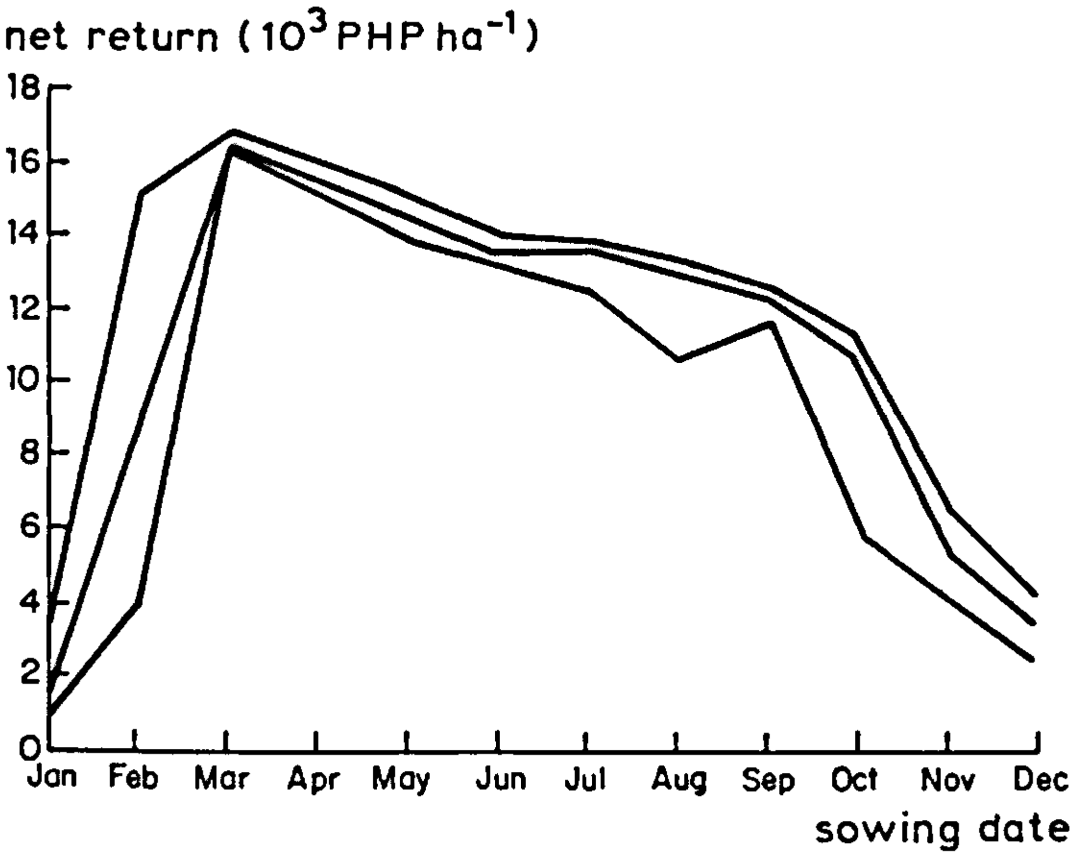

Figure 26. The simulated potential net profit of soya bean production (in 1000 PHP ha^{-1}) that corresponds with 80% of the values of Figure 25 (20 PHP is approximately 1 USD). The lines represent profit levels with a 25% (upper line), 50% (middle line) and 75% (lower line) chance in any year of being exceeded. Source: Penning de Vries et al., 1990.

two months to grow soya bean profitably at this location on deep soils. On shallow soils, however, the window lasts only a few weeks (not shown). From such charts, farmers and agro-industries can draw conclusions with respect to planting date, turn-around time, crop duration. If the potential result is positive after comparison with the potential for alternative crops, research can focus on specific soya bean problems and develop improved technologies.

The third example is an advisory model for farms (Dowle et al., 1988). It simulates annual grass production as a function of latitude, average rainfall and method of grassland exploitation. The output is grass production and growth of sheep and cattle, both in weight and financial value. The model is intended to help farmers in the U.K. to set their annual production plans by trying alternative schedules and choosing the one that fits best.

6.4.2 *Strategic decisions*

Crop models similar to those for tactical decisions can help to prepare strategic decisions. But they are now being used to investigate a wider range of options (different crops, production levels, etc.) over longer time periods and for future conditions that are more distant and less certain. Year-to-year variability is an aspect, particularly with unreliable rainfall. Different scenarios of developments in the production environment can be considered in simulation studies for devising a strategy for successive farm production plans and major investments. Since the future environment is less certain, intuition plays a larger role than in the case of tactical decisions. Dynamic models on sustainability and environmental issues, such as on soil fertility (Wolf et al., 1987) and soil erosion (Haith et al., 1984) may also contribute information for strategic decisions.

At a regional scale, crop simulation, economics and sociological considerations can complement each other to make explicit the realistic alternatives for crop production in a certain area, with crop modelling providing many of the essential input/output relations. Linear programming is used for choosing between the alternative opportunities. Flinn et al. (1980) concluded that their economic multiple goal linear programming model for farms needed results from crop production studies to become more practical.

My first concrete example refers to crop models used by the International Benchmark Sites Network for Agrotechnology Transfer (IBSNAT, 1985). Among others, IBSNAT uses 'systems analysis and soil, crop and weather models to predict the performance of crops and management systems'. Collaborators are encouraged to collect basic data and evaluation data in standard formats. The crop models include aspects of the soil water balance and fertility. The authors state that their models allow predictions of crop potential and performance at locations where the crop has not yet been grown. Whereas this statement may be overly optimistic for the current state of these programmes, in the hands of skilled users crop models increase the number of options for cropping that can be assessed.

A second example is MIDAS, a Model of an Integrated Dryland Agricultural System (Kingwell & Pannell, 1987), a whole-farm mathematical programming model of the agricultural system of Western Australia's eastern wheatbelt. The purpose of MIDAS 'is to provide a model to answer, from the perspective of the whole farm system, questions posed by researchers and extension workers. The model needs to account for the whole farm objective of profit maximization, the many alternative but feasible uses of farm resources, financial and resource constraints, and biological and other farm relationships'. A crop model was used to establish some of the input/output relations. A wise footnote is that 'to be effective, the model needs not only to be accurate but also to be seen by end users to be accurate, relevant and complementary to models stored in their minds', such as their concepts of the socio-economic system in which they live.

For a third example, I choose recent work done by de Wit and his colleagues. They developed and applied a particular form of finding optimal solutions for land use planning (de Wit et al., 1988; van Keulen, Chapter 15). Both the temporal and the spatial horizon are wider than individual farms. The approach encompasses an extensive use of input/output relations obtained by simulation and aims at quantifying concrete alternatives for agricultural land use, both in diversity and intensity, for agricultural planners and researchers. Using Interactive Multiple Goal Linear Programming, their program determines the best mix of activities to reach one of several main goals, while secondary goals are met at a minimum acceptable level. In a study in Egypt, these goals were employment, income and extent of pastoral land use (Table 5). Optimizing successively for these goals yielded alternative options for agricultural development. The cost of meeting one goal can then be expressed in terms of reaching fewer the other goals. The possibilities, limitations, and acceptance of this promising technique need to be ascertained.

Table 5. Upper and lower limits for three goal variables in a region of Egypt over a 15-year period.

Goal maximized	Values of goal variables		
	consumable income (USD 10^6)	employment (10^2 person–year)	traditional systems (10^3 ha)
After one set of iterations			
cons. income	197	135	112
employment	50	192	100
trad. systems	50	58	742
After two set of iterations			
cons. income	144	113	600
employment	90	131	600
Final result			
cons. income	135	125	600

Source: de Wit et al., 1988

6.4.3 *Operational decisions*

Farmers use agronomic information for day-to-day planning when production plans have to be adjusted to unusual weather, outbreak of pests, break-down of machinery or other disturbances. To redress the situation, farmers irrigate, fertilize, spray, or hire equipment. Agronomic information that permits farmers to choose the best alternative in terms of yield, resource use efficiency and profit must be presented in a comprehensive form and consists of guidelines (i.e. rules, equations, charts, tables). Such guidelines are usually summaries of crop responses derived from field trials, but they can also be obtained by simulating crop growth under different environments and management inputs.

Deriving guidelines for operational decisions is not yet common, but it seems that crop modelling has a large potential for this use, particularly for countries with rapid changes in agriculture and with too few experimental stations to address all local differences. Calibration can to a limited extent (if done by experts) replace parts of models that are still weak.

Expert systems that support operational decisions on farms are being developed, in which the expert knowledge consists of facts, guidelines and even dynamic simulation models (J.R. Lambert, personal communication). They could become part of expert systems for advising and training farmers and the extension service (Heong, 1990).

One example of indirect use is the advice on irrigation in different climatic zones (Doorenbos & Kassam, 1979); the guidelines were derived with a crop–soil model. CROPWAT (FAO, 1988), a successor to this study, is a crop model to compute irrigation requirements for specific situations. It can be used on personal computers by farm managers.

Another example is the comprehensive formula for calculating grass production on grazed land (Lantinga, 1985), which was derived by simulation. It is used to determine the optimal cattle stocking rate.

Real-time indirect decision support, using up-to-date or forecasted weather instead of average data, could become an interesting form of application of crop models. It would permit general guidelines to be adjusted to current weather conditions, and be of particular value for regional advice on crop protection and irrigation. Zadoks & Rabbinge (1989) indicate that in the Netherlands modelling supports protection of field crops by supplying computer-generated guidelines shown on TV or provided by telephone service. The dissemination by mass media (radio, newspaper) of general guidelines and of adjustments related to actual weather may become practical in developing countries (S.K. Sinha, personal communication). Optimizing nitrogen fertilization with crop models, however, has not yet been successful (van Keulen, personal communication).

'Real-time' crop modelling can help in yield forecasting for operational decisions by government organizations. The Department of Agriculture in the Philippines, for instance, uses a modelling project to predict the rice yield before the harvest (F. Lansigan, personal communication). In the future, dynamic crop models may support operational decisions on farms in well monitored and controlled situations by simulating crop and soil processes with time steps of hours or less. Challa (Chapter 8) elaborates this for glasshouse crops and Seligman (Chapter 14) for a cotton irrigation model. Such models demand much field-specific data and real-time information on variable conditions of crop and environment. However, it may be that summary models, derived for specific objectives, are all we need, even for these conditions.

6.5 Economics and crop modelling

Let me finally reverse the question raised by the research leader in the introduction (Section 6.1) and ask: have crop models a place inside dynamic agro-economic models? I will argue that the answer is 'yes', and present two examples. In economic models that simulate water consumption, crop growth could be simulated dynamically. Calibration of certain parameters, derived from specific experiments or observations, is probably often necessary to ensure that realistic results are obtained. The crop model should be a summary model, containing only the most significant processes and components, to prevent the total model from becoming biased in the attention it pays to certain aspects and in its data requirements. Unfortunately, summary crop models are still weak in dealing with soil fertility and pest damage.

One model simulates day-to-day water distribution to and use on fields at different distances from channels in a diversion irrigation system in the Philippines (Rosegrant, 1985). The background to this study is the concern for the efficiency of irrigation systems, and the hypothesis that 'improved management of water distribution could improve both the total benefits from the system and the distribution of benefits'. The model consists of three parts: water distribution among irrigation channels, a farm level water balance model, and a farm decision component. Simulation of water balances for several years provided an average number of stress days in the fields. Rice yield per field is obtained with a regression equation, and net income is derived from yield and associated inputs. The equation is based on more than 3000 trial results and contains 11 variables, including the number of stress days. The model simulates two alternative irrigation schedules: continuous supply to all fields (head fields get more water than tail fields) and rotational irrigation (in turn, every field gets a full supply). Rosegrant concludes that income distribution would be more equal for the rotational pattern, but that the total production remains almost the same. The study is being extended to other parts of Southeast Asia (IFPRI, 1988).

A key relation is the response of yield to irrigation. Our crop-soil model (Penning de Vries et al., 1989), calibrated to attain at the full-irrigation yield levels (mimicking nutrient shortage and pests), produced curves somewhat different from Rosegrant's (Figure 27). This is at least partly due to the nature of the curves (average, versus a particular case). The simulated unirrigated dry season yield could be low because a water table may have been set too deep (1 m in the dry

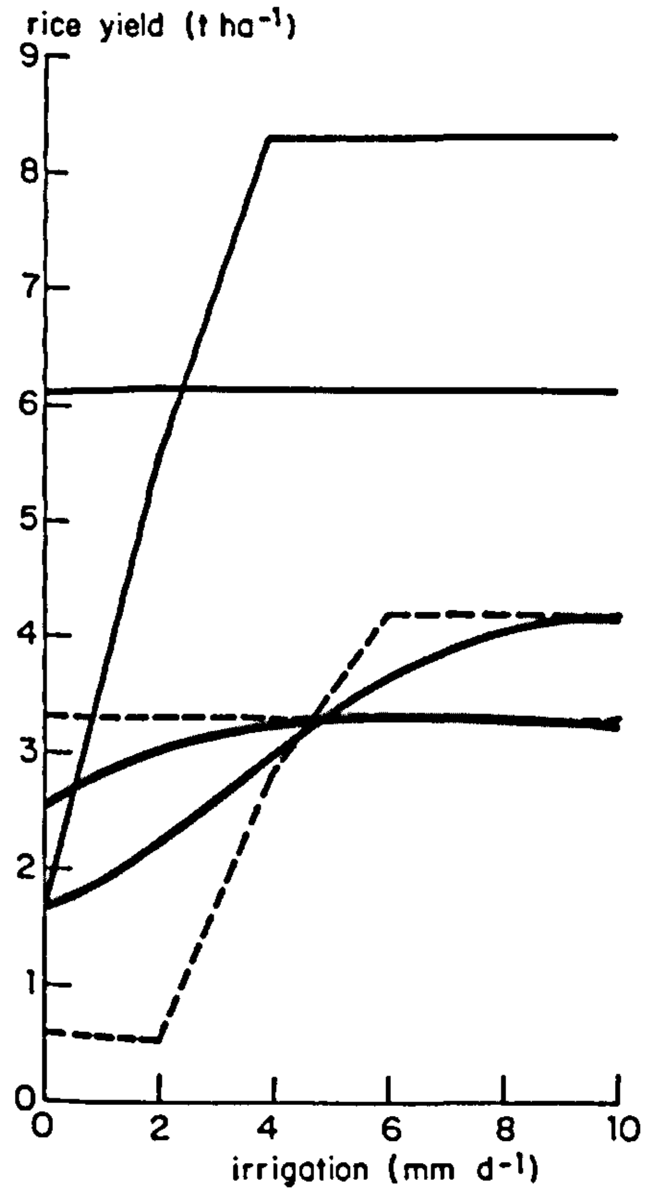

Figure 27. Response curves of rice yield to water supply in an irrigation system in the Philippines. Bold lines are from Rosegrant (1985); the light (rainfed potential) and broken lines (calibrated) were computed with MACROS modules (Penning de Vries et al., 1989); for each pair of lines, the line with the highest unirrigated yield refers to the wet season.

season) and our model is sensitive to this. Simulation shows that response curves reach higher values and that their shape can change with high inputs (Figure 27).

Adding an explanatory crop model to this economic model would lead to a more flexible tool for analysis. This would then avoid simulating water balances independently of crop growth and relating yield to the average stress pattern rather than simulating it in response to varying levels. Such changes would probably modify the outcome. A combined model can be used for other rice varieties, crop species, soils and weather and water table patterns. For crop production in situations with nutrient shortage, specific field trials are needed for calibration.

The second model simulates day-to-day water use on small rice farms in tank irrigation systems (Palanisami & Flinn, 1988). Irrigation water is the runoff from a catchment area, collected in a large, communal tank. This system is widespread in southern India. The authors examined 'tank irrigation system performance using productivity increases and income equity as performance criteria under existing and improved physical and management strategies, and to evaluate the financial viability of alternative improvement strategies to help guide future investments in tank improvement'. The model simulates the water balance of fields at different positions along irrigation channels and access to pumped groundwater. The crop part is represented by a regression equation of final yield versus number of stress days, developed by Palanisami & Flinn (1988):

$$Y_t = a_t - b_t SD_t \qquad (t = 1,2,3) \qquad \text{Equation 17}$$

where Y_t represents the rice yield in t ha^{-1}; a_t the base yield, given no stress days; SD_t the number of stress days observed; b_t the estimated reduction per day of stress; and 1,2,3 are the successive periods of differing sensivity.

In Equation 17, sensivity to stress depends on crop age. Net income per field is derived from the financial value of outputs and inputs.

As a result of calibration, the equation and constants summarize the specific condition in one tank adequately. However, the equation is only valid in one location because values of its constants depend, among other things on crop duration, fertilization level and water table depth. Other equations will be more suitable in other conditions. Moreover, the equation applies only to rice production, even though it is important to consider other crops that require less water in a part of India where rainfall is scarce and the price of water may go up. In fact, by using this model it is almost implied that one must choose from a narrower range of options than really exists.

6.6 Conclusions

Economic and sociological factors can be used to set boundary conditions, management rules and to develop objectives for using crop models, but they cannot play a dynamic role in them.

However, crop simulation can supply agronomic information that can be used jointly with economic information and other data, to arrive at management decision. With respect to developing countries, it seems that crop modelling can provide support at a tactical level of farm management to decisions about the annual farm production plan, at the strategic level for long-range planning by quantifying consequences of alternative options, and at the operational level by preparing guidelines for day-to-day actions. It seems to me that there are already many opportunities for deriving guidelines for specific crops, soils and weather patterns, in spite of the infancy of applied crop modelling and of environmental data bases.

Combining dynamic agro-economic models with dynamic crop models can improve results, raise the number of alternatives for management or planning assessed, expand the area to which the new model is applicable (soil, climate, crop varieties), and broaden the range of agronomic options studied (crops, fertilization). There is a challenge in combining crop and economic models.

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7 Integration of activity in the higher plant

R.S. Loomis, Y. Luo and P.L. Kooman

7.1 Introduction

Multicellular organisms face special problems in coordinating the growth and development of their various parts. Higher plants, for example, have numerous meristematic centres, each capable of expanding some dimension of the organism. Their collective potential use of substrates can easily exceed supplies and, without coordination of what grows when and how rapidly, growth would be chaotic and inefficient, if not fatal to the organism. Qualitatively and quantitatively understanding how such activity is coordinated remains perhaps the most significant problem facing plant scientists.

Integrative control is apparent at all levels of biological organization. The information on which it is based is ultimately found in genetic material, giving force to reductionist science. Our expectation has been that knowledge of cellular and molecular levels will 'explain' the behaviour of the whole and, given the complete set of enzymes found in plants and their operating rules, that we can some day predict how they produce cells and whole plants. Control and explanation also derive from the higher levels, however. The genome supplies the machinery and rules about its operation, but those metabolic systems operate in the ambient environment and at the mercy of carbon and nutrient supplies and water status determined through the display of roots and leaves at the community level. As a result, the assimilation of nitrogen, for example, is relatively insensitive to properties such as V_{max} and K_m of key enzymes, but highly sensitive to nitrogen and carbon supplies and to the rate at which amino acids are used in protein formation (Novoa et al., 1981).

Control and regulation by higher levels are evident in most aspects of plant growth, including the pattern of exponential growth observed in young plants where the rate of carbon supply and growth expand concomitantly with leaf area.

With the current emphasis on moleculair research, it is easy to forget that our need is to understand whole plants and vegetation, because it is at those levels that we manage crops and vegetations. The catalogues of molecular biology tell us what plants can do, but there is enormous latitude in what is done, how fast, and to what degree. That plasticity and the multiplicity of controls and feedback elements involved, as well as the remoteness of molecular aspects from organismal traits, have limited our progress in integrative physiology and morphology. Clearly, special techniques must be employed to encompass the complexity involved: Simulation models that integrate activity over several levels of biological organization emerge as the principal tool for the study of integrative control. The involvement of several levels opens the possibility that the properties of one level may explain behaviour at another (in the sense that a rational hypothesis explains) (de Wit, 1982). The certainty of such explanations improves with each failure to disprove them, and as alternative explanations are disproved.

Given our experience that the simulation of enzyme sequences is strongly regulated by substrate, and thus subordinated to organismal and community properties, those levels must be included as explanatory levels in models concerned with integrative behaviour. R. Brouwer and C.T. de Wit (Brouwer & de Wit, 1969) opened the door to that approach with their ELementary CROp Simulator, ELCROS, for the study of carbon dynamics in crop communities. It is now 20 years since that seminal paper appeared and it is worth reflecting upon our progress in using simulation to explain the behaviour of organisms. First, let us examine the control systems that need to be considered in such models.

7.2 Control systems of higher plants

Selection has favoured systems of integrative control that balance the patterns and timing of growth in ways that lend fitness for particular environments. By timing development relative to seasonal and diurnal variations in the environment, for example, activities such as reproduction are placed and completed during favourable times of the year. Full use of scarce resources of carbon and nutrients generally follows and is also implicit in fitness. The expanding capability of shoots for the utilization of nutrients and water, for example, is forced into balance in a homeostatic way, in accordance with the ability of the root system to take up those resources (Brouwer, 1983), and limiting supplies of nitrogen are distributed to sunlit leaves in preference to those in shade (Hirose & Werger, 1987; Sinclair, Chapter 3).

In state-variable models, as in real plants, processes (e.g. photosynthesis, expansive growth, transport) are regulated and this affects the state of the system. Our objective here is to create model structures that parallel the regulatory mechanisms found in real plants. The difficulty is that many regulatory mechanisms, such as those based on membrane properties, are too fine-structured for our present abilities to construct models of organisms. In such cases, the fine structure must first be aggregated into general properties of tissues and organs. This is illustrated in the following sections, in which four aspects of control and regulation are examined: phenological advance, the role of growth substances, the influence of substrate supply, and the influence of diurnal variations in the environment.

7.2.1 Phenological advance

The phenostages of germination, flowering, and maturity mark key events in the life of annual plants. The advance through those stages follows a temperature-dependent developmental rate (*DVR*) seen in the plastochron intervals in the production of new leaves and in the duration of phenophases. We still know very little about the processes involved. Leaf initiation involves cell division in primordia at the stem apex, so growth and development are closely linked in that case (e.g. Horie et al., 1979), but what determines the number of such events within a phenostage is unknown. Unfortunately for modelling, little attention has been given to the dependence of development on substrate (Sachs, 1987), and the dependence on temperature has been characterized adequately for only a few species. The *DVR*-temperature relation follows an optimum curve, with slow rates at both low and high temperatures. That response (substrate not limiting) appears as a simple continuous function but is undoubtedly a summary of several fine-structure processes including a threshold related to activation of key enzymes, an autocatalytic phase dependent upon collision of substrates and enzymes, a saturation phase limited by transport of substrates or enzyme capacity, and an injury phase.

In some higher plants the initiation of flowering is controlled solely by such developmental advance, whereas others depend on phenological switches and are induced to flower by exposure to low temperature (vernalization) or by a phytochrome-mediated response to changing photoperiod. Regardless of the mechanisms involved, developmental advance and phenological switches are essential control components in integrative models. Fortunately, they are also easily modelled phenomenologically as functions of current weather. The difficult part is extracting response functions and rules appropriate to particular species and cultivars from the existing literature (Roberts & Summerfield, 1987). Phytotrons have not lived up to expectations in this area. The number of skilled phytotron practitioners remains small, in part because such research is costly and carries a sense of frustation imposed by acclimation phenomena and by the plurality of important genotypes. As a result, many modellers take too simple a view of *DVR* and employ linear temperature summations to advance their models, thereby ignoring the optimum response of real plants.

7.2.2 Control by growth substances

F.Went (1926) was the first to isolate from plants a specific growth substance that behaves as a hormone. That substance, auxin, is involved in the dominance that stem apices exert over adjacent meristems and in the control of expansive growth, rooting, and other aspects of morphogenesis. Went's discovery led plant physiologists to concentrate enormous research attention on how such materials might control the activity of distant centres of growth. Such phenomena fit neatly with current ideas about nuclear control through 'signals' and 'targets'. The view is that environment can serve as a signal to the genome in one tissue, eliciting the production of a hormone that acts as a signal recognizable by distant tissues. Initiation of secondary growth, tuber formation, and graft-transmissible floral induction stimuli, as well as apical dominance, fit that concept. The list of growth substances has grown to include variants of cytokinins, gibberellins, ethylene and absisic acid, and recent work has demonstrated that hormones may act through mRNA formation.

The problem for modelling is that growth substances seem to be produced by most tissues and their effects may differ from one tissue to another in bewildering ways. The modes of action of a growth substance may be common at some level, in an effect on membranes, for example, but the phenotypic responses can be quite different. Growth substances frequently exist as steady-state fluxes or concentrations and their effects are evident only when perturbed, as through decapitation of *Avena* coleoptiles. One has to wonder whether hormones are 'aimed' at specific 'targets' or if susceptible tissues simply fall victim to the modified internal milieu. In radish (*Raphanus sativus* L.), shoot-supplied auxin and cytokinin are involved in the control of the vascular cambium of the central axis (Loomis & Torrey, 1964; Radin & Loomis, 1973). In that case, the hormones can be represented as on/off switches; as is the case with other root crops, once cambial activity is induced in receptive cells it continues unabated except as regulated by the influences of substrate, temperature and water status. It seems that initiation of a growth substance flux and its recognition by receptive cells are the key events.

After 60 years of research on growth substances, it is now clear that a general theory of coordination cannot be constructed from hormones alone (Trewavas, 1982, 1985). Our failure to recognize this sooner is due in part to a failure to consider the interactions between growth substances and substrates. It is surprising how much of the work in hormone physiology has been done with plants grown with low levels of light, and thus low supplies of photosynthate, leaving uncertain the significance of hormones in normal coordination. In the case of apical dominance, Mitchell (1953) and McIntyre (1977) found that the expression of dominance was greatly weakened in the presence of adequate carbon and nitrogen substrates. Trewavas (1985) and Digby & Firn (1985) have summarized such problems for control of leaf growth – in that case, substrates play the dominant role.

The Wageningen group (Brouwer & de Wit, 1969; de Wit & Penning de Vries, 1983) have made important contributions to whole-plant physiology by showing how the coordinating roles of growth substances can be represented phenomenologically in models of organisms as messages and rules governing meristem activity. In other words, growth substances, as is the case with enzyme pathways, can be viewed as subordinated systems.

7.2.3 Substrate control

The number, kind and ability of the various meristems provide a basic control over the distribution of growth. That is particularly so whenever their potential for growth exceeds the supply of new carbon and nitrogen assimilates. Substrate limitations are a normal condition, particularly in competitive stands, and are easily demonstrated in experiments where carbon supply is varied by changing leaf area, light, or CO_2 levels, by reducing competition, or by supplemental feeding with carbon or nitrogen substrates. The conservation law imposes very powerful limits over what those meristems can do, since substrate embodied into biomass or respired cannot then be expended elsewhere. Trewavas (1985) has expressed this view nicely:

> '...what one growing area removes from circulation is not available to another. This represents a form of communication between the two areas...[and] since the different growing areas...have qualitatively different growth material requirements, reducing the growth rate...of some will result in qualitative changes in what is left...[Those] changes could then act as effective signals for developmental change.'

This 'nutritional theory' of coordination is not new. The roots of the concept can be traced at least to G. Klebs of Heidelberg (Klebs, 1903; 1910) who successfully manipulated the growth and development of fungi through substrate supply. He also was able to modify the flowering times of higher plants through variations in temperature and light. That work inspired Kraus & Kraybill (1918) at the Oregon Agricultural Experiment Station (U.S.A.) in their efforts to explain flowering trough a 'carbon/nitrogen balance'. Plant scientists subsequently found C/N explanations inadequate in many cases, especially where photoperiod influences flowering, and the nutritional theory lost favour. It has lingered, mainly in the teaching of whole-plant physiology, under headings such as 'growth-differentiation balance' (Loomis, 1932). (As a youth, R.S.L. received lessons in growth-differentiation balances from W.E. Loomis – proper axe handles, for example, were highly elastic and came only from *Fraxinus* trees that grew with abundant water and nutrients so that the wood was composed of large xylem elements with a minimum content of lignin, a differentiation product.) Recently, the concept has been employed effectively in explaining insect resistance in trees (Lorio, 1986; Lorio & Sommers, 1986).

Plant physiologists are gradually returning to the study of nutritional control. In addition to work in developmental physiology, it is also seen as an extension of work on long-distance transport (Cronshaw et al., 1986). It is now realized that phloem loading, and velocity, and capacity for transport, seldom serve as the principal limits to sink activity. Control of sink development sometimes rests on the rate of phloem differentiation towards and within a sink, but once the sink is established, the relative activity of the sources and sinks, as well as their position on the common trough, create a very strong regulatory environment. Progress is being made in understanding the related phenomenon of feedback inhibition in source leaves (Foyer, 1988) and phloem unloading, but we still know little about the dependence of sink activity on internal substrate supply. Growth response to substrate level is probably hyperbolic (Hunt & Loomis, 1976; Moser et al., 1982; Penning de Vries et al., 1979) and apoplastic conductivity may play a critical role (Hampson et al., 1978; Wyse, 1986).

7.2.4 *The special case of diurnal control*

Much less attention has been given to the control imposed by the pulsating environments in which plants grow. Alternation, day and night, of temperature, water status and photosynthetic activity leads to rhythmic sequences of limitations on the growth of different meristems. Shoots, for example, are exposed to the most extreme variations in temperature and moisture status, whereas remote roots may suffer from periodic deficiencies of carbon substrates.

Our attention has been given more to issues in circadian rhythms than to the logistics of assimilation and growth over the diurnal period. It helps to ignore the concept of an 'internal clock' and look for more direct influences of environment. Cell division, for example, can be synchronized in algae by cyclic changes of light (Tamiya, 1957) due apparently to variations in substrates. Cell division in roots is dependent on substrate (van 't Hof & Kovacs, 1972) and in some cases is synchronized by the daily pulse of carbohydrate supply (Webster & Langenauer, 1973). Temperature also has strong effects on cell-cycle stages (Rost, 1977) and there seems no reason why entrainment would not occur with appropriate temperature regimes. Cell enlargement is similarly dependent on temperature and substrate. Cyclical environments can thus lead to cyclic patterns of substrate use, leading to interactions between competitive sinks. A focus on the logistics of sink activity over diurnal periods should give rewarding insights into integrative control.

The extent of diurnal variation in control of growth is illustrated for leaves in Figure 28 (Thut & Loomis, 1944). In this case, leaf extension rates (*LER*) of maize (*Zea mays* L.) grown in the field at Ames, Iowa (U.S.A.), a subhumid environment, were measured with simple auxanometers and related to diurnal patterns of temperature and plant water status. *LER* tracked temperature closely except during midday when plant water status, observed as a rapid flux of eosin dye in excised culms, was low. Shaded plants were much less affected by the midday water stress. In the afternoon, *LER* accelerated as water status was restored, and then declined, in a pattern suggestive of substrate limitations, to ca. 4 mm h^{-1} during the night (T_{min} = 19 °C). In the same environment, asparagus (*Asparagus officinalis* L.) having small cladophylls instead of leaves showed no midday depression in the extension growth of stems.

Similar patterns of maize leaf growth have now been observed using more modern methods. Acevado et al. (1979) worked in an arid environment at Davis, California. With minimum temperatures near 10 °C, *LER* dropped to near 2 mm h^{-1} at night. Water status led to strong midday depressions of *LER* at Davis just as it had at Ames. One counter-intuitive result was that at Davis, despite greater evaporative demand during the day, 80% of the daily leaf extension occurred during daylight hours and was strongly dependent upon osmotic adjustment. At Ames, where nights were warmer, 40% of the elongation occurred during the night.

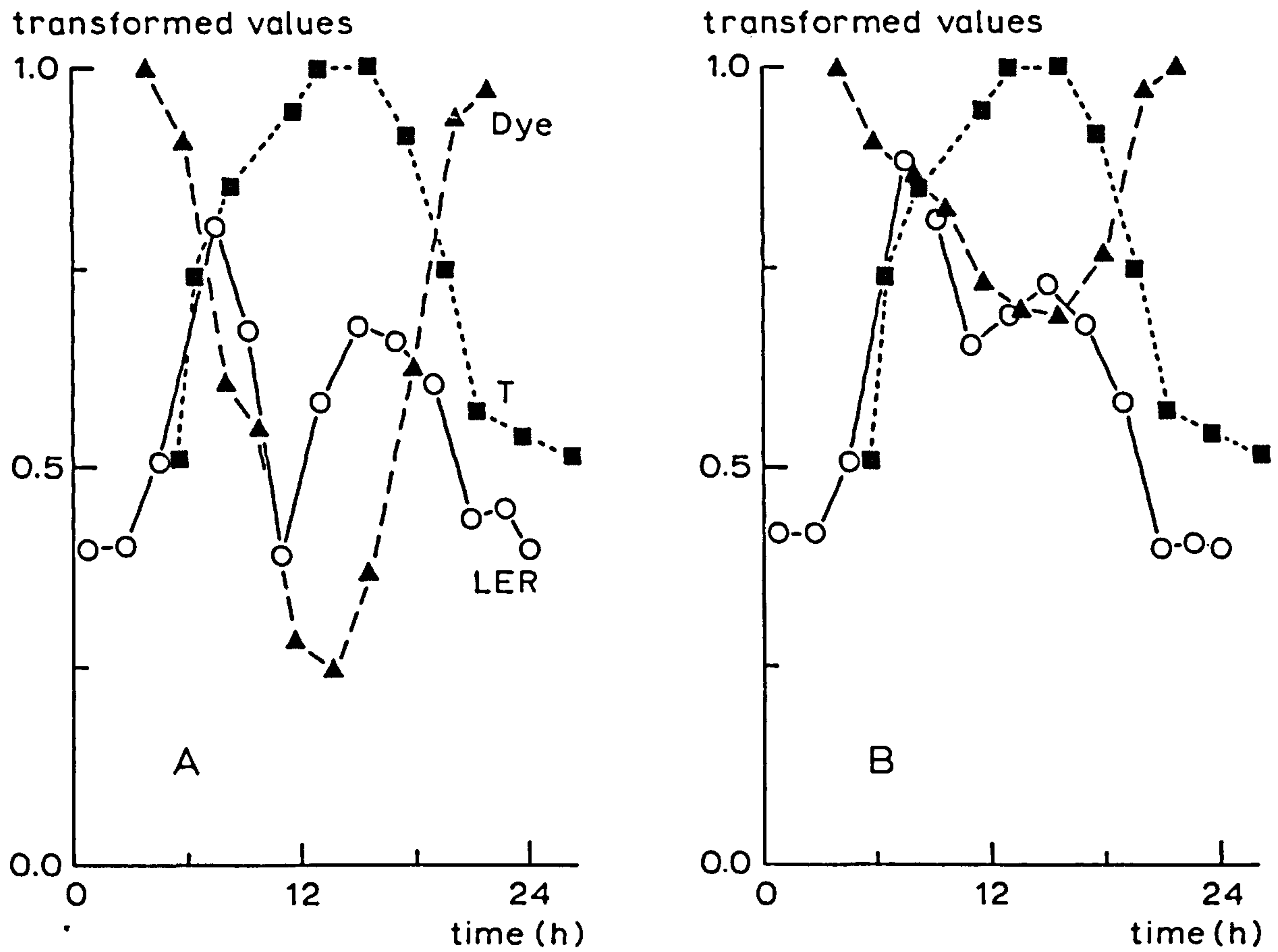

Figure 28. The diurnal pattern of leaf extension rate (*LER*), air temperature (*T*), and water status (*Dye*) for maize crops in midsummer. The original data were subjected to linear transformations for plotting. Water status was measured as the rate of dye movement in excised culms and is plotted here as a subtraction from 1.0 so that the smaller the value the lower the plant water status. A: In full sun; B: shaded from direct sunlight. After: Thut & Loomis, 1944.

7.3 Simulation of integrative control

The de Wit-type of crop models that attempts to explain community behaviour from morphological and physiological information comes in several forms. Some 'allocate' new assimilates to respiration and to the growth of various organs in fixed patterns (van Keulen & Wolf, 1986). A problem in teleology arises with many popular uses of the term allocation – a model may allocate, but real plants lack such central control. Allocation is suitable in a model for the simulation of normal crop production, since partitioning patterns are then relatively constant, but such models are greatly limited for the study of integrative control.

Models that simulate partitioning from tissue- and organ-level information are necessary for studies of integrative phenomena, but they are also more complex and thus less transparent to the researcher (Passioura, 1973; Seligman, Chapter 14). Although still in their infancy, the more complex models offer promise in the study of integrative physiology, ideotype specification and bioclimatology. With hourly or shorter time advances, the influence of diurnal pulses can be analysed. The embodied conservation laws assure dominance by the nutritional theory and allow testing of hypotheses about genotypic control (including hormones) expressed in sets of response functions and in 'rules' about patterns of behaviour.

Below, we illustrate some simple examples of integrative control with models of sugar beet (*Beta vulgaris* L.), potato (*Solanum tuberosum* L.) and alfalfa (lucerne, *Medicago* spp.). These models are structured along the lines of ELCROS with time steps of 1 h but with greater morphological detail and greater attention to physiological controls of growth.

7.3.1 Root–shoot relations in Beta vulgaris

The ELCROS model inspired our efforts to construct an integrative model for sugar beet (Fick et al., 1973; 1975). Coordination in beet involves balancing carbon use among leaves, fibrous roots, and a storage axis. Some types of *B. vulgaris* resolve that conflict in favour of large leaves (e.g. var. *Cicla,* known as chard or spinach beet) while others favour large roots (sugar beet and fodder beet). It was unknown whether real beet roots become large only when leaves cannot use the available assimilates, or whether the leaves are small because the root is extremely competitive in the use of assimilates. The beet model simulated the contrasting habits of sugar beet (large storage root axis, small leaves) and chard (small axis, large leaves) using several alternative hypotheses involving manipulations of the capacities for growth in either leaves or storage root (Loomis et al., 1976).

The compatibility of sugar beet and chard in grafts enabled that question to be resolved. Chard leaves from scion apices grafted to sugar beet stocks were smaller than normal and sugar beet leaves on chard stocks were larger than normal, whereas the root sizes were not affected (Rapoport & Loomis, 1985). Regulation of leaf size appeared to reside in the intrinsic capacity of the roots for growth. The temporal pattern of cambial formation and cell division were very similar in the two root types and the very large differences in root size resulted from the ability of a few cells of beet roots to enlarge to very large dimensions, rather than to some difference in cell number (Figure 29) (Rapoport & Loomis, 1986). Thus, genetic control of leaf size might be brought about in many ways, including through changes in root-wall polysaccharides affecting cell expansion, in the conductivity of the root apoplast to substrates, or in menbrane transporters found in root cells.

7.3.2 The influence of diurnal temperature pattern on the integration of growth in potato

The POTATO model described by Ng & Loomis (1984) has recently been revised as POTATO 2 (Pinto, 1988). Programming that gave incorrect simulation of low densities was corrected, and a layered soil with distributed root growth and soil water balance routines have been added. This new model permits rainfed and

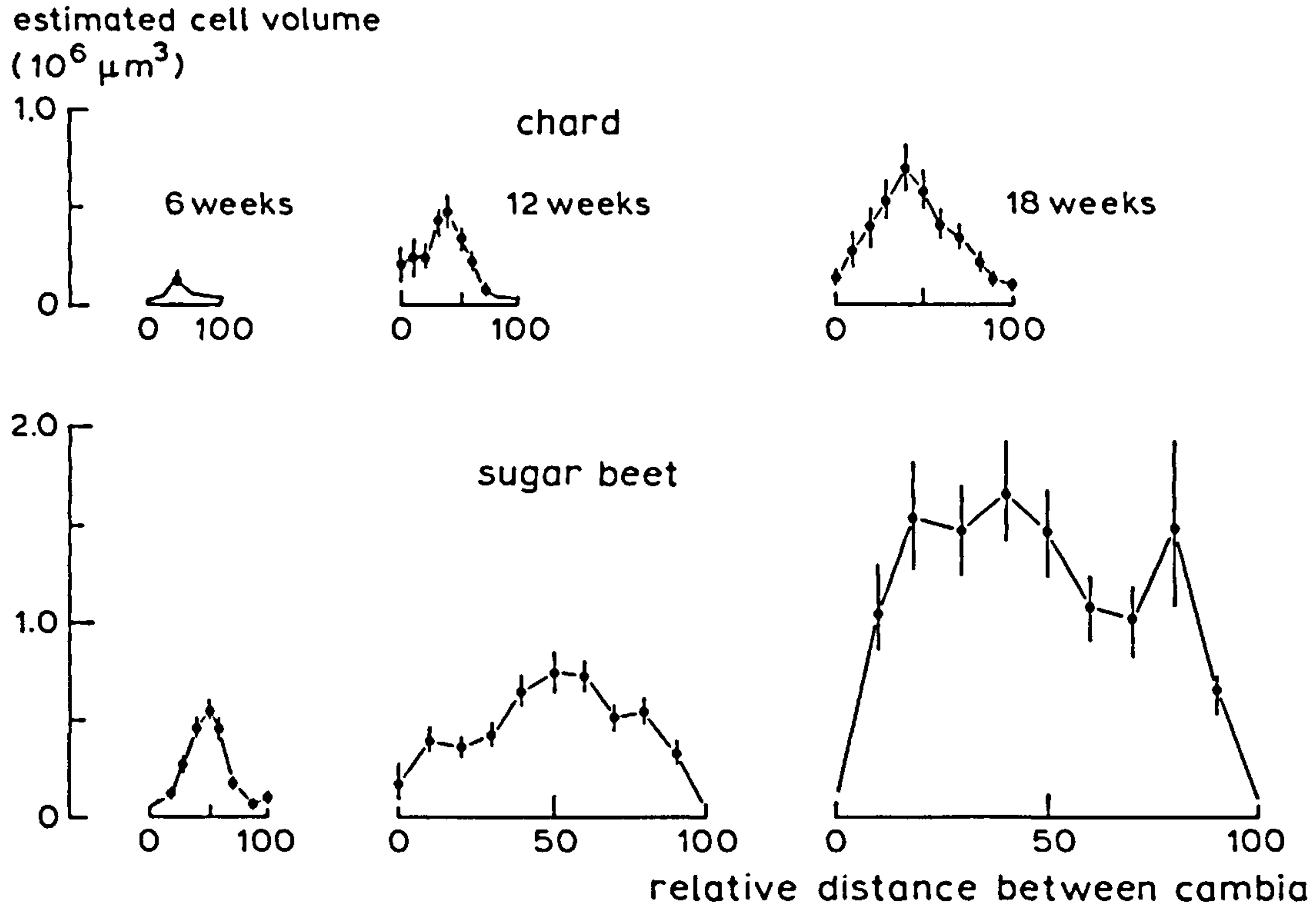

Figure 29. Distributions of cell sizes in the interzonal parenchyma between cambia 2 and 3 (numbered from the interior) of sugar beet and chard roots, 6, 12 and 18 weeks after emergence. The vertical bars represent ± 1 SE. The mean volume of the cells of that zone for sugar beet at 18 weeks was near $1.5 \times 10^6 \mu m^3$ compared with less than 0.5×10^6 for chard. That difference appears to account for the large difference in the strength of the two roots as sinks. After: Rapoport & Loomis, 1986.

irrigated conditions to be simulated. The input routines were restructured for the simulations reported here on diurnal temperature as an agent of integrative control (POTATO 2.1).

Very strong effects of amplitude (0 to 2 times the normal value) of diurnal temperature are shown in Figures 30 and 31, which illustrate the simulated limitations to leaf and tuber growth imposed by internal substrate supply and ambient temperatures 40 days after emergence at Davis on 26 April. The parabolic response of growth to temperature included in the model restricted leaf growth in late night and midday at this time of the year (Figure 30). The restrictions were greater with greater diurnal amplitude. Tubers, protected from those extremes in temperature, were influenced much less than leaves. The integrated effect of temperature on the carbon balance took a different pattern (Figure 31). Carbon supply was maximum during the daylight hours and was depleted during the night to the point that tuber growth ceased. Substrate was so limiting that fibrous roots (data not shown) only grew for a few hours in late afternoon. Diurnal temperature had only a small influence on the carbon concentration because of intervening effects of the developmental rate on carbon use.

The model was based on the hypothesis that the temperature response of

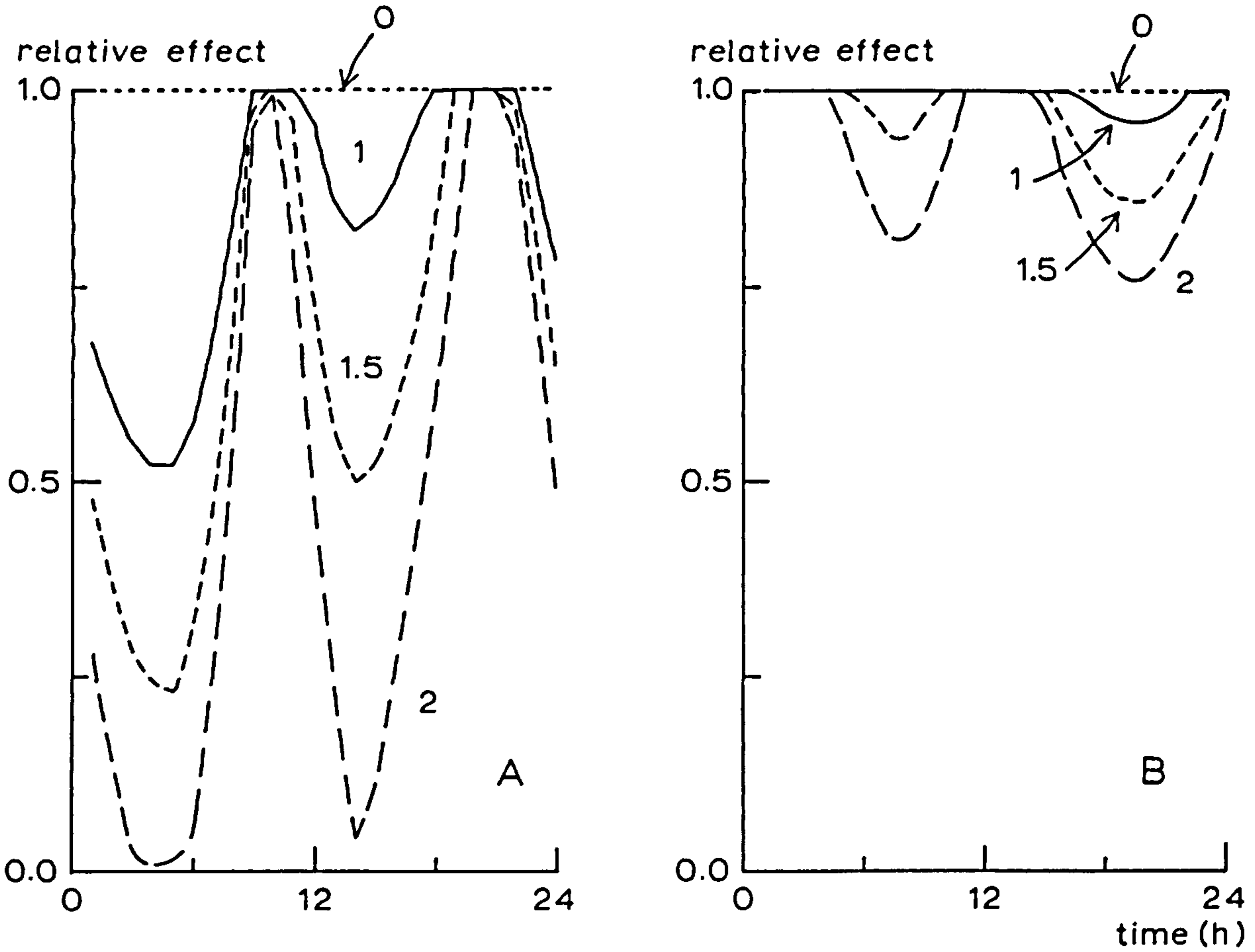

Figure 30. A: Diurnal variation in the relative effect of temperature on leaf dry matter growth in POTATO 2.1 40 days after emergence when the amplitude of air temperature was varied between 0, 1, 1.5, and 2 × normal. B: The effect of temperature on tuber dry matter growth under the same circumstances.

photosynthesis has a broader optimum than the temperature response of growth. This was expected to give the crops subjected to a large amplitude of diurnal temperature a larger resource of substrate relative to growth. The tubers were protected, however, and treatments with a small amplitude of diurnal temperature spent more hours each day near the optimal temperature for development and therefore initiated branches, branch leaves, and tubers more rapidly than those with large amplitudes (Table 6). With zero amplitude, the second tuber was initiated 26 days after emergence and competition from the tuber sink suppressed the development of the second branch and additional leaf area. This changing balance of sources and sinks, in particular the more rapid expansion of leaf area with intermediate amplitude of diurnal temperature, offset the photosynthese–temperature relation.

All of these amplitude treatments had the same daily mean temperature and therefore experienced the same accumulations of thermal units as usually calculated. The simulated differences in development shown here illustrate why thermal units have only limited merit and why nonlinear summations over the diurnal

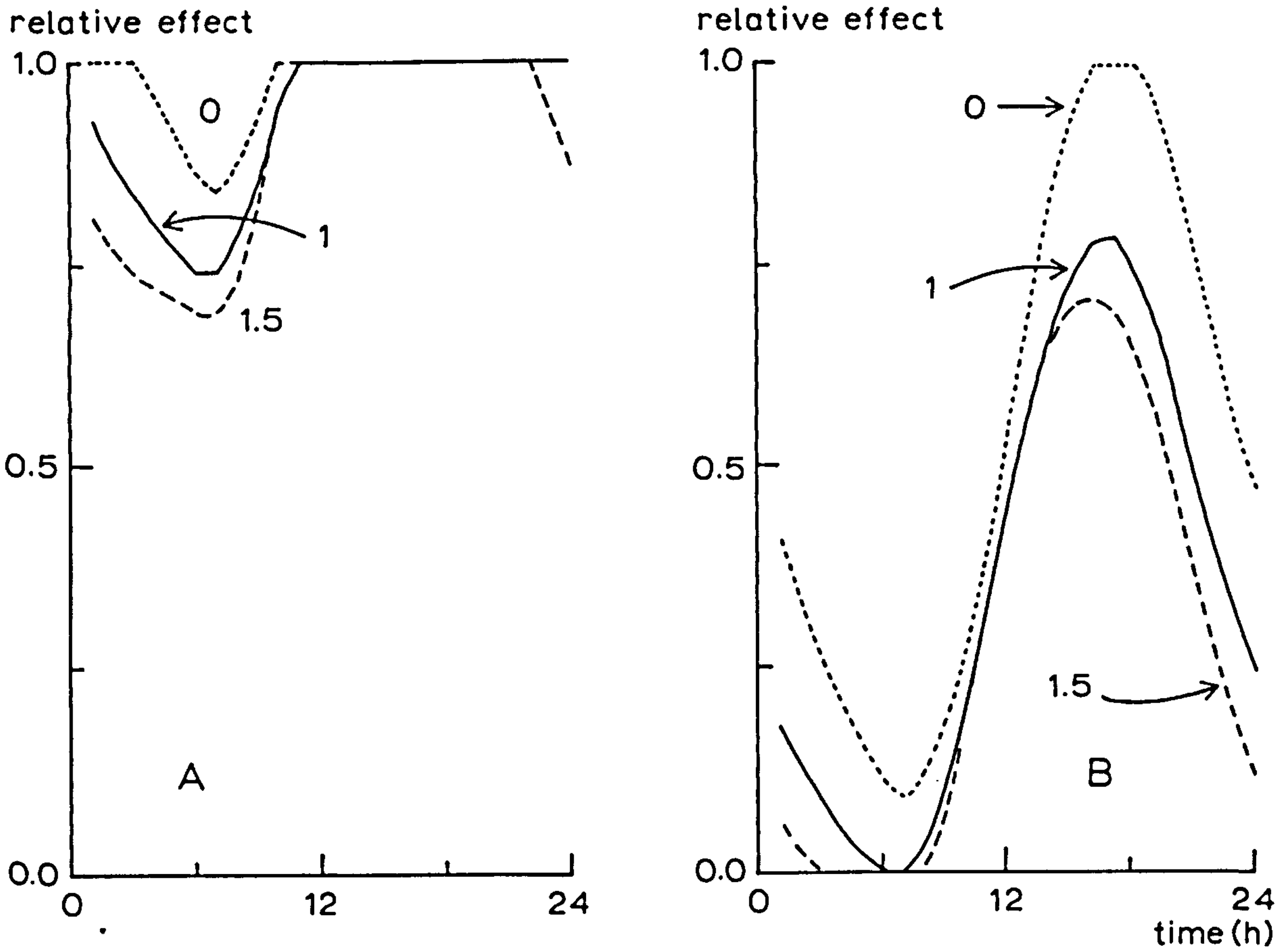

Figure 31. A: The simulated diurnal variation in the relative effect of carbohydrate supply on leaf growth in POTATO 2.1 on Day 40. Details as in Figure 30. The curve for 2 × amplitude is similar to that for 1.5 × and has been omitted. B: The substrate limit to tuber growth on Day 40 (2 × amplitude is omitted).

Table 6. Progress of crop development in POTATO 2.1 with varying diurnal amplitude of temperature. Emergence was on 26 April with 12 main stems m^{-2}.

Diurnal amplitude	Numbers on Day 50		LAI on Day 50	Maximum LAI		Initiaton of tuber 2 on Day
	branches	leaves		Day	value	
0	1	23	5.9	47	5.8	26
1	2	23	5.3	51	7.2	32
1.5	1	23	3.5	59	6.0	33
2	1	20	2.3	81	6.2	37

Table 7. Yield of plant parts 85 days after emergence simulated with POTATO 2.1 involving various diurnal amplitudes of temperature superimposed on the long-term average weather for Davis, California. Emergence was on 26 April with 12 main stems m^{-2}. Dry matter yields in g m^{-2}.

Diurnal amplitude	Stem	Living leaves	Fibrous roots	Tuber	Total
0	103	11	169	1700	1980
1	95	102	174	1370	1740
1.5	105	149	172	1330	1760
2	89	252	151	785	1280

range correlate better with crop development (Gilmore & Rogers, 1958).

The influence of these environments on the state of the crops 85 days after emergence (normal harvest date) is seen in Table 7. The zero-amplitude crop has completed its growth (nearly all leaves had senesced as is normal in potato) and the large-amplitude crops were closing the yield difference imposed by their initial disadvantage in development. These simulations illustrate the importance of interactions between the initiation and growth of various organs. Formulation of the opinions governing these processes is often the Achilles heel that defeats an integrative model. The opinions used in POTATO regarding leaf longevity, for example, are open to criticism (E. Ewing, personal communication), and we are unsure about the proper way to model that aspect of development.

7.3.3 Altered temperature and light on integration in alfalfa

The newly developed ALFALFA model (Version 1.4; Denison & Loomis, 1989) is similar to POTATO in its structure. One major difference is that the distributions of radiation and photosynthesis within 25 canopy layers are simulated rather than being drawn from look-up tables. This allows carbon supplies, growth and persistence of 5 successive cohorts of stem classes to be simulated separately. The carbon pools of the 5 classes interact with a common crown–root carbon pool. Growth and maintenance of fibrous roots, taproot, crown buds and young shoot classes are supplied by the crown–root pool. Beyond a certain size, the shoot classes may transfer carbohydrate to the crown but they are not allowed to draw from it when shaded below their photosynthetic light-compensation level.

Alfalfa crops are more complex than simple annual crops such as potato. Plant spacing is variable, the crop is subject to repeated cycles of cutting and regrowth, underground biomass is large, and overwintering is a necessary part of the simulation. ALFALFA 1.4 was developed and validated as an established crop with large crowns and rooting through a deep profile of soil. Fibrous root growth and senescence were restricted to real values. The simulations reported here were done with an experimental version (2.X) currently being developed that begins from seedling stands. For that, a more realistic behaviour of fibrous roots was necessary, and that was found to require separation of an active carbohydrate compartment in the crown and fibrous roots from a 'reserve', less active, pool in the taproot. When the crown–fibrous root pool is starved (e.g. following cutting), the taproot pool unloads carbohydrate at a level sufficient for maintenance respiration and bud growth but insufficient for fibrous root growth. Transpiration is simulated from radiation and energy balances for the canopy and in proportion to the current vapour pressure deficit. The old water routines behaved stiffly in this new version and a simple predictor-corrector was added. Although its structure is still preliminary, ALFALFA 2.X gives results in validation tests that are similar to version 1.4.

ALFALFA 2.X is used here in a study of the integration of the crop's response to large differences in light and temperature. The crop was 'grown' to full cover (LAI = 3.2 and midday light interception of 0.93) using long-term average,

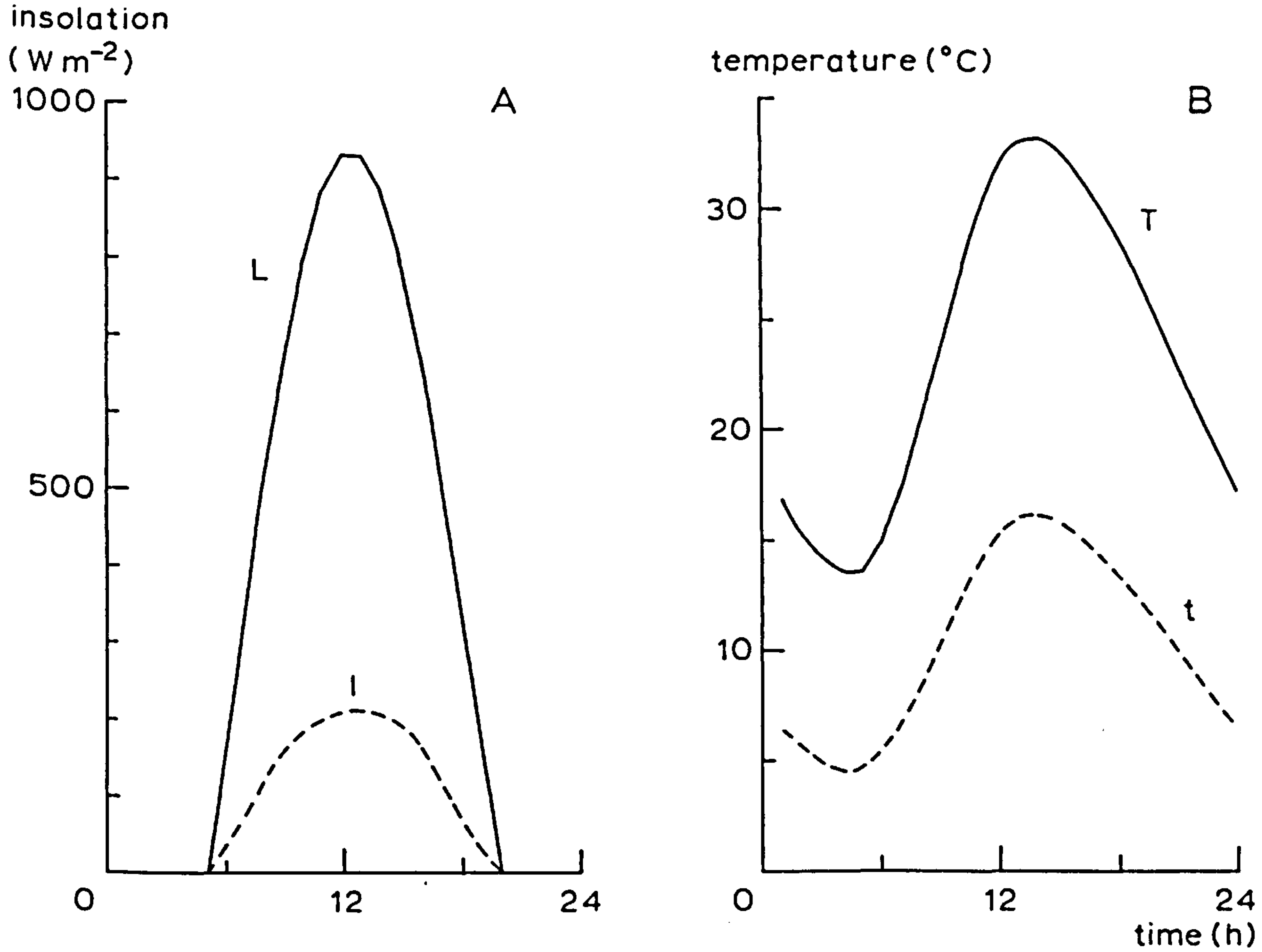

Figure 32. A: The diurnal course of short-wave radiation on 22 June simulated in ALFALFA 2.X using the observed long-term daily totals on that date (*L*) and for mid-February (*l*) at Davis, California. B: The diurnal course of air temperature on 22 June simulated using daily maximum and minimum temperatures for that date (*T*) and for mid-February (*t*).

spring weather for Davis, California. The state variables at that point were then used as initial conditions for simulations with four weather treatments. The simulations extended over several days beginning 19 June with normal summer solstice weather (high temperature and radiation) or with alternative light and temperature levels characteristic of early spring weather (Figure 32). The treatments were: *LT* for the normal light and temperature levels of June; *lt* for those of mid-February; and *Lt* and *lT* for the crossover environments. The solar track and thus daylength in all of the simulations were those for June.

The simulation presented in Figure 33 illustrates the time course of leaf dry matter growth over a period of 6.5 days following transfer to *lT* weather. During each iteration, the model restricts potential leaf growth by temperature, water, or substrate, depending upon which is most limiting at that time. Substrate was nonlimiting to leaf growth during the first two diurnal periods (1–48 h), since the initial conditions included high levels of nonstructural carbohydrates reflecting growth under moderate spring light and temperature. For those days, leaf growth was limited at night by temperature and during the day by water status. That pattern is very similar to those observed for extension growth by Acevado et al. (1979) and by Thut & Loomis (1944) (Figure 28). This close correspondence implies that extension growth is dependent on the synthesis of new materials, as is generally the case. Substrate supply declined during acclimation to the lower radiation and was the principal limit to leaf growth during the remainder of the simulation. That result indicates that if Thut and Loomis had extended their

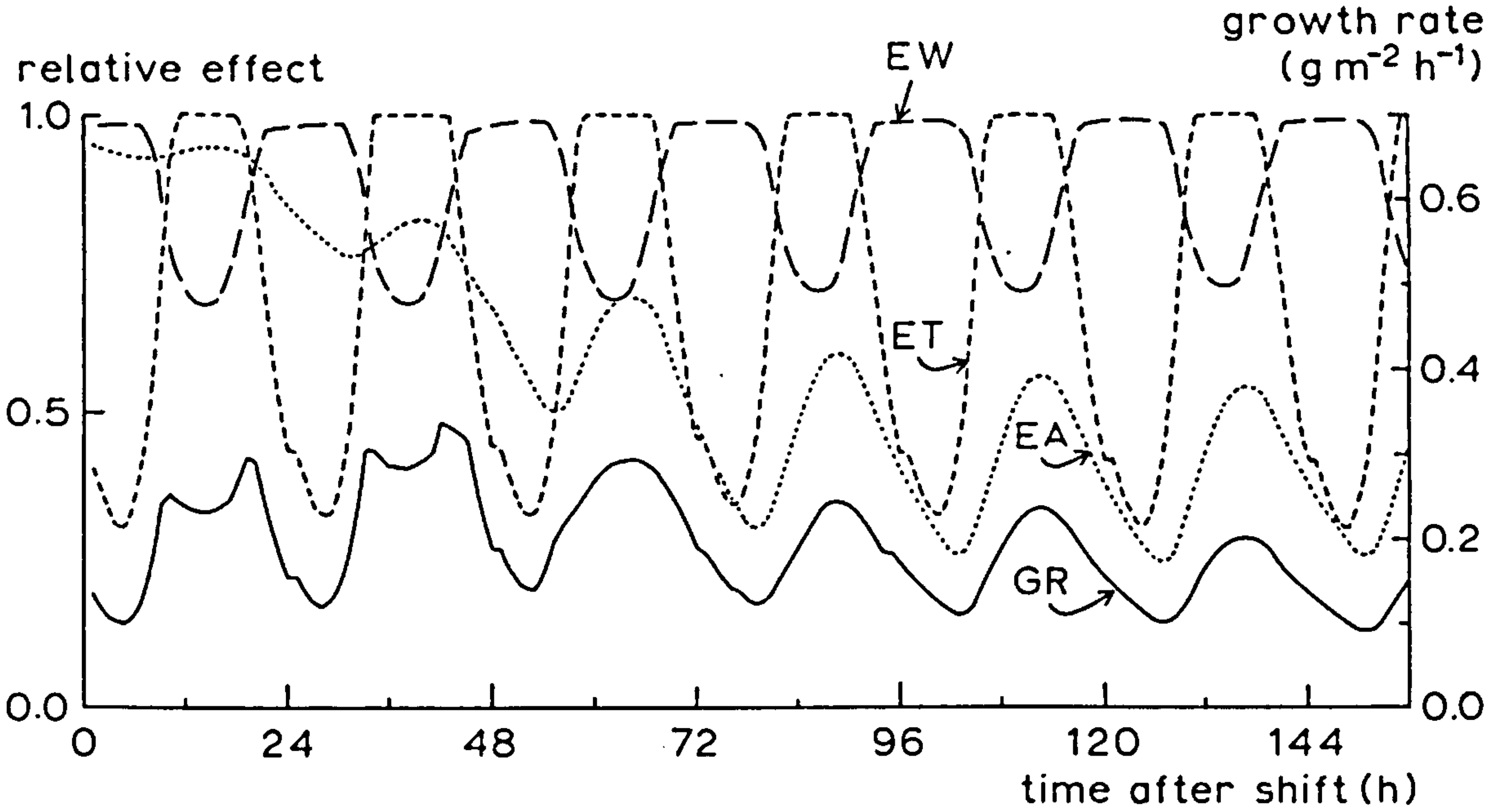

Figure 33. The time course of community leaf dry matter growth and the limits to leaf growth simulated for alfalfa. The simulation began on 19 June with a change from the cool temperature and moderate light of spring weather to the low-radiation, high-temperature treatment (*lT*). EW is effect of water stress, ET is temperature effect, EA is the effect of limiting substrate and GR is leaf growth rate effect.

shade measurements for several days, the midday water deficit would probably have disappeared. The effect on simulated growth of fibrous roots was even more dramatic. During the first day (19 June, 1–24 h) with moisture stress, the ratio of fibrous root growth to leaf growth was 1.8; on the sixth day (24 June; 121–144 h) with substrate stress, it was 0.2.

Five to six days were needed for substrate status to become adjusted to the new conditions. By contrast, water status adjusted within a few hours, whereas other aspects of acclimation, such as variation in leaf number and size and relative proportions of fibrous roots and leaves, require much longer times, as was evident for potato in Table 6.

The diurnal course of simulated leaf dry matter growth for all four treatments on 24 June (121–144 h in Figure 33) are presented in Figure 34A and the limits to growth are seen in Figure 34B (temperature) and Figure 35 (water and substrate). The *LT* treatment was still affected dramatically by a water deficit at midday, as was the case for the first two days of the *lT* treatment, but the effect was less on each successive day as fibrous root mass increased. Temperature limited *LT* at

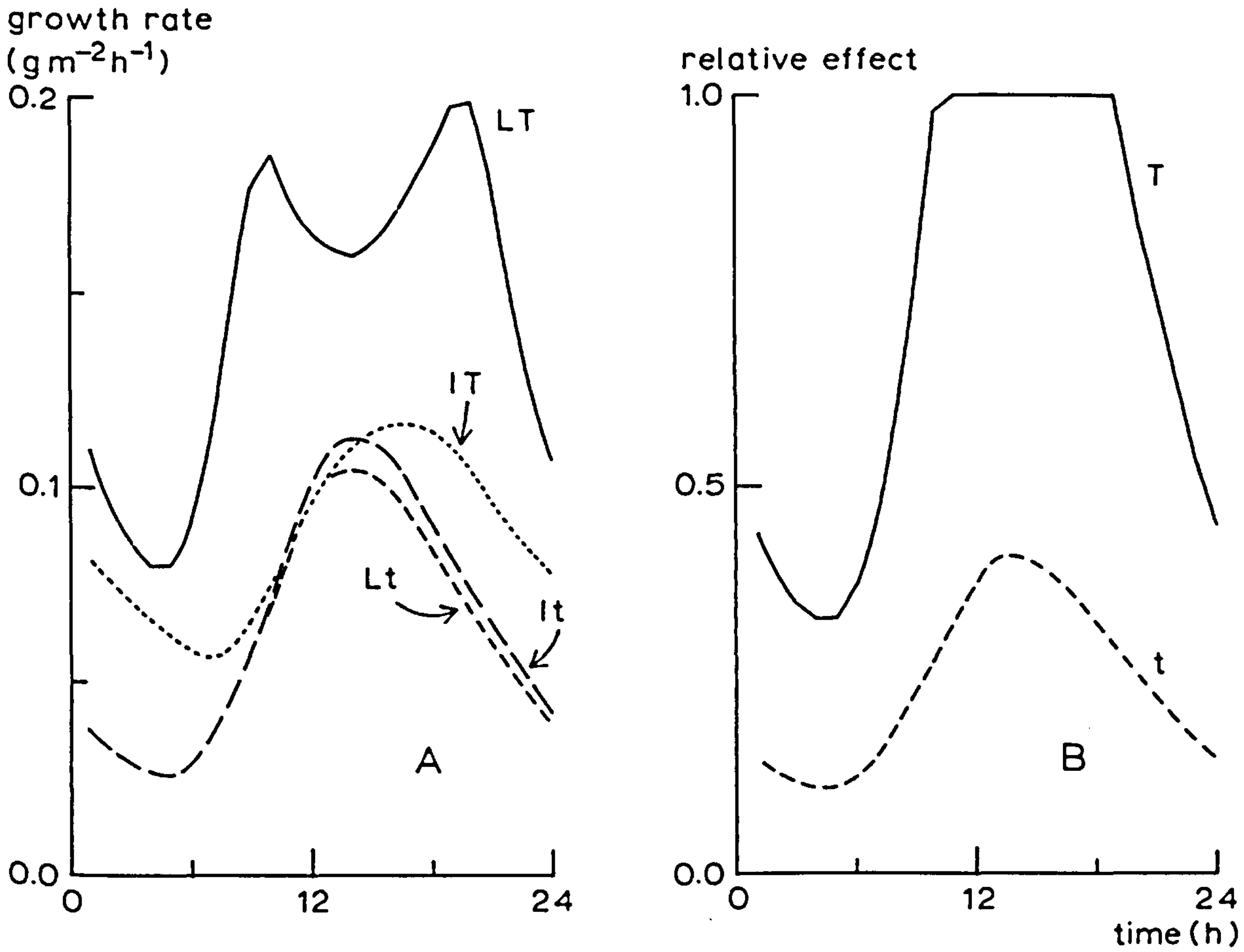

Figure 34. A: The diurnal course of community leaf dry matter growth rate on 24 June simulated for alfalfa with treatments *LT*, *Lt*, *lT* and *lt*. B: The daily pattern of the temperature effect on leaf growth for *T* and *t* on 24 June. The close correspondence with the main patterns of leaf growth reflects the dominance of that factor in the simulations.

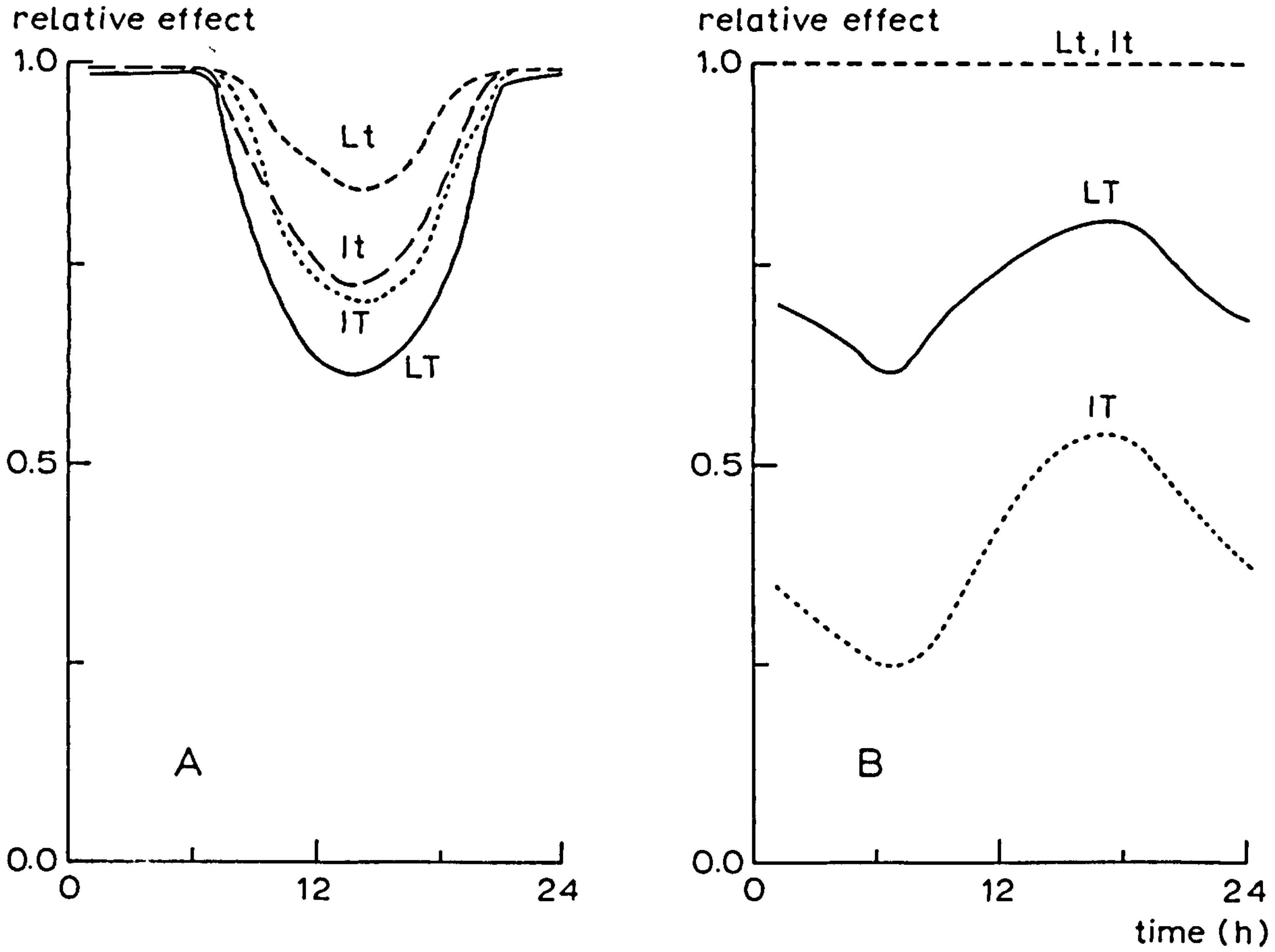

Figure 35. A: Diurnal course of the effect of water status (from simulated relative water content of the plant) on alfalfa leaf growth simulated for four environments on 24 June. The strong midday depression accounts for the reduction in leaf growth seen for the *LT* treatment in Figure 34A. B: The diurnal course of substrate limitations to leaf growth.

night and at all hours in *Lt* and *It* whereas, as we have just seen, substrate supply was the most limiting factor at all hours for *IT*.

Our present opinion is that the integrative behaviour of ALFALFA would not be influenced significantly by a further subdivision of the shoot substrate pool into 'starch' and 'active sugar' fractions (Thornley, 1977). The simulated patterns of substrate production and 'long-distance transport' (represented in the model by use in remote organs) are similar to the patterns observed in alfalfa (Holt & Hilst, 1969) and other species (Hendrix & Huber, 1986; Gordon, 1986) that accumulate starch in leaves. A starch pool in the leaves would be important, however, if we were to include leaf solute potential in the model or were to refine the present simple opinion about feedback inhibition of photosynthesis.

7.4 Overview

It is now 225 years since Robert Hooke published his *Micrographia* with its legacy of the term 'cell' to describe the structure of plant tissues. How cells coordinate to form an organism still remains the central question in plant biology.

Modern research is concentrated on understanding cells but it is unlikely that progress there can overcome the problems that arise when cellular processes are heavily subordinated to organismal properties.

Solutions to that question require quantitative integration across levels, but few tools are available for such work. Because plants are both complex in structure and plastic in behaviour, purely experimental approaches are generally limited to specific solutions and qualitative extrapolation. Attempts at purely mathematical statements are similarly defeated – the limitations of analytical mathematics force us very quickly towards approximate representations of reality. State-variable models employing both numerical and analytical relations and having the conservation law as a central element permit more detailed expression of hypotheses about such complexity in ways that favour realistic behaviour of the models. Pioneering efforts by C.T. de Wit and his colleagues have been a major factor in establishing state-variable models as the basic tool for integrative studies.

Waggoner (Chapter 9) and others have argued for simplicity in models and for the application of 'Ockham's razor' in their design. Progress with state-variable models of crop growth since Kees de Wit provided us with ELCROS has moved, on one hand, towards relatively simple 'summary' models. The key advantage of such models is transparency, leading to ease of understanding and to broad use. However, they lack sufficient morphological detail to address serious questions in integrative biology and the formulation of ideotypes. The alternative, increasingly possible as the cost of computing declines is, as in backcross breeding, to develop one robust structure into which ever-increasing detail is added. Experience and effort are concentrated, and when this approach is successful, models of broad utility are possible. The disadvantage is that all too often, complex models are only adequately understood and interpretable by their makers. Consequently, the user base is narrowed and validation of the added detail is difficult.

The three models used in this chapter are simple by physiological criteria but complex by ecological standards. As yet, they only touch on the frontiers of cell and molecular research and only the sugar beet model has been formulated with routines involving cell division. What we can do now, however, is to link the properties of aggregated cells, i.e. tissues and organs, with those of the whole plant. Our progress at Davis towards understanding integration is limited in part, because funding sources have caused us to give more emphasis to additional crop models than to increasing the depth and competence of existing models. We have yet to make extensive use of the models in integrative work, but the promise of powerful solutions and insights remains tantalizingly close.

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8 Crop growth models for greenhouse climate control

H. Challa

8.1 Introduction

In the last 20 years various different models have been developed to describe and explain crop growth under various conditions. These explanatory models have mainly been used for research to elucidate the often quite complex relations between crop environment and yield. Their practical significance has been mainly through this improved understanding, rather than the direct use of their output.

Models, however, basically do have great potential for practical use in agriculture in general (Penning de Vries, 1983) and in horticulture in particular (Challa, 1985; 1988). In general, their use (which is still very limited) is in the field of decision-making at the three levels of farmer's involvement that are usually distinguished, depending on the decision horizon (Table 8). Spedding and van Keulen give examples of the use of models for strategic decisions (Chapters 13 and 15, respectively). Penning de Vries (1983) mentions models being used for decision support at the operational level in the case of pest management and irrigation. Decisions about process control, an important item in greenhouse culture, are usually considered within the framework of the operational decisions. In my opinion, however, process control should be considered as a special category (Table 8). The principle difference between operational decisions and process control is that the latter lacks human interference. The operator checks the process from time to time and may adjust the control procedure, but the actual control is delegated to the control system.

The main reason we need to use models to control biological systems is because of the difficulty of measuring the relevant processes directly and the inherent need to interpret on-line measurements in the terms desired. In the second place it is often quite difficult to predict a required action in order to obtain a desired reaction. Process control, as described here, is characteristic for protected cultiva-

Table 8. Decision levels and horizons and the involvement of the manager.

Decision level	Horizon	Involvement of manager
Strategic	1 – many years	+ +
Tactical	≤ 1 year	+ +
Operational	days – months	+
Process control	≤ 24 h	–

tion, though with the introduction of fertigation, horticulture in the open air will also have to deal with it to a certain extent.

In this chapter the need to use crop growth models and their potential in relation to the optimization of greenhouse climate control will be considered. Certain characteristics of models constructed for this purpose and difficulties related to the practical implementation of strategies of optimization in control systems will be discussed. The required interaction with the grower and the grower's knowledge wil be highlighted. The net financial response to the control of CO_2 pressure and greenhouse temperature and its sensitivity to a number of relevant parameters will be elucidated.

8.2 Control in greenhouses

The greenhouse shelter profoundly modifies the climatic conditions inside the greenhouse. This is true not only for temperature, but also for CO_2 pressure, radiation and water vapour pressure. The temperature inside the greenhouse is usually higher than that outside. Apart from the energy supplied from the heating system, this rise in temperature is caused by radiative energy from the sun being trapped in the greenhouse because of a strong decrease in turbulent air exchange with the outside air and a decreased long-wave exchange with the sky (Bot, 1983). In an equilibrium situation the energy supplied to the greenhouse is released to the environment by convection and ventilation (sensible and latent heat). In the light, CO_2 is assimilated by the crop and this loss is compensated for by exchange with outside air and additional CO_2 supplied by the grower. The greenhouse cover transmits only part of the radiation, and the reduction of light can be substantial especially when the sun is at a low angle (Bot, 1983). Furthermore, crop transpiration causes the water vapour pressure inside the greenhouse to be higher than that outside.

The greenhouse climate can be controlled by means of a number of actuators (Figure 36), the major ones being: heating pipes (*p*), ventilators (*v*) and a CO_2 supply system (*c*). In addition, the root zone can be controlled with respect to temperature and, in the case of soilless cultivation, the mineral composition and the osmotic potential of the nutrient solution. Greenhouse culture may be considered as the most intensively managed form of agriculture.

Originally, climate control of greenhouses was primitive: only extreme conditions were avoided and the actuators were operated manually. Later, automation was introduced primarily to save labour. Advances in electronics enabled more refined control procedures to be developed, e.g. to regulate set-points for ventilation and heating in accordance with the prevailing radiation level. In the Netherlands these improved procedures were primarily based on a systematic survey of common practice of climate control among 'good' growers (Strijbosch & van de Vooren, 1975), whereas scientific research contributed more to improved average regimes over longer periods of time. When digital computers replaced electronic controllers this was mainly for reasons of efficiency: one controller was able to

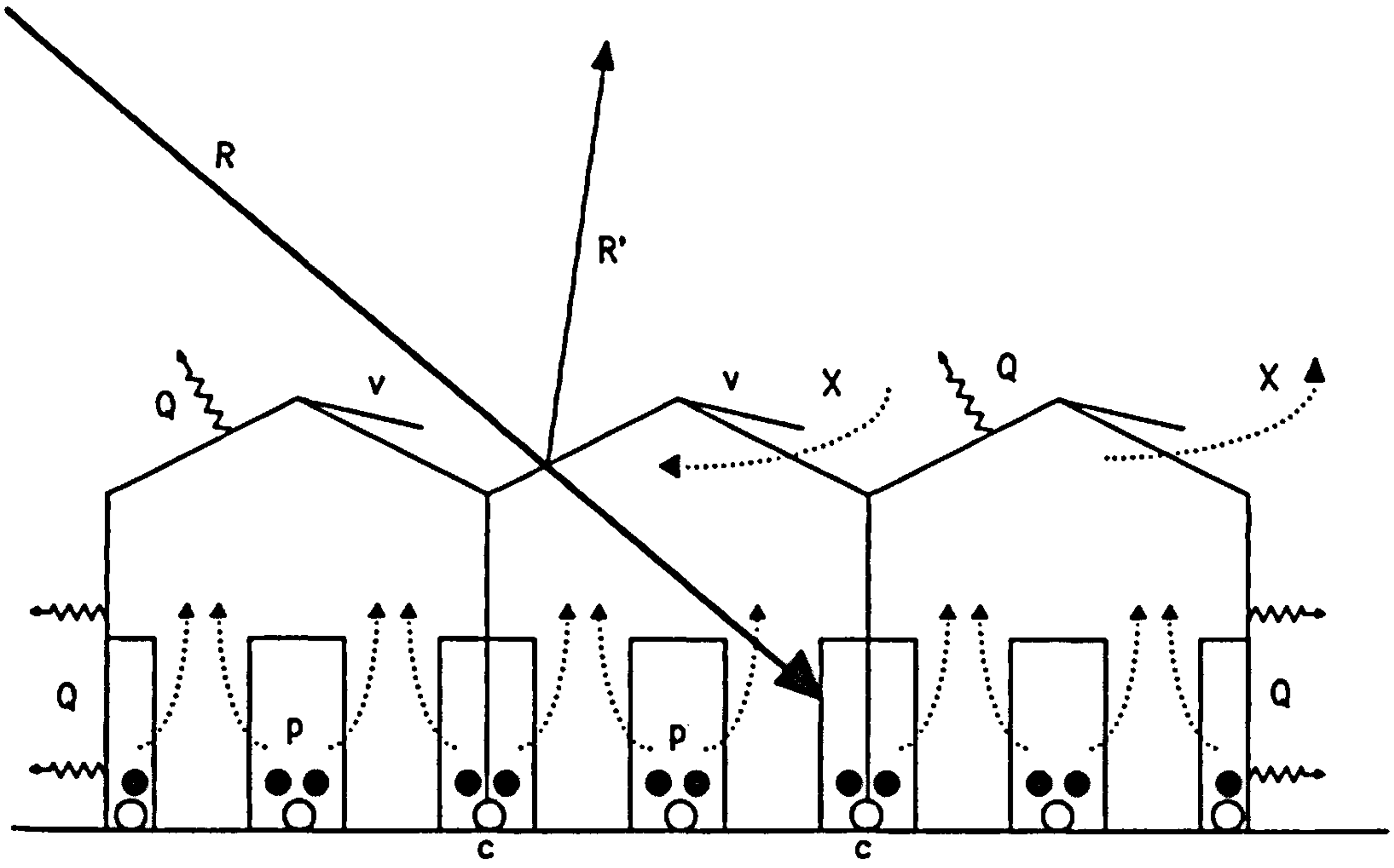


Figure 36. The major actuators for the control of greenhouse climate and the physical processes that are involved. Actuators: ventilators (*v*), heating pipes (*p*, solid circles) and CO_2 supply (*c*, open circles). Processes: transmission of short-wave radiation (*R*) from the sky, air exchange (*X*), including exchange of CO_2 and water vapour, and convective energy loss (*Q*) through the greenhouse cover.

handle a number of greenhouse compartments and this was cheaper than having an electronic controller for each compartment. Other advantages of the use of computers for climate control that played a role in this change were the possibilities of registering the actual climatic conditions and the greater flexibility that allowed other control procedures to be implemented easily, without changing the hardware. More recently, requirements for data exchange between the process control system and the management computer system have also promoted the widespread use of computers for climate control.

In spite of many improvements in hardware and software, little has changed in the underlying philosophy. The control algorithms are still primarily derived from the experience of growers and owe little to scientific research. The basic scheme followed (Figure 37) is that set-points for heating and ventilation are obtained using a classic, usually a *PI* (proportional-integrating) control algorithm (Udink ten Cate, 1980). This control loop (Loop 1) is the inner control loop with the fastest response time. The set-points are selected according to simple procedures (Loop 2), essentially characterized by separate heating and ventilation set-points for day and for night and a somewhat clumsy procedure for controlling air humidity because there is no separate actuator for its control (Anonymous, 1987). The procedures followed at this level are (as mentioned above) primarily derived from the experience of growers. The grower adjusts the control system occasionally (Loop 3) for best performance, on the basis of his observations of the crop and his knowledge of crop requirements. This knowledge

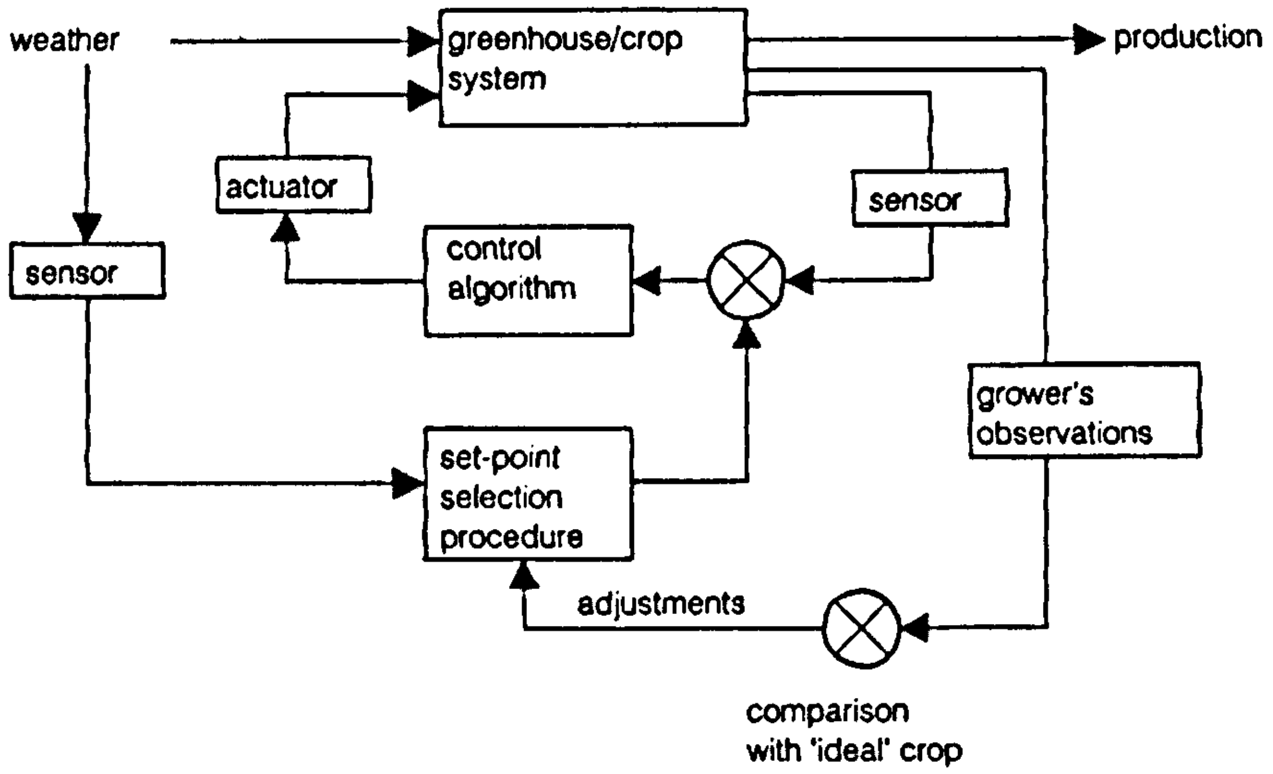


Figure 37. Schematic representation of climate control in greenhouses. There are three loops with different time coefficients: the fast inner loop for maintaining set-points, a second loop where set-points are established and a third loop in which the grower is involved and where the algorithms can be adjusted for optimal performance.

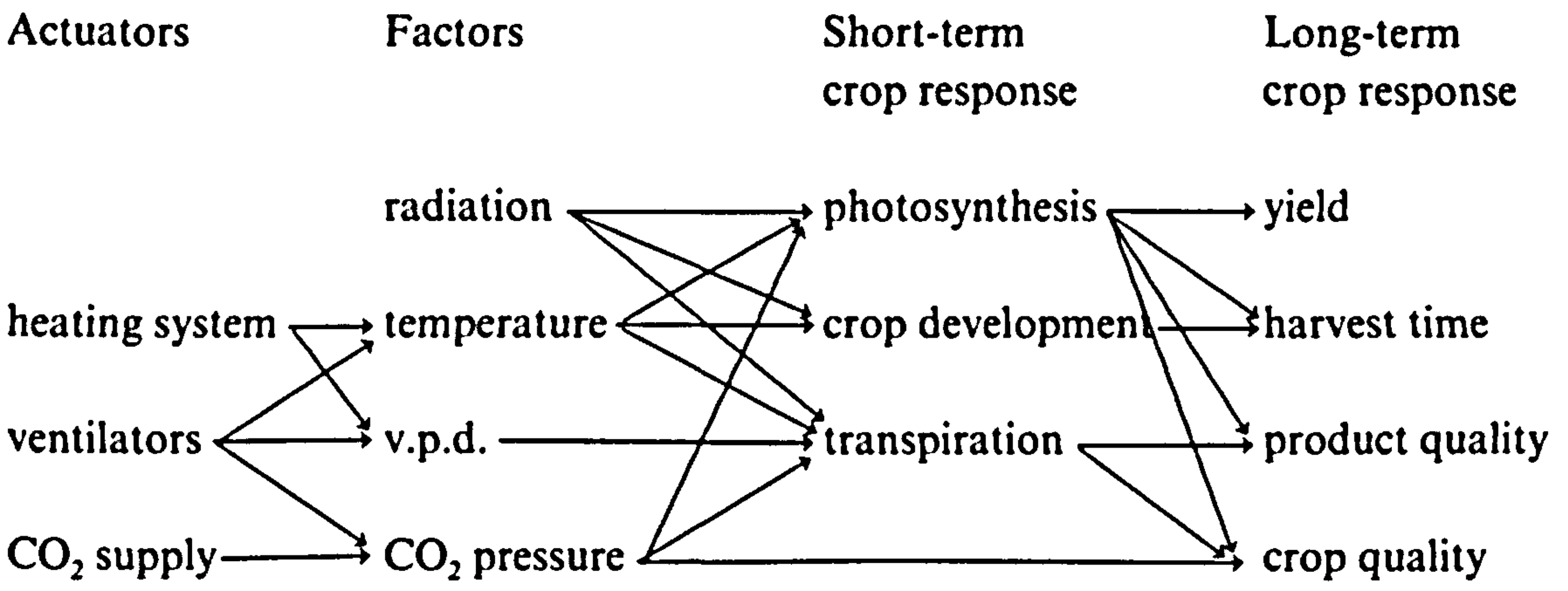
is a blend of results from scientific research and own experience. The grower's decisions in Loop 3 may be considered as operational decisions, whereas Loops 1 and 2 belong to 'process control'.

8.3 Optimal control

As pointed out above, the basic principles of climate control have evolved pragmatically. Hence, although growers are able to grow their crops very well with their current techniques it is unlikely that they achieve their goal(s) in an optimal way (Challa et al., 1988). As will be discussed later in this chapter, a number of objectives play a role in relation to climate control. Below, however, I will focus on one, important aspect, namely the question of optimal use of inputs in relation to the expected output, within the time-scale $\leq$ 24 h.

The grower's great handicaps at this control level are his inability to observe the fast response of crops to the instantaneous conditions and the very indirect and complicated relation between the setting of his control system, the factors to be controlled and the processes with a fast ($\leq$ 24 h) and a slow (days to weeks) response time (Table 9). The main problem of climate control in greenhouses is that there is no simple relation between actuators, environmental factors inside the greenhouse, short-term crop response and long-term results. The system consists of strongly interacting processes and subsystems. In addition, the grower is dealing with a control system which, on the one hand can increase economic yield (e.g. by raising temperature or CO_2 pressure), but on the other hand can raise the cost of operation. Optimization of the system is achieved when conditions are such that further increase of the input of relevant cost factors is just counterbalanced by the increase in yield (Figure 38). The question of optimization, of course, is

Table 9. Some important relations between actuators, factors and short- and long-term crop response (v.p.d. = water vapour pressure deficit of the greenhouse air).



relevant when variations in the input give rise to variations in the associated costs (Seginer, 1980). In the case of greenhouse climate control, the CO_2 pressure and temperature and humidity of the air are the major factors to be considered. The optimization problem for CO_2 and temperature is schematically depicted in Figure 39 and will be worked out below. As Figure 39 shows, crop photosynthesis responds to radiation, CO_2 and temperature and there is a strong interaction at the control level as well as at the process level.

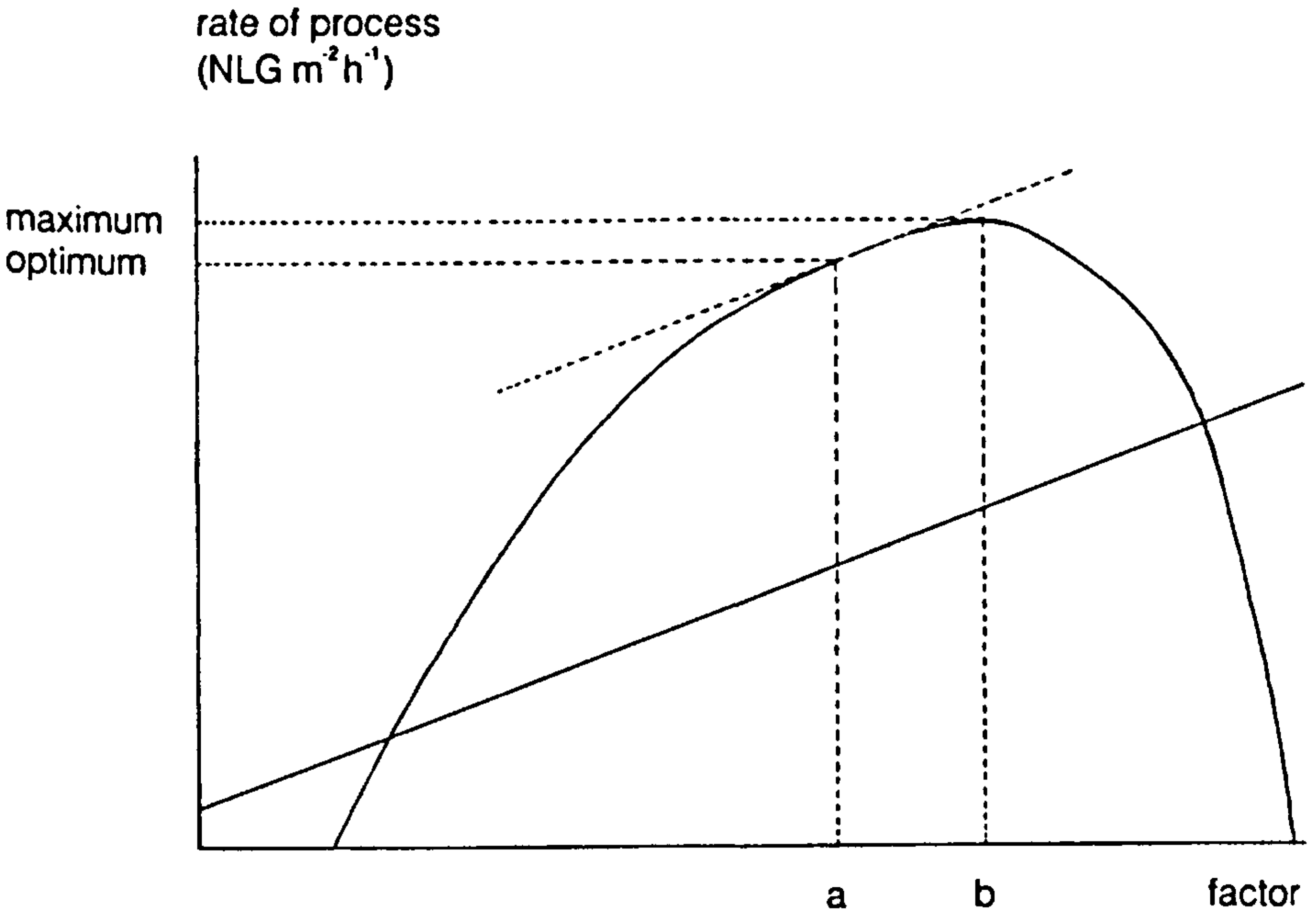


Figure 38. The principle of optimization explained with one input factor related to the rate of one process (optimum curve) and the rate of input requirement (solid straight line), both expressed in financial terms. The break-even point, where the increase of the cost of the input factor equals the increase of the financial output is obtained at an input level *a*. At an input level *b* the maximum output is obtained, which, however, gives rise to a lower net financial output than an input *a*.

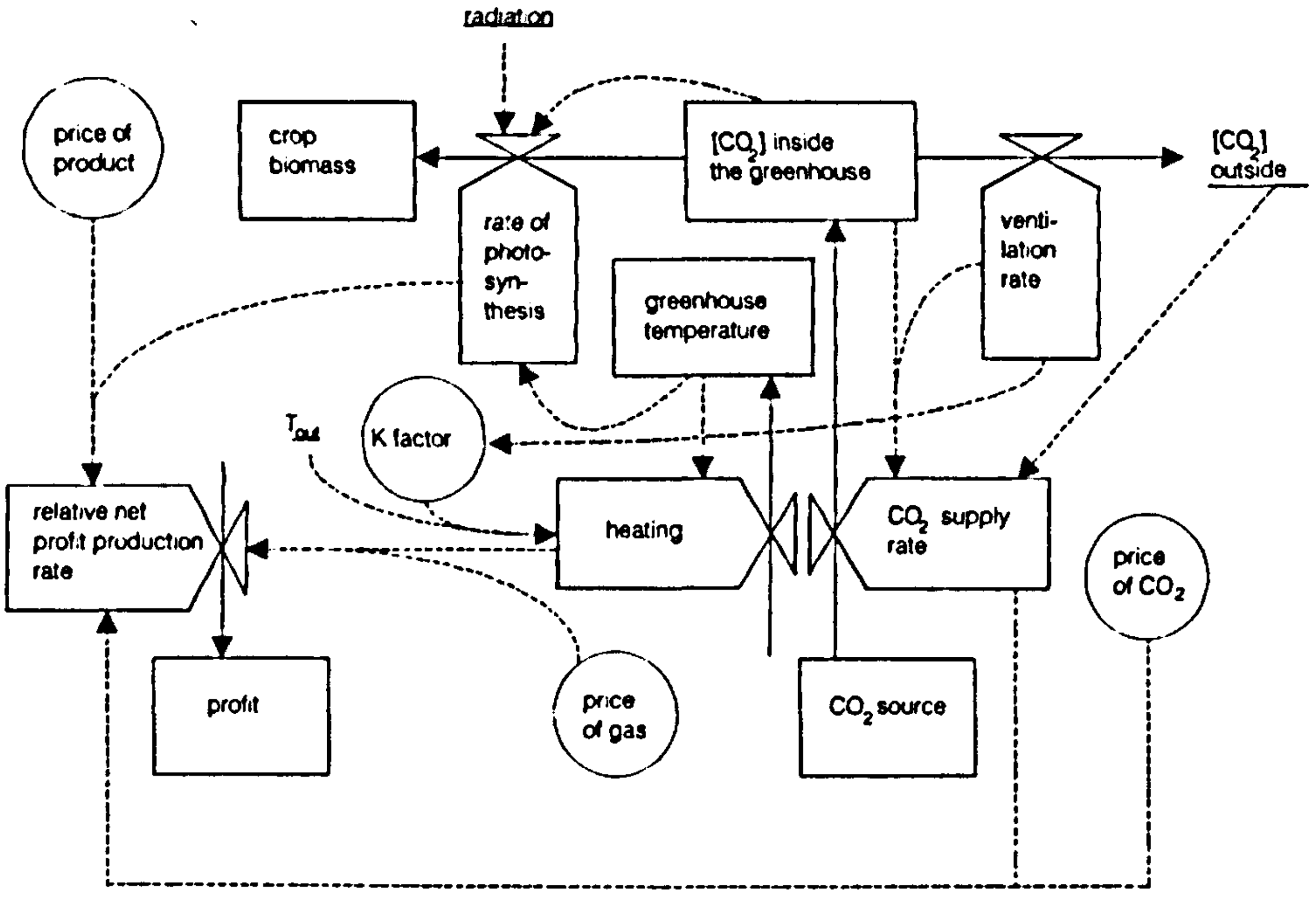


Figure 39. The optimization process with CO_2 and temperature control in greenhouses.

Although other factors such as crop water-status, or sink activity may limit crop performance, there are good arguments for considering crop gross photosynthesis as the key process in relation to short-term optimization of greenhouse climate control (Challa, 1989). According to Penning de Vries & van Laar (1982) the rate of production of a crop can be described by

$$Y_f = f_{wo}\,\alpha\,(P_g - R_m)/C_{dm} \qquad \text{Equation 18}$$

where

Y_f = rate of production (harvestable fresh weight) (g m^{-2} h^{-1})
f_{wo} = fraction of assimilates diverted to harvestable product (g g^{-1})
α = conversion efficiency CH_2O to structural dry weight (g g^{-1})
P_g = gross photosynthesis rate (CH_2O units) (g m^{-2} h^{-1})
R_m = rate of maintenance respiration (CH_2O units) (g m^{-2} h^{-1})
C_{dm} = dry matter content of the product (g g^{-1})

To optimize the environmental factors with respect to the expected net financial output, it suffices to consider only differences in yield, ΔY_f in relation to variations in the relevant inputs (Challa & Schapendonk, 1986)

$$\Delta Y_f = f_{wo}\,\alpha\,\Delta P_g/C_{dm} \qquad \text{Equation 19}$$

provided that R_m is independent of the factors considered. The factors involved are CO_2 pressure, air temperature and air humidity and it is clear that temperature does affect the rate of maintenance respiration. A reasonable approach, however, is to accept the principle that, in the long term, a grower wants to achieve a given average temperature suitable for the crop, and in that case short-term variations in maintenance respiration will be averaged out in the long term. Therefore, these effects have to be neglected here. Likewise, although it is well known that the fraction of assimilates diverted to harvestable product (f_{wo}) may change, for example, with changing climatic conditions (Evans, Chapter 5), it is assumed here that these are reactions to the average climatic conditions and therefore play a negligible role in short-term control. Later in this chapter the relation between short- and long-term control will be considered.

Hence, differences in the rate of gross photosynthesis (P_g) multiplied by a conversion factor ($f_{wo}\ \alpha/C_{dm}$) and multiplied by the expected price should be evaluated financially in relation to the associated differences in the rate of consumption of energy and CO_2. In other words, the rate of financial output minus the rate of financial input of the factors considered, called the relative net profit production rate, *RNPPR* (Challa & Schapendonk, 1986), should be maximized, where

$$r_{vn} = \mathrm{d}(V_p - V_i)/\mathrm{d}t \qquad \text{Equation 20}$$

where

r_{vn}	= relative net profit production rate	(NLG $m^{-2}\ h^{-1}$)
V_p	= the economic value of dry matter produced	(NLG m^{-2})
V_i	= the economic value of the inputs considered	(NLG m^{-2})
t	= time	(h)

In Equation 20 those cost factors that are independent of the inputs considered are ignored, because they do not play a role in the optimization problem considered here. Therefore, values of *RNPPR* cannot be used to evaluate the actual profit to the grower.

In an earlier paper (Challa & Schapendonk, 1986) only the factor CO_2 pressure was considered. Here I propose to elaborate the discussion by introducing temperature control in the optimization, because it interferes strongly with the control of CO_2 pressure as well as with the response of the crop to CO_2. Although the control of air humidity certainly deservers attention it will be ignored here, because the effects on crop performance are too little understood and therefore cannot be handled quantitatively at present. Air humidity will therefore be considered here primarily as one of the factors that should be dealt with in the context of other objectives that should be involved in the overall management of greenhouse climate control, as will be discussed later.

To maximize *RNPPR* in relation to the inputs considered, it is necessary to calculate the instantaneous rates of P_g, CO_2 supply and of energy consumption in relation to the environmental factors inside and outside the greenhouse and the relevant greenhouse properties. Dynamic models that predict crop photosynthesis (Challa, 1989) and greenhouse behaviour (Bot, 1983) have been developed to do this. These models have to be integrated because the greenhouse and the crop are interacting systems: the greenhouse modifies the environment of the crop and the crop interferes in the CO_2, water vapour and energy budgets of the greenhouse.

Optimizing control algorithms will have to deal with dynamic aspects of the system: optimal set-points in a stationary situation may differ from optimal set-points under varying conditions, because the way in which the desired set-points are arrived at and the time required to realize those conditions play an important role (van Henten, 1989).

Although maximization of *RNPPR* is important in terms of economic operation of the greenhouse, it neither should nor can be the only criterion for climate control. Instead it should be considered as a fine tuning, at a level of refinement that the grower can have no actual knowledge of. This aspect of optimization should therefore fit into a wider framework that involves other objectives. Later in this chapter I will come back to this point.

8.4 The model

I now propose to examine the response of *RNPPR* to temperature and CO_2 pressure inside the greenhouse in a static approach, using cucumber as an example. The benefit of this approach is that insight is obtained in the characteristics of the response surface and in the order of magnitude of gains that could be obtained through optimization at this level. Because of the exploratory character of this study, rough approximations are made to account for the behaviour of the greenhouse. The model used to describe the instantaneous rate of crop photosynthesis was essentially derived from SUCROS87 (Spitters et al., 1989) but extended with a much more elaborate version of the module for leaf photosynthesis developed by Farquhar et al. (1980). This detailed, biochemical model of leaf photosynthesis is able to deal adequately with the combined effects of CO_2 pressure and temperature on the rate of gross CO_2 assimilation of a leaf (Berry & Raison, 1981; Farquhar & von Caemmerer, 1982; Schapendonk & Brouwer, 1985).

The approach adopted by Farquhar and colleagues was used and their parameters were adopted in order to obtain the response of leaf photosynthesis to temperature (Figure 40). This response follows the well-known optimum curve, which is most pronounced when irradiation and CO_2 pressure are high. The temperature for maximum photosynthesis is a function of radiation and CO_2 pressure. At low radiation and CO_2 pressure maximum photosynthesis is observed at low temperatures. It should, however, be noticed that in the low temperature range (< 17 °C) the model overestimates leaf photosynthesis for cucumber, because certain processes are not considered in the model (data not shown). This discrepancy is probably caused by changes in the membrane configuration at low temperature, a reaction that is characteristic of thermophylic plants such as cucumber (Berry & Björkman, 1980).

The distribution of light interception within the crop and the integration of leaf photosynthesis over crop height was calculated according to SUCROS87 (Spit-

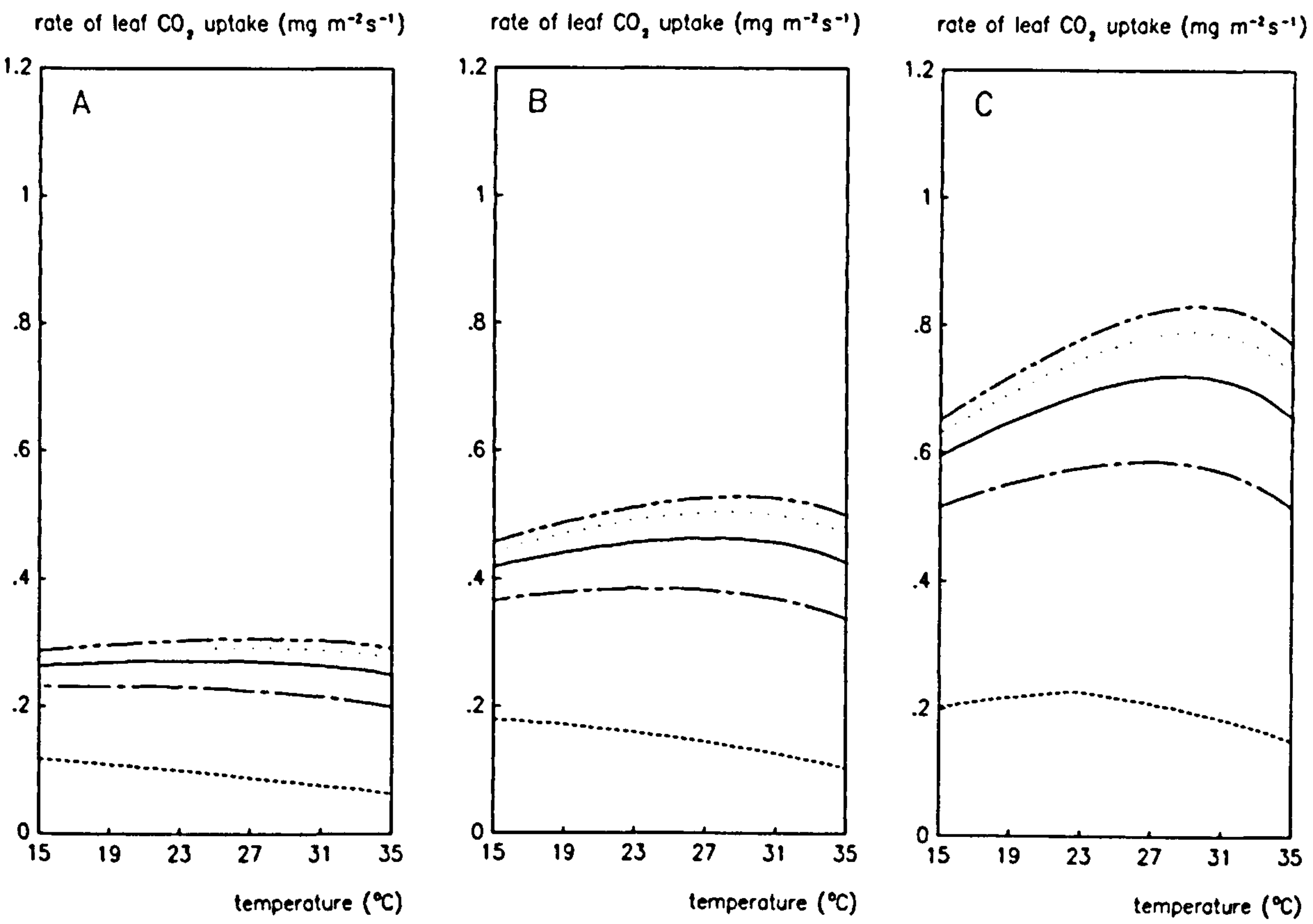


Figure 40. Simulated rate of gross photosynthesis of a single leaf as function of temperature at photosynthetically active radiation of 25 W m^{-2} (A), 50 W m^{-2} (B) and 100 W m^{-2} (C). CO_2 pressures are: (---) 10 Pa; (— — —) 32.5 Pa; (——) 55 Pa; (···) 77.5 Pa and (— — — —) 100 Pa. Absorption coefficient of leaf = 0.8. Other parameters are given in Table 10.

ters et al., 1989). For illustration, fixed values were selected here for the height of the sun and the fraction of diffuse radiation (Table 10). The response of the rate of crop photosynthesis to CO_2 pressure and temperature essentially resembles that of individual leaves (Figure 41). Apart from the absolute levels the main differences are observed in the response to temperature at high radiation, a difference that may be attributed mainly to a lower average irradiation of leaves in the crop situation. The effect of CO_2 pressure predominates but the effect of temperature cannot be ignored, especially at high CO_2 concentrations.

The rate of CO_2 supply (C_s) required to maintain a certain CO_2 pressure inside the greenhouse depends on the pressure difference with the outside air, the rate of CO_2 uptake by the crop and the air exchange rate which is used here as an input parameter, but, of course, in reality is related in a complicated way to ventilator opening and various other conditions (Kozai & Sase, 1978; Bot, 1983)

Table 10. List of parameter values used for the model calculations, and abbreviations and symbols used in this chapter.

Symbol	Meaning	Value	Units
–	chlorophyll per unit leaf area	0.45	g m^{-2}
–	CO_2 resistance stomatal + boundary layer	120	s m^{-1}
–	combustion energy of gas	35.2	MJ m^{-3}
–	concentration of enzyme sites in chlorophyll	87.0	µmol g^{-1}
–	conversion PAR to quanta	4.59	µE W^{-1}
–	dark respiration at 25°C	1.1	µmol m^{-2}s^{-1}
–	price of CO_2	0.20	NLG kg^{-1}
–	price of fuel (natural gas)	0.20	NLG m^{-3}
–	price of product (fresh weight)	0.004	NLG g^{-1}
–	turnover number of RuP2 carboxylase	2.5	s^{-1}
A_c	rate of CO_2 assimilation by the crop	–	g m^{-2} h^{-1}
C_o	CO_2 pressure of outside air	34	Pa
C_i	CO_2 pressure inside the greenhouse	–	Pa
C_s	rate of CO_2 supply	–	g m^{-2} h^{-1}
C_{dm}	dry matter content	0.035	g g^{-1}
d	density of CO_2	1800	g m^{-3}
e	efficiency heating system	0.9	J J^{-1}
f_{dif}	fraction of diffuse radiation	0.5	J J^{-1}
f_{wo}	fraction of dry weight in harvestable product	0.7	g g^{-1}
h	average height of greenhouse	3	m
l_{la}	leaf area index	3	m^2 m^{-2}
K	energy transfer coefficient (floor area basis)	–	J K^{-1} m^{-2} s^{-1}
K'	K factor at $\Phi = 0$	7	J K^{-1} m^{-2} s^{-1}
K_c	Michaelis-Menten constant for CO_2	31	Pa
K_o	Michaelis-Menten constant for O_2	15.5	Pa
NLG	Netherlands Guilder (≈ 0.5 USD)		
P	pressure of the air	10^5	Pa
P_g	gross photosynthesis rate (CH_2O units)	–	g m^{-2} h^{-1}
Q	energy consumption for heating of greenhouse	–	J m^{-2} h^{-1}
R_g	global radiation inside the greenhouse	–	J m^{-2} s^{-1}
R_m	rate of maintenance respiration (CH_2O units)	–	g m^{-2} h^{-1}
$RNPPR$	relative net profit production rate (r_{vn})	–	NLG m^{-2} h^{-1}
r_{vn}	relative net profit production rate	–	NLG m^{-2} h^{-1}
t	time	–	h
T_i	temperature inside the greenhouse	–	°C
T_o	temperature outside the greenhouse	–	°C
V_{co}	V_{omax}/V_{cmax}	0.21	–
V_{cmax}	maximum rate of carboxylase reaction	–	µmol s^{-1}
V_i	economic value of the inputs considered	–	NLG m^{-2}

Table 10 continued

Symbol	Meaning	Value	Units
V_{omax}	maximum rate of oxygenase reaction	–	$\mu mol\ s^{-1}$
V_p	economic value of dry matter produced	–	NLG m^{-2}
Y_f	rate of production (harvestable fresh weight)	–	$g\ m^{-2}\ h^{-1}$
α	conversion efficiency CH_2O to structural dry weight	0.7	$g\ g^{-1}$
β	angle of sun height	0.3	rad
Φ	rate of air exchange	–	$m^3\ m^{-3}\ h^{-1}$
ρC_p	volumetric heat capacity of air	1200	$J\ m^{-3}\ K^{-1}$

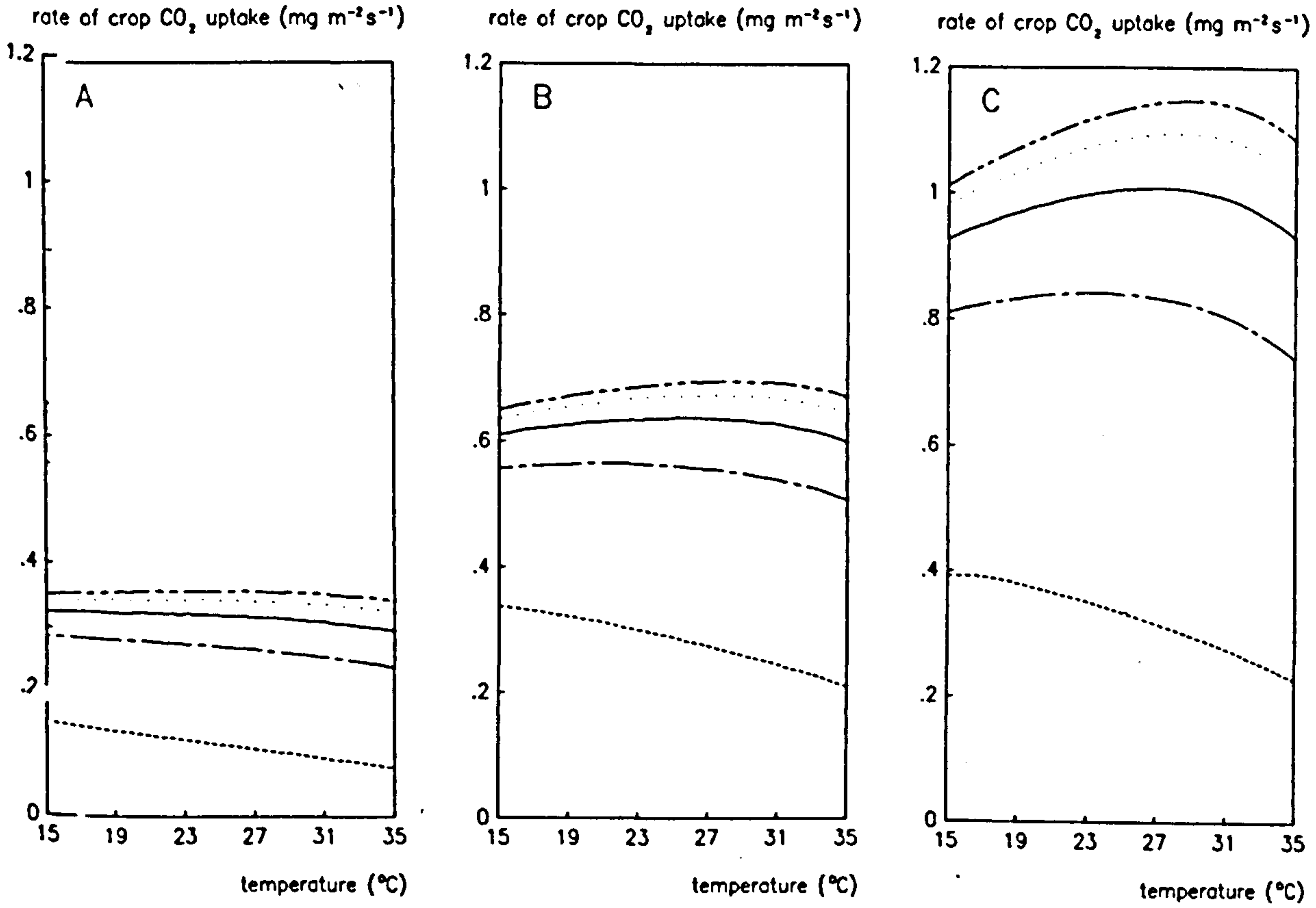


Figure 41. Simulated rate of gross photosynthesis of a crop as a function of temperature at photosynthetically active radiation of 25 W m^{-2} (A), 50 W m^{-2} (B) and 100 W m^{-2} (C). CO_2 pressures as in Figure 40. Leaf area index = 3. Other parameteres are given in Table 10.

$$C_s = A_c + \Phi\, h\, d\,(C_i - C_o)/P \qquad \text{Equation 21}$$

where
C_s = rate of CO_2 supply ($g\ m^{-2}\ h^{-1}$)
A_c = rate of CO_2 assimilation by the crop ($g\ m^{-2}\ h^{-1}$)
Φ = rate of air exchange (h^{-1})
h = average height of the greenhouse (m)
C_i = CO_2 pressure inside the greenhouse (Pa)
C_o = CO_2 pressure outside the greenhouse (Pa)
d = density of CO_2 ($g\ m^{-3}$)
P = pressure of the air (Pa)

Energy consumption required to maintain the temperature difference between inside and outside was estimated very roughly using

$$Q = 3600\, e\, K\,(T_i - T_o) \qquad \text{Equation 22}$$

where
Q = energy consumption ($J\ m^{-2}\ h^{-1}$)
e = efficiency of the heating system, including the boiler ($J\ J^{-1}$)
K = factor (definition follows from Equation 22) ($J\ K^{-1}\ m^{-2}\ s^{-1}$)
T_i = temperature inside the greenhouse (°C)
T_o = temperature outside the greenhouse (°C)

and where K is estimated, ignoring the latent heat loss, according to

$$K = K' + \Phi\, h\, \rho C_p/3600 \qquad \text{Equation 23}$$

where
K' = K factor without ventilation ($J\ K^{-1}\ m^{-2}\ s^{-1}$)
Φ = rate of air exchange (h^{-1})
h = average height of the greenhouse (m)
ρC_p = volumetric heat capacity of air ($J\ m^{-3}\ K^{-1}$)
For $h = 3$, Equation 23 reduces to $K = K' + \Phi$.

The cost of maintaining the desired level of CO_2 is obtained by multiplying the CO_2 supply by the price of CO_2. Likewise, the cost of maintaining the desired temperature is obtained by multiplying the fuel consumption required to cover the rate of energy consumption by the price of fuel. All parameters used for the calculations are presented in Table 10.

8.5 Response surfaces

The models and equations presented in the previous section enable response surfaces of *RNPPR* to be constructed as a function of the two inputs considered, air temperature and CO_2 pressure inside the greenhouse. These response surfaces only provide a static description; the dynamic aspects of the physical and physiological responses that, as pointed out previously, have to be taken into accont for control, are ignored. Two principally different situations are considered in the case of a cucumber crop:

1. 'Heat demand', with a heat demand and given air exchange rate.
2. 'Ventilation requirement', where ventilation is required in order to maintain the temperature set-point, and where the air exchange rate is a function of the temperature inside the greenhouse, the outside temperature and the global radiation.

When there is a ventilation requirement, the rate of ventilation Φ is calculated according to Equation 23 and the definition of K

$$\Phi = ((R_g/(T_i - T_o)) - K') \, 3600/(h \, \rho C_p) \qquad \text{Equation 24}$$

where

Φ	= rate of air exchange	(h^{-1})
R_g	= global radiation inside the greenhouse	($J\ m^{-2}\ s^{-1}$)
T_i	= temperature inside the greenhouse	(°C)
T_o	= temperature outside the greenhouse	(°C)
K'	= K factor without ventilation	($J\ K^{-1}\ m^{-2}\ s^{-1}$)
h	= average height of the greenhouse	(m)
ρC_p	= volumetric heat capacity of air	($J\ m^{-3} K^{-1}$)

For $h = 3$, Equation 24 reduces to $\Phi = (R_g/(T_i - T_o)) - K'$.

8.5.1 Situation 1, heat demand

When the greenhouse is heated the optimization problem is that energy and additional CO_2 are required to maintain a given temperature and CO_2 pressure (Figure 39). In the Netherlands, CO_2 is usually available for free when there is a heat demand, because exhaust gases from the central boiler are used as a source, and in that case only temperature control has to be optimized. Below the more complicated case where liquid CO_2 is used as a source is worked out, where a financial input is required for both temperature and CO_2 control.

The results of the calculations of *RNPPR* are presented in the form of contour plots because two factors are involved. The slope of the response curve is expressed by the density of the contour lines (Figures 42 and 43). Two situations have been considered, a low rate of ventilation of 1 $m^3\ m^{-3}\ h^{-1}$ (Figure 42A, C, E) and a high rate of ventilation of 10 $m^3\ m^{-3}\ h^{-1}$ (Figure 42B, D, F). At high radiation the optimum is very pronounced (Figure 42E, F) and the optimum conditions are little affected by ventilation, indicating that the effect on the cost of the inputs is small compared with the effect on the value produced. At lower radiation levels the effect of ventilation is much greater and there is a clear shift of the optimal conditions towards lower CO_2 concentrations and lower temperatures. Furthermore, there is an obvious interaction of CO_2 pressure and temperature: at low CO_2 pressure the optimum temperature is lower than at high CO_2 pressure. At 25 W m^{-2} and high ventilation (Figure 42B) the optimum conditions

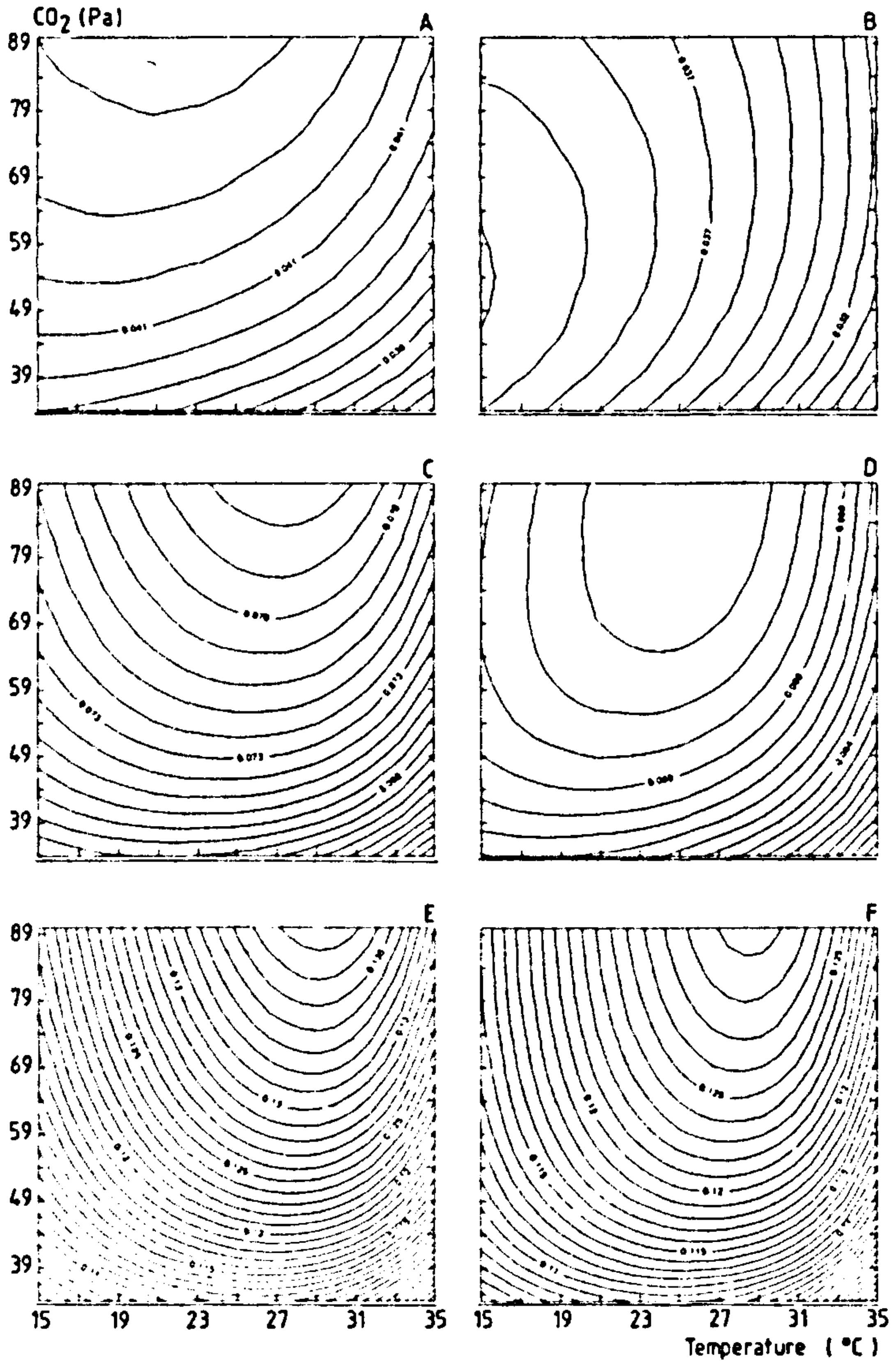


Figure 42. Relative net profit production rate (NLG m^{-2} h^{-1}) as a function of CO_2 pressure and temperature. Temperature controlled by heating. Photosynthetically active radiation inside the greenhouse of 25 W m^{-2} (A, B), 50 W m^{-2} (C, D) and 100 W m^{-2} (E, F). Fixed air exchange rate of 1 m^3 m^{-3} (A, C, E) or 10 m^3 m^{-3} (B, D, F). Price of CO_2 is 0.20 NLG kg^{-1}, price of gas is 0.20 NLG m^{-3}, price of cucumbers is 4.00 NLG kg^{-1}. Outside temperature is 10 °C.

shift to temperatures where the validity of the model is questionable: the model does not account for the strong decrease of photosynthesis at temperatures below ca. 17 °C, as has been pointed out previously.

The same situation was also investigated in the case of higher prices of CO_2 and fuel, a situation that is likely to occur in the Netherlands in the future (Figure 43) and that is probably more common in many other countries. The results obtained show a clear difference with Figure 42: the effect of ventilation on the response surface is much more pronounced, even at high irradiation. Furthermore, these examples clearly show the importance of dynamic optimization. Optimal climate conditions are indeed not only a matter of maximizing photosynthesis but may

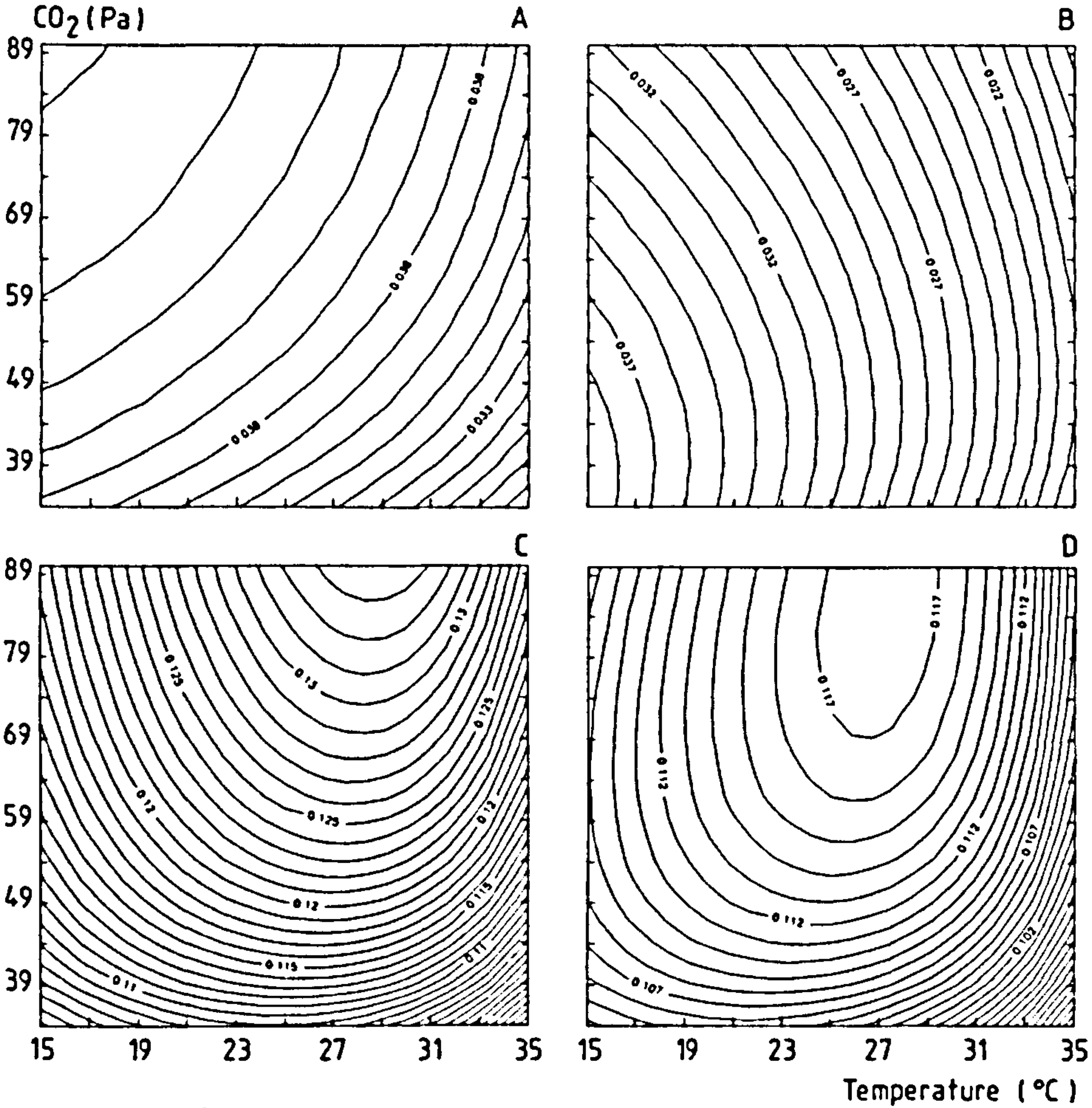


Figure 43. Relative net profit production rate (NLG m^{-2} h^{-1}) as a function of CO_2 pressure and temperature. Temperature controlled by heating. Photosynthetically active radiation inside the greenhouse of 25 W m^{-2} (A, B) and 100 W m^{-2} (C, D). Fixed air exchange rate of 1 m^3 m^{-3} (A, C) or 10 m^3 m^{-3} (B, D). Price of CO_2 is 0.40 NLG kg^{-1} and price of gas is 0.40 NLG m^{-3}. Other parameters as in Figure 42.

depend strongly on various economic factors, such as the price of the product, of fuel and of CO_2 (Compare Figure 42 with Figure 43).

8.5.2 Situation 2, ventilation requirement

When only ventilation is required to maintain a given temperature set-point, because there is a surplus of energy as a result of solar radiation, the main cost factor in this optimization problem is maintenance of the CO_2 pressure desired (Figure 44). In this case optimum temperature is high at both low and high radiation because the high ventilation rate that is required in order to maintain a low temperature leads to a high demand for CO_2. The range of temperatures is smaller than in Situation 1, because only ventilation control is considered and the maximum temperature that may occur depends on the energy supply by radiation.

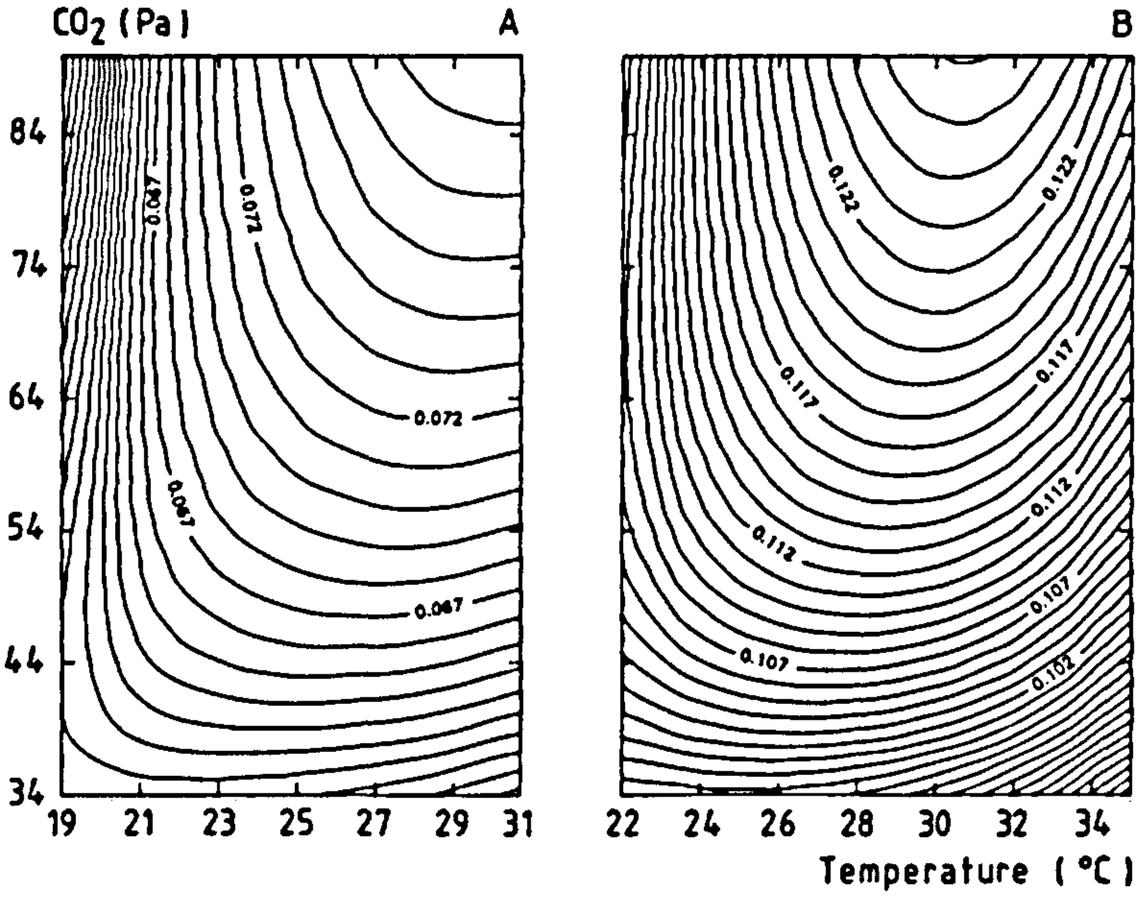


Figure 44. Relative net profit production rate (NLG m^{-2} h^{-1}) as a function of CO_2 pressure and temperature. Temperature controlled by ventilation. Photosynthetically active radiation inside the greenhouse of 50 W m^{-2} (A) and 100 W m^{-2} (B). Price of CO_2 is 0.20 NLG kg^{-1}, price of gas is 0.20 NLG m^{-3}, price of cucumbers is 4.00 NLG kg^{-1}. Outside temperature is 17 °C.

8.5.3 Conclusions

The simple examples that have been discussed make clear that dynamic optimization may be important because substantial benefit can be obtained. For an early planted cucumber crop in the Netherlands, the value produced during the first 83 days of the production cycle (the period where the price used in our calculations prevails) is in the order of NLG 29 per square metre of greenhouse floor (Anonymous, 1988). Assuming an average daylength of 10 h, the average value produced per hour is about NLG 0.035 m^{-2}. In Figures 42, 43 and 44 the iso-*RNPPR* lines differ by NLG 0.001 m^{-2}, or 3% of the average value produced. *RNPPR* differences of this order of magnitude are certainly relevant, because the extra cost for a system providing optimal climate control will be small. A better evaluation of optimized climate control requires extensive simulation runs using generated average weather conditions and a greenhouse model more elaborate than the simple version used here.

Optimal conditions depend on a great number of factors, which will change from moment to moment, from year to year, and from grower to grower. It is, however, important to notice here that the price of the product at the time of harvest is normally unknown at the moment the required assimilates are produced. Because this price depends strongly on the situation of the market it is impossible to obtain accurate predictions. As a result, accurate optimization is, in general, impossible, even if the crop models are very accurate.

In any case it is clear that in order to improve present greenhouse climate control systems, models that enable all relevant input and output factors to be evaluated in real time are required. The rapid development of powerful hardware will make it feasible to introduce models as a tool for optimizing greenhouse climate control. Horticulturists, engineers and plant physiologists are faced with the challenge of developing systems that are able to use the great potentials of modern greenhouse technology adequately.

8.6 The future

It has been pointed out already several times that, of course, maximization of the relative net profit production rate (*RNPPR*) is not the only objective of climate control. In general the following objectives can be formulated:

- high yield at reasonable cost
- optimal planning of production (labour requirement, market)
- product of good quality
- risk minimization
- maintenance of the production potential of the crop
- good labour conditions.

Maximization of *RNPPR* should thus be considered within the overall framework of the objectives mentioned. It will not be easy to integrate these objectives in future control systems, however. A proposal for an integrated system of short-term optimization and long-term planning of production was presented previously (Challa, 1985). In that set-up, requirements resulting from long-term decisions were linked to short-term optimization in terms of fixed limits for acceptable climatic conditions and average target conditions for humidity and temperature. The disadvantage of this one-way approach is that the knowledge that is available at the short-term level is not used to modify those limits. Thus, for example, if a minimum air humidity is formulated as a general rule for all conditions, it is obvious that refinements can be made if other instantaneous conditions that interfere in the problems caused by low humidity are also taken into account. Otherwise, the range of conditions that are defined as acceptable may be so small that little room is left for optimization.

In fact, more dynamic limits could be established if the relevant processes and their relations to the condition of the crop and the prevailing situation were understood. Unfortunately, this kind of knowledge is mainly present in the form of the grower's practical knowledge and therefore has a poor scientific basis and is badly documented.

A systematic survey of this 'grey' knowledge is urgently required and should be supplemented by a careful scientific analysis to enable it to be integrated with quantitative knowledge of physiological processes. Future climate control systems for greenhouse culture must rely on symbiosis of qualitative (knowledge systems) and quantitative models, in which the interaction with the grower is essential (Figure 45). The grower's knowledge that could be used is primarily qualitative and can be expressed in term of 'if... then' rules. Quantitative models

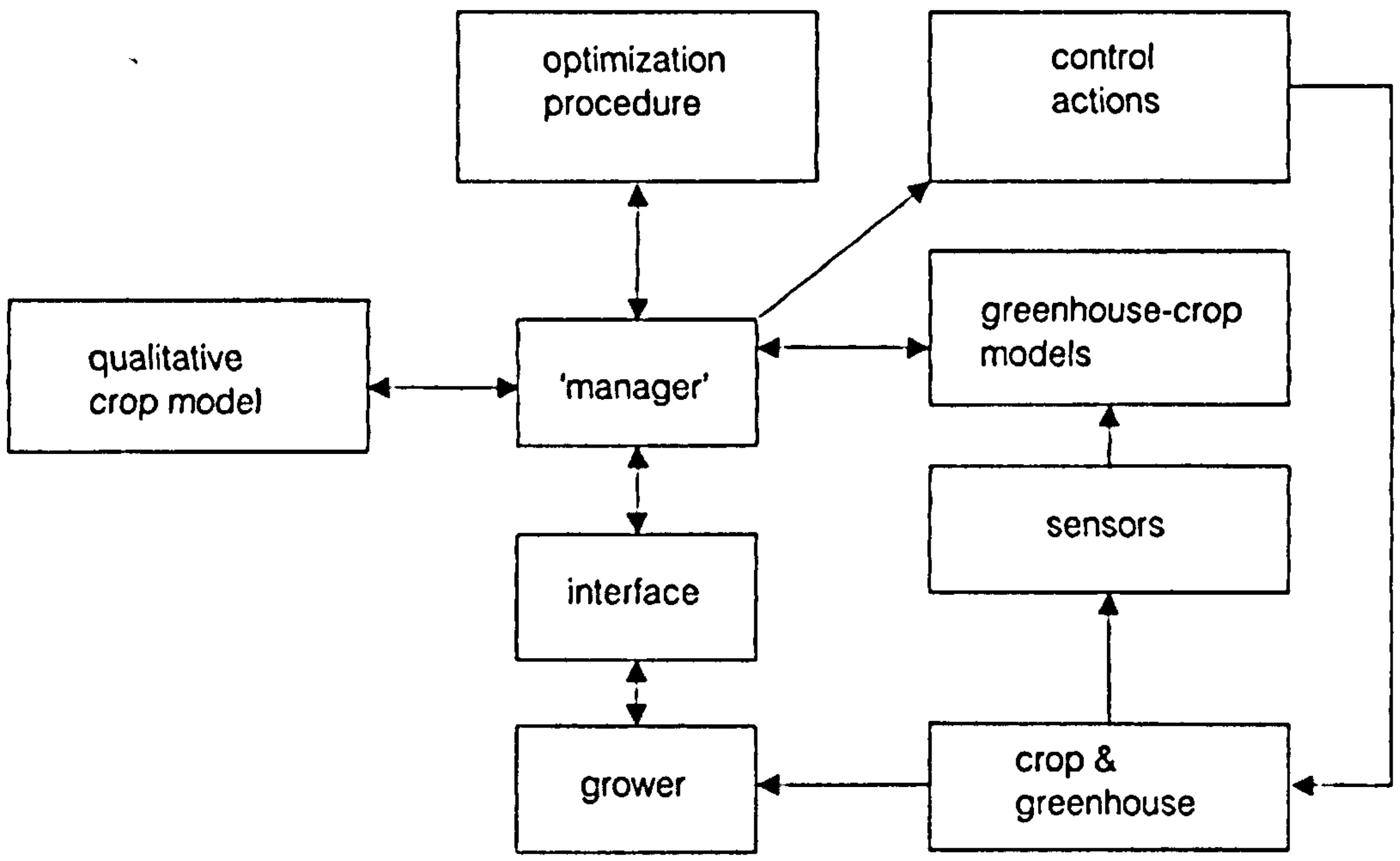


Figure 45. General architecture of future control systems.

support the qualitative model as one of the knowledge bases that can be consulted. In addition, the qualitative model will receive information from the grower who, by observations of the crop, possibly supported by a decision-support system, and given his general management policy, is able to manipulate the crop in the way desired.

Depending on the deviation from the 'ideal' situation, the qualitative model determines the room for optimization (Figure 46). Under 'normal' conditions a standard strategy is followed (blueprint), which is a sub-set of the conditions that could be generated by the optimizing control system. The room for optimization can be limited further if problems are expected. In that case the grower will switch to the 'prevent strategy', where priority is given to preventing the problems that might occur, rather than to optimization, if there is a conflict between these objectives. The smallest range of acceptable conditions is generated in the case of the 'recover strategy'. Of course the 'prevent' and 'recover' strategies are directly related to the problems that might or do occur, and are not general strategies.

Greenhouse climate control systems such as those described here are still wishful thinking. As stated before, knowledge required for their construction is still largely lacking. In addition, artificial intelligence is a new area and consequently obtaining proper and reliable tools is also a problem. Others (Jones et al., 1989; Schmidt-Paulsen, 1989) have also argued in favour of a combined approach that uses quantitative and qualitative models. This approach is probably essential, if models are to be used in agriculture.

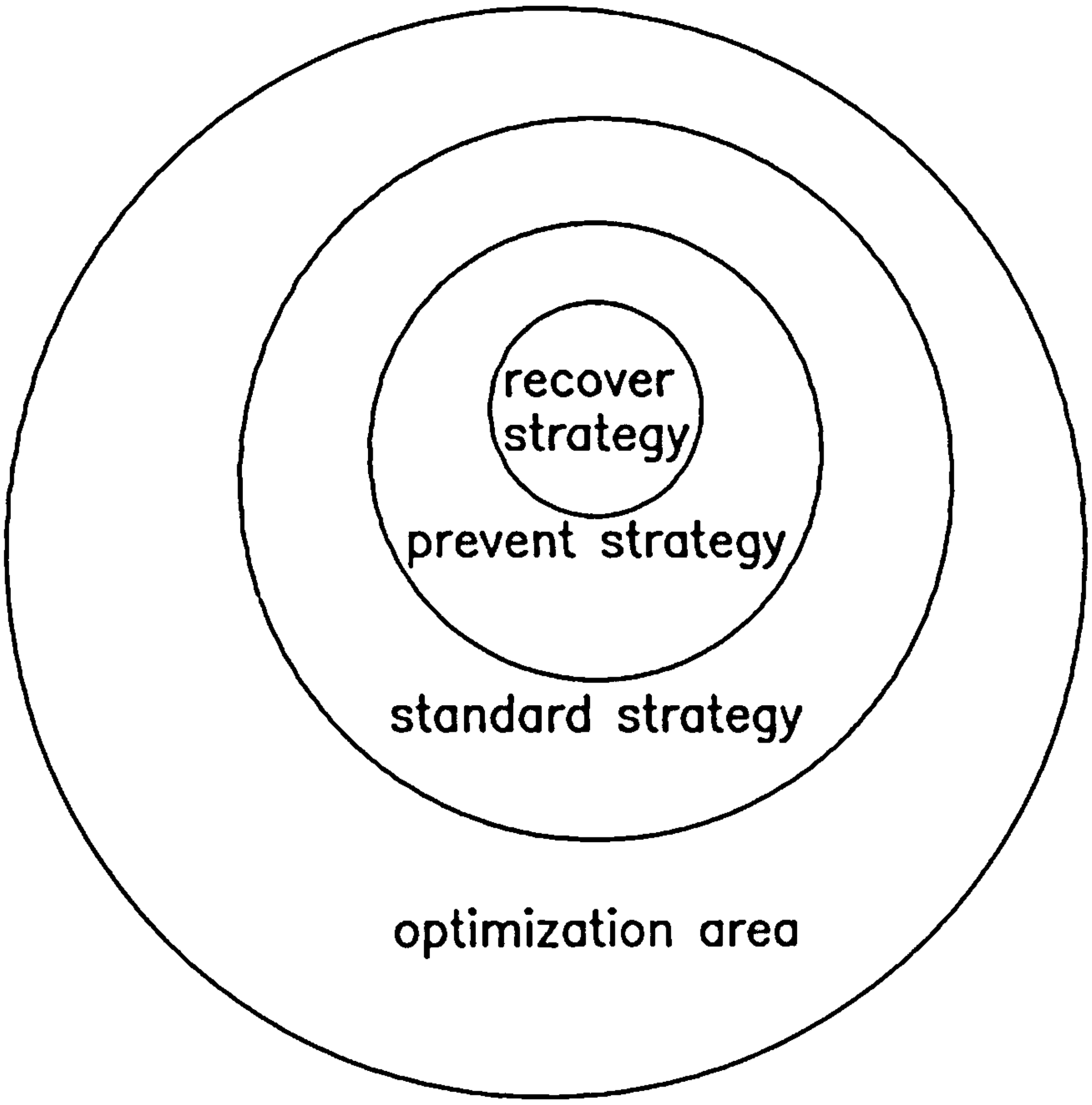


Figure 46. The optimization space and the limits set by 'standard', 'prevent' and 'recover' strategies.

8.7 Acknowledgments

The assistance of Dr G.P.A. Bot, Department of Agrotechnique and Physics, Wageningen Agricultural University, the Netherlands, in setting up a simplified procedure for the calculation of CO_2 and energy requirement is acknowledged. My thanks are also due to J.A. ten Cate, Centre for Agrobiological Research, Wageningen, who kindly provided me with a FORTRAN implementation of the routine for photosynthesis according to Farquhar et al. (1980).

Numerous discussions with Drs L. Maris, Department of Computer Sciences, Wageningen Agricultural University, and our students, T. van Dijk and P. Schotman, were of great value when developing the concepts mentioned in the section on the future.

I wish to thank my colleague Ir. E. Heuvelink for carefully reading the manuscript and making valuable comments.

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PESTS, DISEASES AND WEEDS

9 Defoliation, disease and growth

P.E. Waggoner

9.1 Introduction

One of the definitions of 'eponym' is 'a person whose name has become synonymous with an era, practice or the like'. De Wit is the eponym of the era and practice of computer simulation of photosynthesis, metabolic partitioning, and plant competition. The era and practice even encompass the simulation of pest attack, especially its harm to the crop (de Wit & Goudriaan, 1978; Rabbinge, 1982; Rijsdijk, 1986).

It was not always so. A faded card in the Soils Department of The Connecticut Agricultural Experiment Station still states that de Wit wrote *Het Verloop van de Grondwaterstand ten Westen van de IJssel in Zomer en Herfst.* He published it when he was 25 years old. We have lost the reprint. Another reprint, still in the files in New Haven, Connecticut and dated 1958 foreshadows the era. In *Transpiration and Crop Yields* de Wit put a simple model in eleven words: 'Photosynthesis appears to be positively correlated with the daily total radiation' (de Wit, 1958).

De Wit and his colleagues went on to compose comprehensive simulators of crop growth in dynamic programming languages. For decades they put in the roles of nutrients like nitrogen, changes like organogenesis and limitations like drought. They put in pests.

They exposed themselves to the Siren's song, 'Fill the computer's hold'. But they were never lured onto the rocks. They remembered the Law of Parsimony: 'Entities are not to be multiplied beyond necessity'. They shaved their ships with Ockham's Razor, consciously shaping summaries.

In *Philosophical Transactions*, de Wit & Penning de Vries (1985) specified what models are good for:

> In spite of early expectations about the predictive power of simulation models, their evolution has been slow and their development is still far from complete. At present there are no predictive models if prediction is defined as the making of precise statements about the future. But even if we had fully satisfactory predictive models of crop growth these would not 'predict' in the above sense, because the weather is an unpredictable variable. To justify the title *Predictive Models in Agricultural Production...* prediction is better defined as *organized thinking about the possible* (italics by Waggoner).

On the occasion of C.T. de Wit's retirement, it is fitting that I should organize thinking about the possible by discussing a summary model of attack by pests, founding the model on experiments but thinking far beyond that experience.

9.2 The foundation of the summary model

A look at plant pests usually starts by discussing how many pests there are and how fast they multiply. I break that convention by starting with hosts. In fact, I start with healthy hosts.

The elemental fact about plants is their conversion of solar energy into food by the photosynthesis in their foliage. The food builds the plant, and the accumulation, called yield, then feeds animals, including us. Thus, long ago physiologists began measuring the area of the foliage that transformed solar energy (e.g. Gregory, 1917). Since solar energy or insolation *I*, is measured per area of land, foliage is measured in the same way. Figure 47 shows a hypothetical distribution of leaf area with height *z* in a canopy of foliage. The foliar area per area of land and per depth swells with height above the soil and then shrinks to zero at the top of the canopy, as the profiles of the speckled shapes show. Its integral from the top of the canopy is the leaf area index, which is the sum of foliage area per land area. Called depth *f*, the integral increases from zero at the top of the canopy to *L* at the bottom. Although *f* and its maximum *LAI* or *L* are dimensionless because they are Leaf m^2/Land m^2, the two areas are of different things. In Figure 47, disease severity is greatest in a focus at the centre of the field. At the top of the figure, the

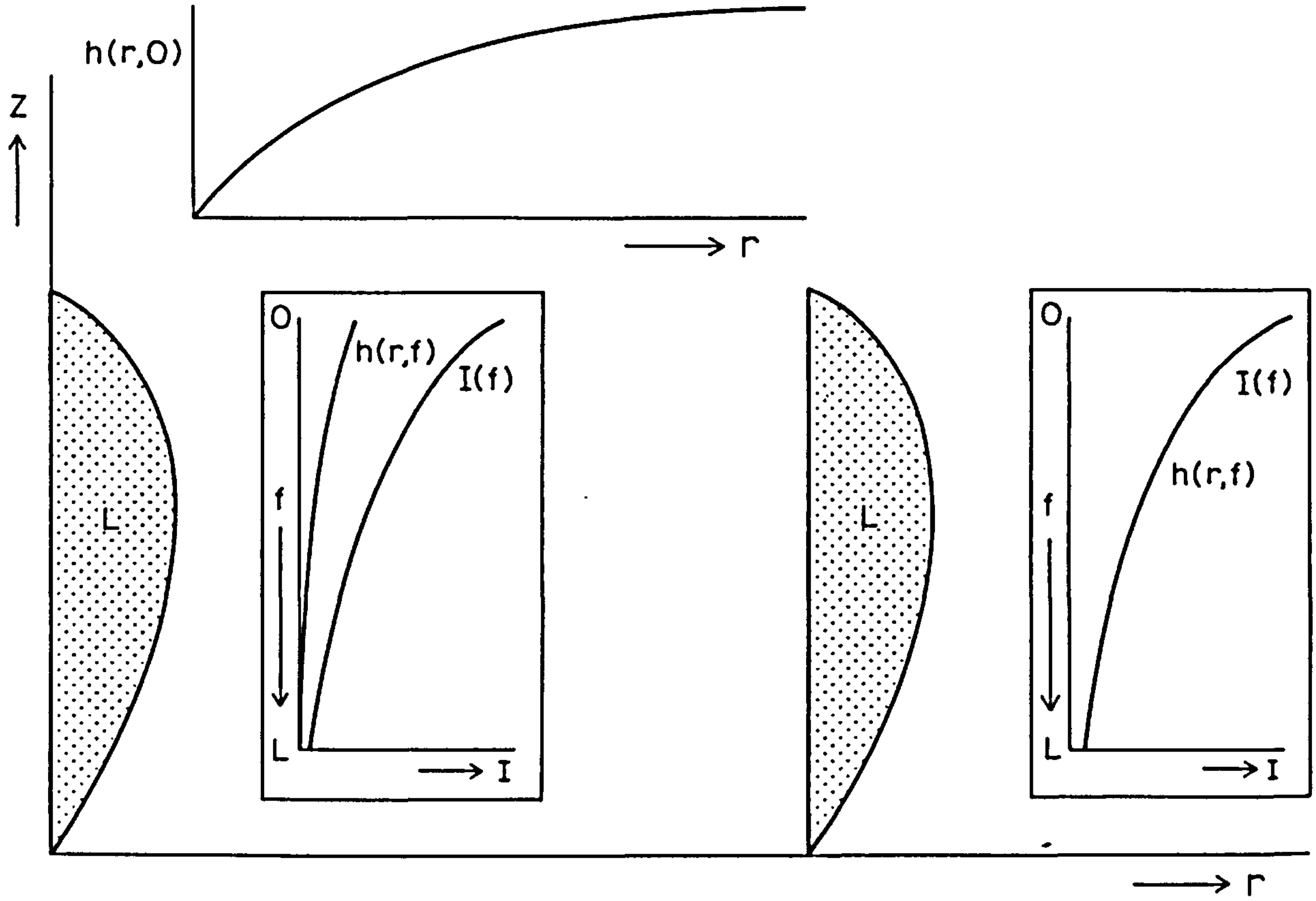

Figure 47. Hypothetical variations of leaf area, health and sun with height *z* and with distance *r* from the centre of a circular field. *f* is depth in the canopy, *h* is health, *I* is sun and *L* is maximum *LAI*.

health $h(r,0)$ at canopy top where f is zero is shown improving with distance r from the centre. In the lower part of the figure, a panel is drawn near the left margin, representing the centre of the field. Down the f of the canopy's depth, it shows the extinction of sun from $I(0)$ at the top. At the top it shows the health $h(r,0)$, and down f it shows the health $h(r,f)$ worsening. Farther along r the foliage is distributed through the canopy in the same way and has the same L. In the panel at the right, sun I is still intercepted with f in the same way. Health is made to coincide with I to show it is better at all depths than near the centre of the field.

A any given moment, photosynthesis may be controlled by leaf area. During a whole season, however, yield is photosynthesis accumulated while leaf area grows and senesces. Watson (1947), therefore, reasoned and then showed by the yields of barley, potato, wheat and sugar beet that yield was greater for the plants with larger integrals of L during the season.

Nevertheless, the absorption of radiation by foliage, not its area, is the crucial matter. The absorption of radiation by a gas in the atmosphere is reckoned by Beer's law. It states that a quantity of gas extinguishes radiation by a constant fraction called the extinction coefficient K_I. This was adapted to foliage by Monsi & Saeki (1953), who made K_I the fraction per foliage f of the solar radiation or insolation extinguished or intercepted by absorption and reflection and thus not transmitted further into the canopy. That is, they made K_I a fraction per leaf area per land area. K_I varies among plants, erect leaves intercepting a smaller fraction of insolation per f and having a smaller K_I than more horizontal ones. K_I only varies from 0.3 up to 1.1 (Monteith, 1969).

In my dictionary the definitions of 'sun' include 'the heat or light radiated from the sun'. To save space, I shall use 'sun' to mean radiation and insolation.

If the sun is $I(0)$ at the top and I at the depth f in a canopy of leaves,

$$dI/df = -K_I I.$$

Thus the sun intercepted in a column of unit area through the entire canopy of area L is

$$\int_0^L (dI/df)\,df = -K_I I(0) \int_0^L \exp(-K_I f)\,df = I(0)[1 - \exp(-K_I L)]$$

Equation 25

Since foliar f rather than height z does the intercepting and since sun is intercepted from the top down, Equation 25 uses the variable f rather than z, and f is measured from the canopy top to the limit L at the bottom.

A simple next step is setting the photosynthesis P proportional to the intercepted sun. The saturation of a single leaf with light in a physiological laboratory discourages setting this proportionality. In a canopy of foliage, however, the tilt of the leaves and the shade deep in the canopy encourage it.

Experiments, in fact, support going beyond the simple rule, 'more light, more photosynthesis' to a proportionality between sun intercepted and photosynthesis accumulated during a season. That is, the weight W of a crop growing from a negligible weight at time zero to the weight W at time t is

$$W = \varepsilon \int_0^t I(0)\,[1 - \exp(-K_\mathrm{I} L)]\,\mathrm{d}t \qquad \text{Equation 26}$$

ε is the efficiency of the crop's conversion of intercepted sun into plant weight. The size of ε depends on whether $I(0)$ is measured as sun from 0.3 to 3 μm or only as its half that can energize photosynthesis. Since the intercepted fraction $[1 - \exp(-K_\mathrm{I} L)]$ includes the reflected quarter of $I(0)$ from 0.3 to 3 μm, the size of ε also depends on reflection. Finally, the size of ε depends on whether W is all the biomass or just the harvested fraction, which is the biomass times the harvest index. The assumption that ε is constant during the season and can be moved outside the integration must also be remembered. Despite all these qualifications, when sun is measured from 0.3 to 3 μm, reflection is ignored, biomass is weighed and variation in harvest index is ignored, the range of ε is only from 1 to 3 g MJ^{-1} (Monteith & Elston, 1983).

A test of Equation 26 for biomass is doubly critical. First, it specifies biomass grows linearly with the integral in the equation. Second, it specifies the slope ε is 1 to 3 g MJ^{-1}. The equation for biomass goes beyond correlation of yield with sunlight. It specifies the shape plus the slope.

Although Equation 26 has an English history, it also has a Dutch history: de Wit's simple 1958 model of assimilation and transpiration proportional to sun. Three decades ago the bottom of de Wit's model of crop yields was the same proportionality between sun and photosynthesis that underlies Equation 26.

9.3 Pests

Now, we come to pests. In a book entitled *How Plants Suffer from Disease*, Horsfall & Cowling (1978) catalogue all the bad things microbial pests can do to plants. Although it begins with less capture of energy, the catalogue includes dysfunction in the flow of food and water, disturbed mineral nutrition and symbiotic relations, teratomas and alteration of growth, disrupted reproduction and rhythms, and senescence and disintegration of tissue. Similar catalogues could be written for insects and weeds. A comprehensive model would have to devour a whole catalogue. In the words of de Wit & Penning de Vries (1985), the gluttonous model would 'contain a wealth of information but ...(be) unwieldy'.

Despite this litany of complications, regressions have been fitted to the damage by pests (James, 1974). In an example, Zaharieva et al. (1984) found a close correlation between the weight of ears of winter wheat and both the fraction of leaves and fraction of foliar surface mildewed at single times. Although damage is correlated with disease at several and even single times, one must still acknowledge that

> The statistical 'blunderbuss' approach ... is not only clumsy, but also uninstructive because it ignores the underlying mechanisms and their interactions. At best, the results describe the existing situation, but they do not help organized thought about the possible (de Wit & Penning de Vries, 1985).

I shall present an alternative, a 'summary model'. De Wit & Penning de Vries (1985) defined a summary model as simple because of conscious and guided reduction of evaluated and well documented comprehensive models. The heart of Rijsdijk's (1986) comprehensive model of disease and crop is an equation making the growth in dry matter proportional to the interception of sun and to the fraction of leaf weight that is not diseased (Rijsdijk's Equations 123 and 124, p. 299). I ask readers to accept Rijsdijk's as an 'evaluated and well documented comprehensive model'. Then I ask they accept my adaptation of Equation 26 to plant disease as its 'conscious and guided reduction'.

Since pathologists study disease, they measure severity, the fraction x of foliar surface infected. They see the loss of yield inflicted by the disease rather than the yield that escaped. Like pessimists, pathologists habitually measure how much disease has emptied the bottle rather than how much remains.

I depart from Rijsdijk's comprehensive model by using the healthy leaf *area* rather than *weight*. I break the pessimist's habit by using the healthy fraction h or *health*, which equals $(1 - x)$. I use leaf area plus health rather than health alone. Like the comprehensive model, the summary includes the interception and shading by both diseased and healthy foliage. I multiply by the sun and the efficiency.

Equation 26 for healthy plants becomes the 'summary model' for diseased plants

$$W = \varepsilon_0 \int^t h\, I(0)\, [1 - \exp(-K_1 \mathrm{L})]\, \mathrm{d}t \qquad \text{Equation 27}$$

Since ε is outside the integration, it must be constant despite health and season. Sun, health and foliage may, however, vary during the season.

The integral of Equation 27 has been called Healthy Area Absorption of sun or *HAA*, and W is then equal to ε times *HAA*. This ignores the fraction reflected and equates absorption with interception, causing an estimate of ε somewhat smaller than if reflection had been subtracted from interception before calling it absorption. The simpler integral of h times L has been called the Healthy Area Duration or *HAD* (Waggoner & Berger, 1987).

The argument underlying the summary model does not distinguish microbial lesions on foliage from damage by an insect or even an environmental factor like smog. L is the foliage that intercepts sun, h the fraction healthy enough for photosynthesis, and ε the constant efficiency.

9.4 Test of the summary model for diseased crops

Despite the catalogue of qualifications and complications, the summary model does work in several crops and diseases. Peanuts were grown at various times during 14 years by four experimenters, leaf area index was changed by manually defoliating the crops, and the sun was estimated from the latitude. The yield of these healthy plants grew in a curvilinear fashion with *HAD*, the integral of L. It grew linearly, however, with *HAA*. The yields and *HAA* themselves are not shown

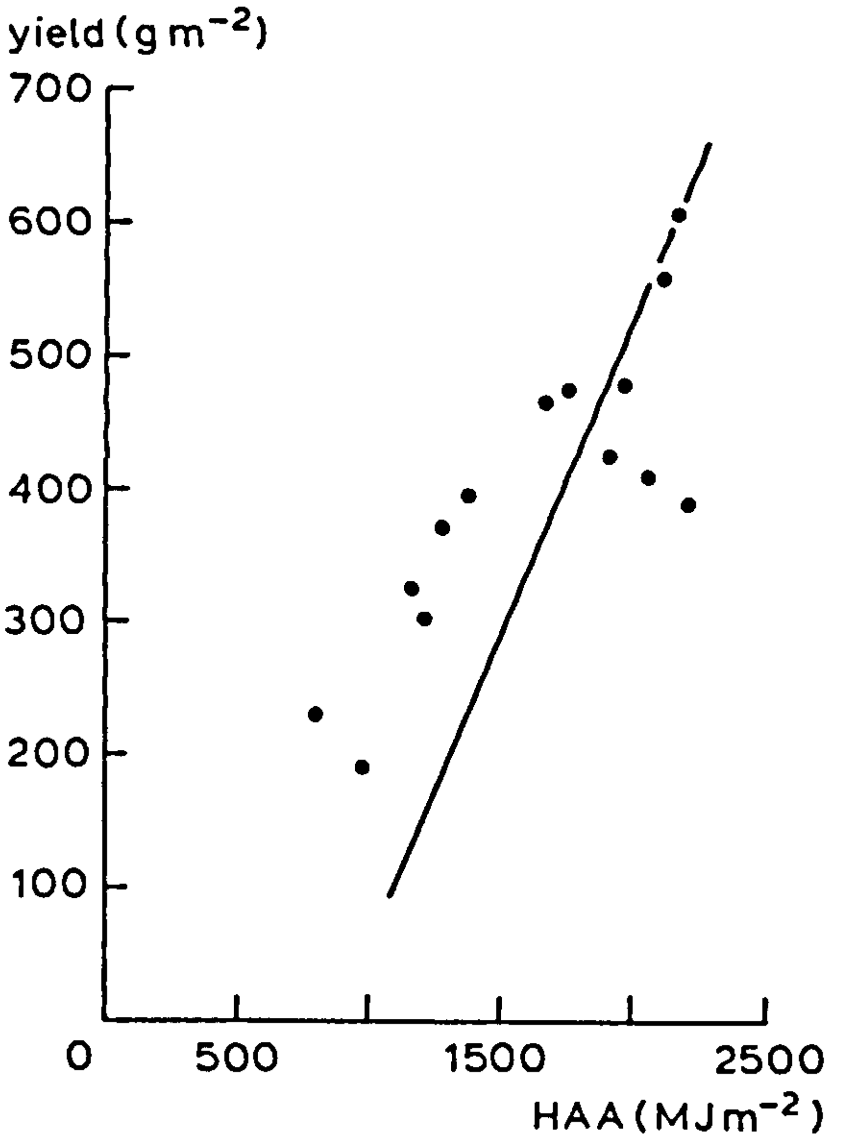

Figure 48. The Healthy leaf Area Absorption *HAA* of sun and pod yield of peanuts grown by Pixley (1985) and by Elston et al. (1976). *HAA* varied because of locality and disease. The line was fitted to other peanuts whose leaf area and hence *HAA* was varied by manual defoliation. Source: Waggoner & Berger (1987).

on Figure 48, but the linear relation between them is. Its negative intercept indicates that no peanuts are set when *HAA* is very small. When its slope is adjusted for 6% water in the harvest, 70% more calories in peanuts than wheat and a harvest index of half biomass harvested as yield, the slope for the peanuts corresponds to an ε of 1.5 g MJ^{-1} for wheat (Waggoner & Berger, 1987).

More pertinent to pests, differences in interception of sun by healthy foliage of peanuts cause the differences in weight predicted by Equation 27. Two experimenters sprayed peanuts in Africa and America with fungicides, causing differences in healthy leaf area. Later, Waggoner & Berger (1987) estimated $I(0)$ from the latitude and integrated it and the observed h and L to obtain *HAA*. The yields of different varieties with different disease on the different continents are compared with *HAA* in Figure 48. Despite all these differences plus the difference between disease and manual defoliation and the estimation of *HAA*, the yields change with *HAA* much as the relation for the manually defoliated peanuts represented by the line in Figure 48.

When the yield of potatoes suffering from late blight is compared with *HAD*, the slope of the line varies about fivefold from autumn to spring (Figure 49). On the other hand, when the yield is related to *HAA*, a single relation is found with an intercept near zero (Figure 50). When its slope is adjusted for 20% dry matter in the yield of tubers and 80% of the biomass in the tubers, the slope corresponds to

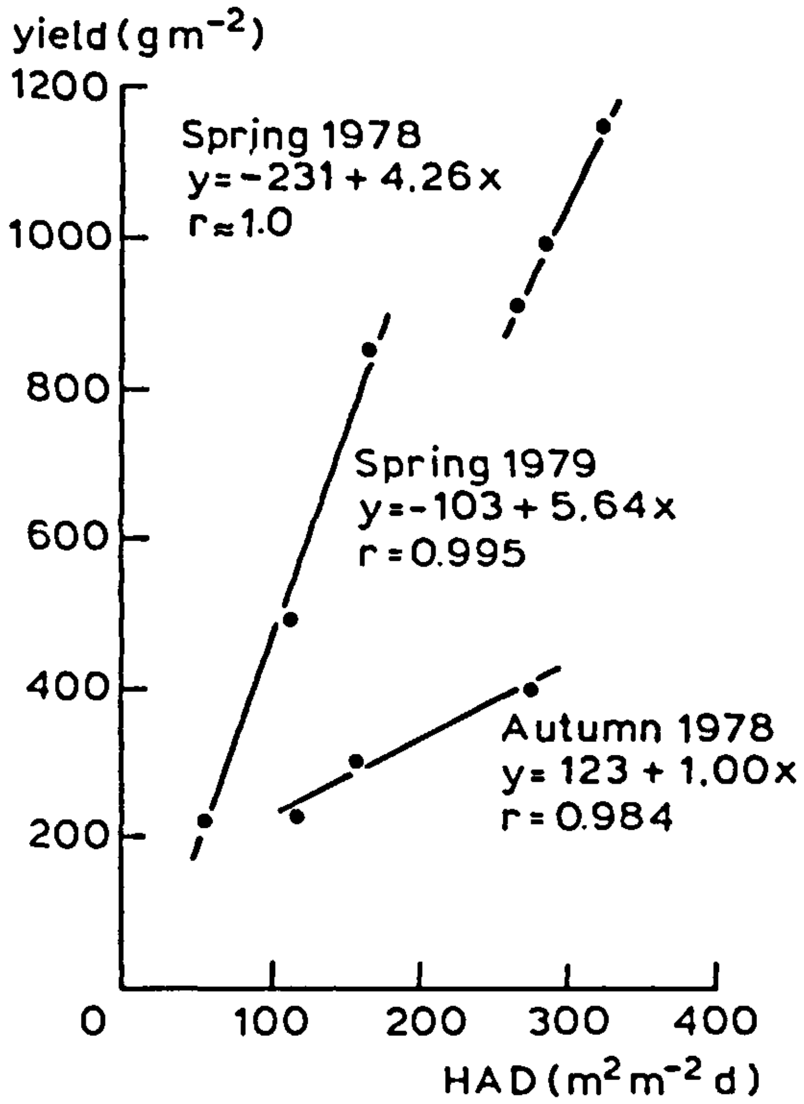

Figure 49. The Healthy leaf Area Duration *HAD* of sun and tuber yield of potatoes grown by Rotem et al. (1983a, b). *HAD* varied because of season and disease. Source: Waggoner & Berger (1987).

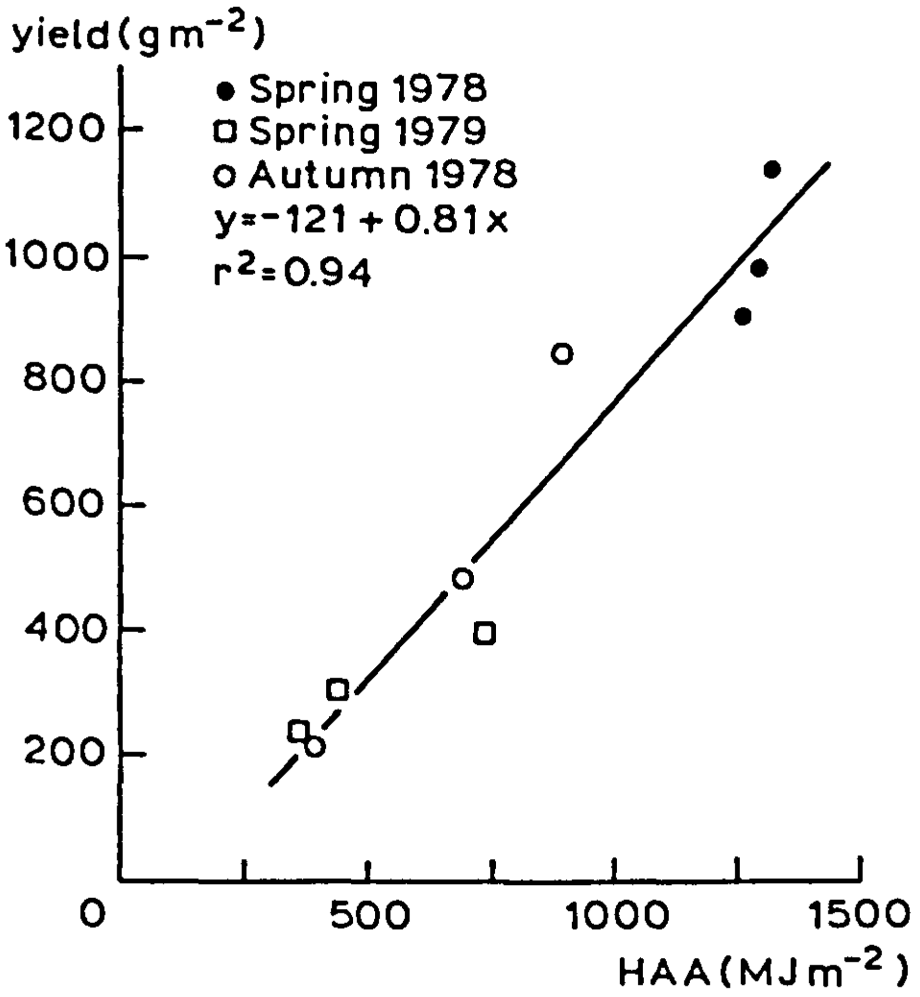

Figure 50. The Healthy leaf Area Absorption *HAA* of sun and the same tuber yields depicted in Figure 49. Source: Waggoner & Berger (1987).

an ε of 2 g MJ^{-1} (Waggoner & Berger, 1987).

Haverkort & Bicamumpaka (1986) found that 'late blight control did not significantly change the radiation use efficiency, either for total dry matter production, or for tuber dry matter production'. They encountered as much as 90% of the foliage destroyed by blight. They stated that the fraction of sun intercepted equalled the fraction of ground covered by green leaves. This statement probably means that the fraction of ground covered by diseased leaves was omitted from 'the proportion of ground covered by green leaves'. Then their 'intercepted radiation' equals $\{I(0)\, h[1 - \exp(-K_I L)]\}$ in the summary model, and their observations confirm the model.

During 1986 and 1987, Ferrandino (1989) measured disease severity and light interception in healthy and blighted potatoes. He found a decreasing return in yield for increasing *HAD*, high coefficients of linear correlation between yield and *HAA*, and no significant difference between the relations of yield to *HAA* in healthy and blighted potatoes. As important as the correlations, his estimate of 1.39 g MJ^{-1} for ε agrees with estimates from other climates, continents and cultivars. He suggested that all potatoes, diseased or healthy, have a universal value for ε.

The summary model works for a disease of maize and one of wheat with an ε of 1 to 2 (Waggoner & Berger, 1987). Griffiths (1984) found the yield of barley attacked by powdery mildew, brown rust or leaf blotch correlated with green leaf area integrated over time. Since Griffiths's variable is proportional to *HAA* or sun intercepted by healthy foliage when sun varies little and leaf area index is not great, his correlations can be taken as evidence that the summary model works.

Recalling how many ways plants can suffer, the reader will not expect that the simple summary model will fit all pests. Griffiths (1984) found little relation between green leaf area integrated over time and the losses to several diseases. His catalogue of explanations was: variations in harvest index, respiration enhanced by infection, photosynthesis lessened beyond lesions, peculiar contributions to yield by certain leaves, and changes in water and growth regulators. Nevertheless, for several diseases he found that yield followed green leaf area.

Earlier I asked you to accept Rijsdijk's as an 'evaluated and well documented comprehensive model' and my equation for *HAA* as 'conscious and guided reduction'. My equation fits some diseases. For any pest it logically removes the straightforward effects of sun, leaf area and disease area. Then we organize thinking rather than speculate sloppily about other effects.

We have established a summary model for our 'organized thinking about the possible'.

9.5 Thinking about simplification

Although the summary model is a conscious reduction, it still goes beyond the pathologist's usual severity x to the labour of measuring $I(0)$, K_I and L. Is avoiding this labour practical? Is further simplification logical?

Two parameters have been proposed to indicate yield of diseased plants. They can be thought of as simplifications of the summary model. Since they relate the yield of the diseased to a healthy crop, the first step is letting L' be the leaf area index of the healthy crop, d be the fraction defoliation and thus $L'(1 - d)$ be the leaf area index of the diseased crop. Let the derivative $\mathrm{d}W/\mathrm{d}t$ of yield be the net assimilation or photosynthesis P. Then from the summary model,

$$P = \varepsilon\, I(0)\, \{1 - \exp[-K_1 (1 - d)\, L']\}\, (1 - x) \qquad \text{Equation 28}$$

When the canopy is deep and shady and K_1 and L' are large and d small, this is approximately

$$P = \varepsilon\, I(0)\, (1 - x)$$

Because the integral of x is called the Area Under the Disease Progress Curve *AUDPC* (van der Plank, 1963), this approximation becomes

$$P = \varepsilon\, I(0)\, [1 - \mathrm{d}(AUDPC)/\mathrm{d}t]$$

The approximation says the integrated loss of yield will be proportional to *AUDPC* when K_1 and L' are large, when d is small, and when efficiency and sun are constant. But James (1974) found, '*AUDPC* was not successful for estimating losses ... because it could not distinguish between early light infections and late severe infection ...'. L' growing from small to large during a season, defoliation d increasing and sun varying all make predictions from the summary model and *AUDPC* practically and logically different.

The second simple indicator can also be an approximation of the summary model. When the canopy is shallow and sunny, K_1 or L' are small. Or, d is large. Then the summary model is approximately

$$P = \varepsilon\, I(0)\, K_1\, L'\, (1 - d)\, (1 - x)$$

Because the integral of $(1 - d)(1 - x)$ is called Area Under the Green Leaf Area Curve *AUGLAC* (Johnson et al., 1987), this approximation is

$$P = \varepsilon\, I(0)\, K_1\, L'\, \mathrm{d}(AUGLAC)/\mathrm{d}t$$

The approximation says the yield will be proportional to *AUGLAC* when the product of K_1, L' and $(1 - d)$ is small, and when efficiency, sun and L are all constant. Johnson et al. (1987) found yields correlated with *AUGLAC*. They found that the constant in the equation for *AUGLAC* differed between some pests: the line relating yield to *AUGLAC* was steeper for attack by leafhoppers than for attack by disease. They argued that the steeper slope and larger constant was evidence of variation in photosynthetic efficiency. Direct evidence that a toxin injected by the leafhoppers inhibits net photosynthesis supports their argument. Or, it would support the argument that the toxin made the fraction of the photosynthesis affected by the pest more than x. One must remember, however, that variation in $I(0)$ or L' will make the integrals for *AUGLAC* and the summary model different. Further, $(1 - d)$ affects *AUGLAC* linearly, whereas it appears in the exponent of the summary model because changes in leaf area grow less important as leaf area grows large. According to Johnson et al. (1987) this curvature of the relation between photosynthesis and *AUGLAC* explains why in some cases the regression lines do not pass through the origin. This implies that potatoes with no green leaf area would still yield tubers.

Since the summary model and *AUGLAC* have not been compared experimentally, I examined some hypothetical epidemics. Predicted yields differed most when the disease was early or the crop grew slowly. Then *AUGLAC* changed much but the summary model little because the early defoliation was multiplied by a small L' and the early x was multiplied by a small interception of sun. These hypothetical epidemics indicate that the predictions could differ practically.

The labour of measuring sun, K_I and L for the summary model seems worthwhile. Its logic and the known range of ε elevate it from the class that de Wit called the statistical blunderbuss to a class that helps organize thought about the possible.

9.6 Thinking about health versus defoliation

Since thinking about the effect of disease encompasses a spectrum of parameters with a spectrum of dimensions, a dimensionless measure is demanded. Economists with this demand use 'elasticity' (Samuelson & Nordhaus, 1985)

$$\begin{aligned} E &= \text{(per cent rise in quanity)/(per cent cut in price)} \\ &= \text{d(quantity)/quantity/d(price)/price} \\ &= \text{d log(quantity)/d log(price)} \end{aligned}$$

Elasticity allows the economist to think about the response to a change in price without worrying whether quantity is in kilograms or pounds and whether the price is in guilders or dollars. It will serve us in the same way, allowing us to encompass factors from P with its complex dimensions of g $\mathrm{m}^{-2}\mathrm{t}^{-1}$ to dimensionless parameters like K_I, L or h. Whatever the dimensions, an elasticity E of 1 means that a 1% change in the independent variable cause a 1% change in the dependent one.

The net photosynthesis P written earlier in Equation 28 and integrated into yield in Equation 27 can be rewritten as

$$P = \varepsilon h I(0) [1 - \exp(-K_I L)] = \varepsilon h I(0) [1 - \theta (I, L)] \qquad \text{Equation 29}$$

where $\theta (I, L)$ is $\exp(-K_I L)$. The mnemonic of $\theta (I, L)$ is 'transmission of sun I through a depth L of foliage'. Equation 29 is the summary model as a photosynthesis rate, which states it is the product of efficiency, sun and the fraction of the sun intercepted. In logarithms,

$$\log P = \log \varepsilon + \log h + \log[I(0)] + \log[1 - \theta(I, L)]$$

Thus the elasticity of photosynthesis P for changes in efficiency ε, sun $I(0)$ and health h is 1. A 1% change in ε, $I(0)$ or h simply changes P by 1%.

Because the response to L decreases as L grows, figuring out the elasticity of P for a defoliation of L is harder. (K_I L) can be considered a single variable called shade, indication how shady the canopy is. For example, when K_I is 0.5 and L is 4 or when K_I is 1 and L is 2, then (K_I L) is 2, and the shade is the same beneath the canopy. Values to 4 are reasonable. The elasticity of P for a change in (K_I L) is

$$E = K_I \, L \, 0\,(I, L)\,[1 - 0(I, L)]^{-1}$$

This elasticity has a maximum of about 1 when the leaf area L is very small, and it falls to only 0.3 when (K_I L) is 2. The elasticity is nearly zero when (K_I L) is very large. In other words, a 10% change in the product of leaf area and its extinction coefficient for sun will change photosynthesis 10% when leaves scarcely shade one another, about 3% in circumstances often encountered and practically none if (K_I L) is even as large as 4.

By defoliating, a disease can lessen L. Thus the relevance to pests of the elasticity of P for h and L is as follows. The h of diseased foliage adhering to the plant has an elasticity of 1, 1% worse health h always decreases photosynthesis by 1%. But the defoliation and change of L by a disease makes an elasticity of 1 only when the leaves do not shade one another; defoliation has little effect when leaves shade each other deeply.

The elasticity of the P of Equation 29 for change in (K_I L) reiterates the difference between the summary model, on the one hand, and *AUDPC* and *AUGLAC*, on the other. Whereas the elasticity of the P of the summary model falls from 1 in thin canopies to about zero in shady ones, the elasticity of *AUDPC* is always zero and *AUGLAC* is always 1.

9.7 Thinking about variable health

The summary model admits only a crop with a single h and L. Common experience teaches that disease is often more severe down in the shade of a canopy than at its top, that disease and leaf area vary over a field and that foliage is aggregated and shaded in rows. One method of coping with this heterogeneity is to use average h, L and K_I.

An average h or L may not, however, accurately predict yield. The point was made by Ferrandino (1989) by comparing the yields from two fields with 10% disease. The disease defoliates 10% of the foliage. The health h of the foliage left on the plants remains 1, and this foliage still photosynthesizes fully. Let K_I be 1 and L be 4. In the first field, defoliation is homogeneous, and all plants have lost 10% of their foliage. This makes their photosynthesis $\varepsilon \, I(0)\,[1 - \exp(-0.9 \cdot 4)]$. In the second field, defoliation is also 10%, but it is heterogeneous: 10% of the plants are completely defoliated, whereas 90% are untouched. In this heterogeneous field, photosynthesis is $\{0.9 \, \varepsilon \, I(0)\,[1 - \exp(4.0)]\}$, making the photosynthesis in the homogeneous field about 1.1-fold that in the heterogeneous one. More defoliation increases the ratio. When defoliation is nearly complete, the ratio approaches $[K_I\, L]\,[1 - \exp(- K_I\, L)]^{-1}$, which exceeds 4 in the example. The yield from a field with a few leaves on all plants could be severalfold the yield from a field with the same number of leaves concentrated on a few plants.

Foci or centres, heterogeneity or unevenness typify diseases because they are, after all, contagious. Naturally, the frequency distribution called 'contagious' by statisticians fits the distribution of lesions (Waggoner & Rich, 1981). Uneven spacing lowers yield by as much as half (Soman et al., 1987), and uneven disease severity obviously lowers yield when the curve of mean yield versus mean severity curves downward (Hughes, 1988).

I shall examine the consequences of this heterogeneity and of averaging the parameters to calculate photosynthesis, first in the dimension f from zero at the top of the canopy to L at the bottom. Then I shall examine heterogeneity over the radius r of a circular field from zero at the centre to R at the periphery.

Variability of health h and sun I with depth f and distance r are illustrated in Figure 47. Disease severity is greatest in a focus at the centre of the field, and in a graph at the top of Figure 47, the health $h(r,0)$ at the top of the canopy improves with distance r from the centre. A panel is drawn in the figure near the left margin, representing the centre of the field. In the panel, foliage area f increases downward as a depth into the canopy, reaching a maximum L at the bottom. Down depth f, sun diminishes from $I(0)$ at the top. Even at the top, health $h(r,0)$ is poor; and into the depth of the canopy it diminishes to $h(r,f)$, becoming ever smaller.

Farther along r, the total foliage L and its distribution do not change. Sun I is still intercepted with f in the same way. In the panel at the right, however, health is better at the top and at all depths than in the canopy near the centre of the field. Heterogeneity of health h is the difference with distance r shown at the top of the figure or down the depth f of the canopy shown in the panels. Along r, it could also be difference of leaf area L or difference of the extinction of h in the canopy. I begin with the difference with depth and later examine differences with distance.

9.7.1 Variation through the canopy, when h(0) is constantly 1

Since moisture usually encourages fungi and bacteria, the blight, mildew and rot usually worsen in the shade of the canopy. Recognizing this, Rijsdijk (1986) divided the comprehensive model into upper and lower strata. In the summary model, I recognize it by making h a function of f.

Let $h(0)$ be the health $h(r,0)$ at the top of the canopy, and let it be extinguished by a fraction per f. Let the extinction coefficient per h be $(c\, K_I)$, proportional to the extinction of sun. At r and f the health $h(r,f)$

$$h = h(0) \exp(- c\, K_I\, f) \qquad \text{Equation 30}$$

If c is 1, the extinction of h equals the extinction of sun, and the health h is proportional to the interception of sun, $-\mathrm{d}I/\mathrm{d}f = I(0)\, K_I \exp(- K_I\, f)$. Since energy is consumed in evaporating the water that encourages microbes, the proportionally is reasonable.

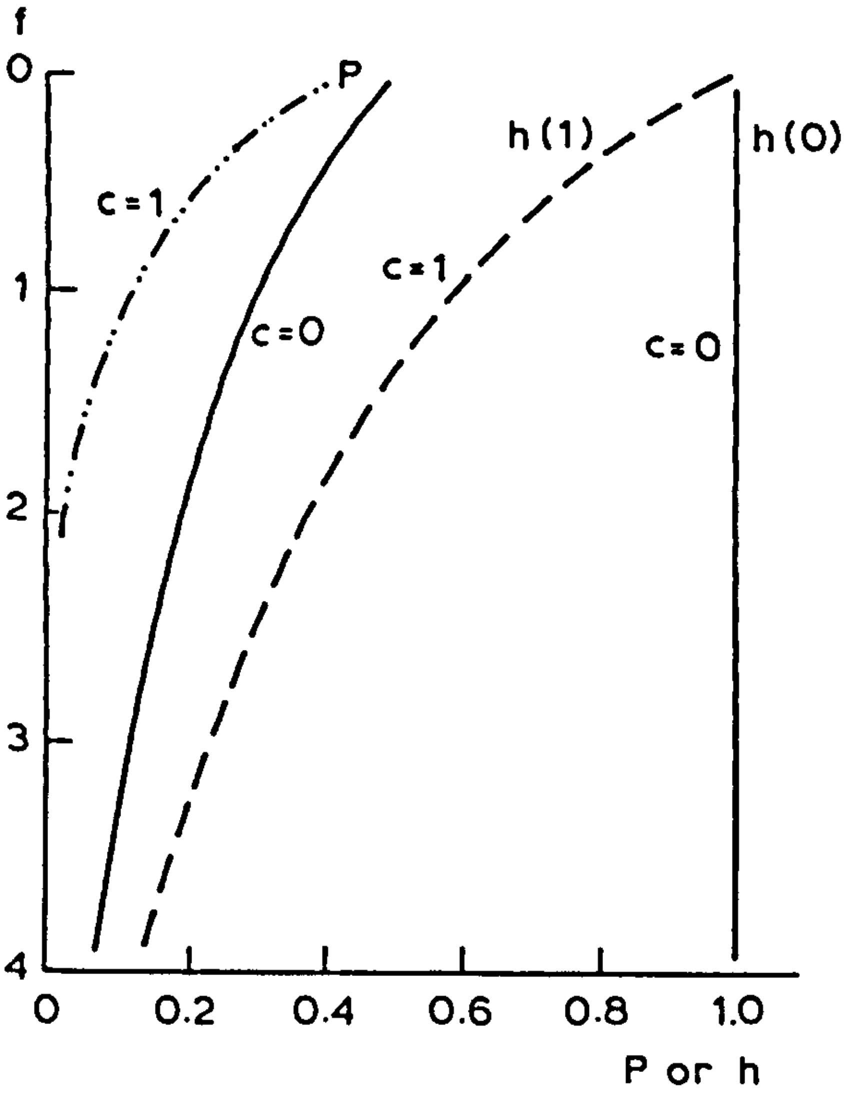

Figure 51. Profiles of the health h and photosynthesis P in a canopy of foliage when the health $h(0)$ at canopy top is 1. f is depth in the canopy and c is the ratio of extinction of healthy area in the canopy to extinction of sun. (— — —) is h in the canopy when c is 1; (——) is the photosynthesis P or $P(r,f)$ in g per land area per time per depth f in the canopy when c equals 0; (—··—) is ditto when c equals 1. The P are for unit ε and $I(0)$, and at canopy top they are 0.5, which equals K_I.

Profiles of I and h with f in the canopy were illustrated in Figure 47. For a specific c of 0 or 1 and K_I of 0.5, profiles of h are depicted in Figure 51. If $h(0)$ is 1 at the top of the canopy and if c is 0, then h is $h(0)$ or 1 from top to bottom (see vertical line on right-hand side of Figure 51). When c is 1, health declines in proportion to the interception of sun (see dashed curve in Figure 51).

The integral through the canopy of the dimensionless h times the leaf area per land area per depth is the healthy leaf area H with dimensions of leaf area per land area

$$H = h(0)\,(c\,K_I)^{-1}\,[1 - \exp(-\,c\,K_I\,L)] \qquad \text{Equation 31a}$$

Let $\theta(h,L) = \exp(-\,c\,K_I\,L)$. Analogous to the transmission $\theta(I,L)$ of the sun, $\theta(h,L)$ is the transmission of health $h(0)$ at canopy top through the depth L. Then

$$H = h(0)\,(c\,K_I)^{-1}\,[1 - \theta(h,L)] \qquad \text{Equation 31b}$$

When c approaches 0 making health uniform through the canopy, H nears $[h(0)\,L]$. The average health h_{bar} in the column is the healthy area H divided by the total area L, making it dimensionless

$$h_{\text{bar}} = h(0)\,(c\,K_I\,L)^{-1}\,[1 - \theta\,(h,L)] \qquad \text{Equation 32}$$

The h_{bar} approaches $h(0)$ when c approaches 0 because health is uniform in the canopy.

Continuing the assumptions underlying the summary model Equation 27, I turn to the photosynthesis P, the $P(r,f)$ per f at depth f in the canopy. I make it the product of the efficiency ε, of the health h from Equation 30 and of the interception of sun, $-\,\mathrm{d}I/\mathrm{d}f = I(0)\,K_I \exp(-\,K_I f)$. Consequently, this P in g per land area per time per depth is the product of efficiency, health and intercepted sun

$$P = \varepsilon\,[h(0)\exp(-\,c\,K_I f)]\,[I(0)\,K_I \exp(-\,K_I f)]$$

Let $0\,(I,h,f) = \exp[-\,(1 + c)\,K_I f]$, which is the product of the transmission of sun and health through the depth f. Then photosynthesis at depth f is

$$P = \varepsilon\,I(0)\,h(0)\,K_I\,0\,(I,h,f) \qquad \text{Equation 33}$$

which is the product of efficiency, health and sun at the top of the canopy, the rate of extinction of sun, and the transmission of sun and health.

The photosynthesis P in the canopy for c of 0 and 1 is depicted in Figure 51. When $h(0)$ is 1 and c is 0, the canopy is completely healthy. Nevertheless, the extinction of sun in the canopy causes slower and slower $P(r,f)$ down into the canopy. The photosynthesis in the foliage with c of 1 and h worsening in the canopy is a smaller and smaller fraction $\exp(-\,c\,K_I f)$ of that in the equally shaded but wholly healthy foliage.

The elasticity of $P(r,f)$ for change in K_I is $[1 - (1 + c)\,K_I f]$, showing that as the elasticity is zero in $f = [(1 + c)\,K_I]^{-1}$ the photosynthesis down to depth f speeds up with greater extinction coefficient K_I and then below that depth slows with greater K_I. For change in c, however, the elasticity of P is $(-\,c\,K_I f)$, indicating that a greater c and extinction of health slows P at all depths but especially deep in the canopy.

Integrated through the canopy, the photosynthesis $P(r)$ per land area per time at location r is

$$P = \varepsilon\,{}_0\!\int^L P(r,f)\,\mathrm{d}f$$

$$P = \varepsilon\,I(0)\,h(0)\,(1 + c)^{-1}\,[1 - 0\,(I,h,L)] \qquad \text{Equation 34}$$

where $0\,(I,h,L) = \exp[-\,(1 + c)\,K_I\,L]$, which is the product of the transmission of sun and health to the bottom of the canopy at depth L. If c is 0 and h becomes $h(0)$ because disease does not vary through the canopy, Equation 34 becomes Equation 29, the summary model for P without depth or horizontal extent. When $(K_I\,L)$ is large and the canopy shady, P is about $[\varepsilon\,I(0)\,h(0)\,(1 + c)^{-1}]$.

The growing photosynthesis P through canopies as shade $(K_I\,L)$ deepens is shown in Figure 52 for c of 0 and 1. The striking feature is the limit of $[\varepsilon\,I(0)\,(1 + c)^{-1}]$ approached by P as shade deepens. When a c of 1 extinguishes health like sun in a deep canopy, the photosynthesis of a shady and diseased canopy will be half that in a healthy one.

The elasticity is 1 for P through a column at r for changes in efficiency ε, sun $I(0)$

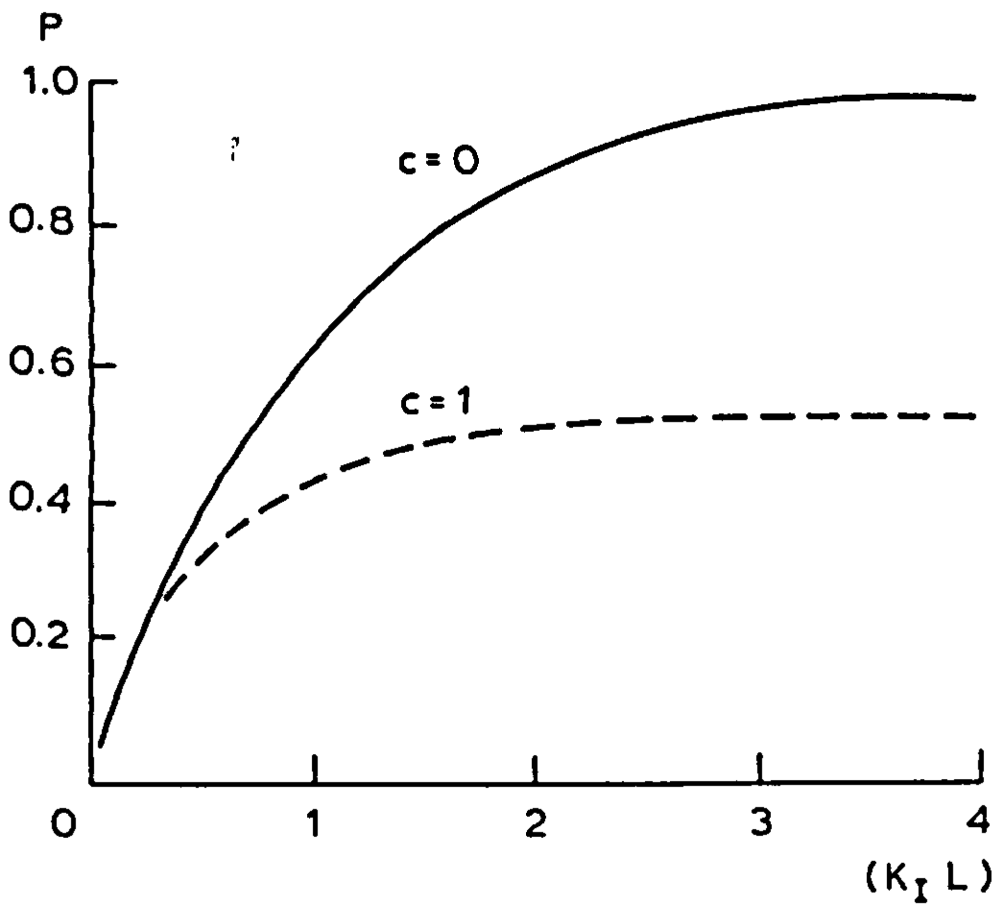

Figure 52. When the health $h(0)$ at canopy top is 1, the photosynthesis P of an entire canopy of foliage with deepening shade (K_I L). (——) is the photosynthesis of a healthy canopy with c equals 0 and h equals 1; (---) is the photosynthesis of a canopy with h extinguished within the canopy because c is 1. The P in g per land area per time are for unit ε and $I(0)$ in Equation 34. P is about $(1 + c)^{-1}$ at large (K_I L).

and health $h(0)$. Change ε, $I(0)$ or $h(0)$ by 1% and P also changes 1%.

For other changes, however, the elasticity of P is a function of c and (K_I L). For change in c, the ratio of extinction of health to that of sun

$$E = c\,\{K_I\,L\,0\,(I,h,L)\,[1 - 0\,(I,h,L)]^{-1} - (1 + c)^{-1}\}$$

In a shady canopy, the elasticity is about $-\,c\,(1 + c)^{-1}$. The change from a c of 0 and uniform health to a profile of health extinguished with depth at first diminishes photosynthesis little. By the stage of c equal to 1, however, the elasticity is − 0.5, and it approaches − 1 when c is large, extinguishing health rapidly near the top where the sun is bright.

The elasticity of P for change in shade (K_I L) is

$$E = (1 + c)\,K_I\,L\,0(I,h,L)\,[1 - 0\,(I,h,L)]^{-1}$$

For little shade (K_I L) the elasticity is nearly 1. As the slopes of the curves for P in Figure 52 indicate, however, the elasticity diminishes rapidly. When a (K_I L) of 2 is reached, the elasticity of P for increasing K_I or L is only 0.3 for a healthy canopy specified by a c of 0 and less than 0.1 for the diseased canopy when c is 1. This echoes the conclusion drawn from the summary model without depth: defoliation of shaded, diseased leaves matters little.

9.7.2 *Variation through the canopy, when the average health is contantly* h_{bar}

Beneath an $h(0)$ of 1, changing K_I, L and c mixes distribution and severity of disease. Distribution in the canopy is better evaluated by holding constant the average through the canopy rather than the health at canopy top. So I replaced $h(0)$ in Equation 33 with $h(0) = h_{\mathrm{bar}} (c\, K_I\, L)\, [1 - 0\,(h,L)]^{-1}$ from Equation 32 and held h_{bar} constant. The h_{bar} must be small enough for no h to exceed 1.

Diverse profiles of h in the canopy are illustrated in Figure 53 for an h_{bar} of 0.25. When c is 0, h is simply the average from top to bottom. When c is -0.5 the health improves from the top downward. In this case, raising K_I and thus $(c\, K_I)$ worsens health h near the top and improves it near the bottom. On the other hand, when c is 1 the best health is at the top. Then, raising K_I improves h near the top and worsens it near the the bottom of the canopy.

The photosynthesis $P(r,f)$ is per land area per time per depth. At a depth f in the canopy this P is

$$P = \varepsilon\, I(0)\, h_{\mathrm{bar}}\, c\, K_I^2\, L\, 0\,(I,h,f)\, [1 - 0\,(h,L)]^{-1}$$

When a c of 1 extinguishes h rapidly in the canopy, photosynthesis declines even faster, Figure 54. Reversing the profile of h by letting c be -0.5 makes photosynthesis much less at the canopy top where health is much worse, whereas deep in the shade of the canopy where leaves are now healthier, photosynthesis is slightly higher.

When c is greater than 0, elasticity of $P(r,f)$ can be calculated. For change in c, it

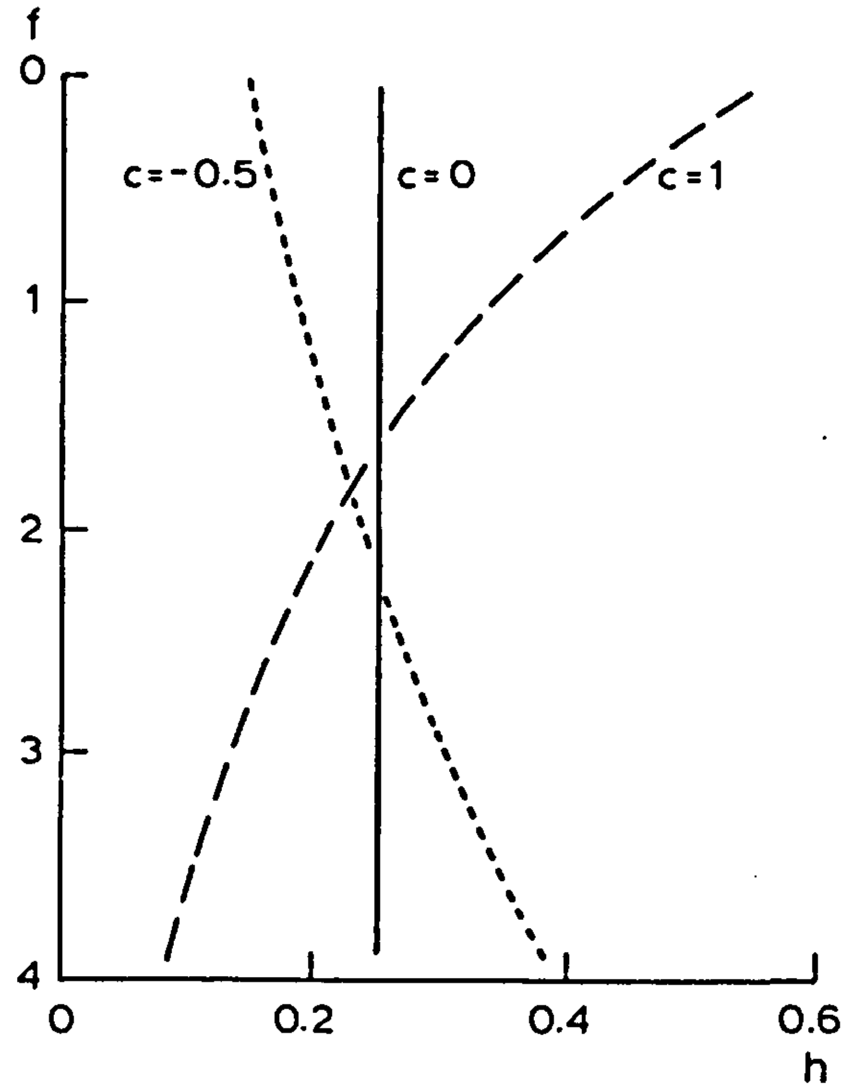

Figure 53. Profiles of the health h with depth f in a canopy when the average health through the canopy is constantly 0.25: (——) when c is 0; (– – –) when c is 1; (- - -) when c is -0.5.

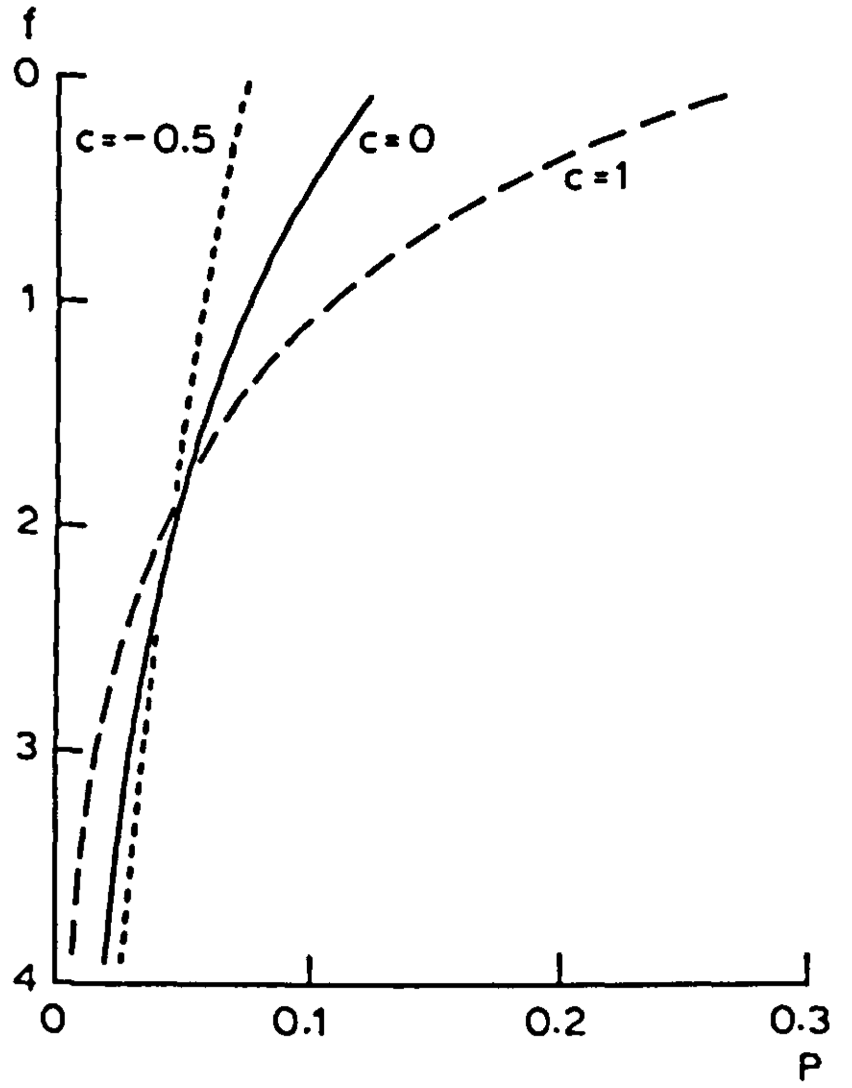

Figure 54. Profiles of photosynthesis P with depth f in a canopy of foliage when the average health through the canopy is constantly 0.25. Photosynthesis P in g per land area per time per depth f in the canopy shown by (——) for $c = 0$, (– – –) for $c = 1$ and (- - -) for $c = -0.5$. The P are calculated for $\varepsilon = 1$ and $I(0) = 1$, $K_I = 0.5$.

is nearly 1 at the top of a deep canopy. Augmenting c 1% steepens the profile of h and improves $h(0)$ to keep h_{bar} constant. Near the top, this speeds up photosynthesis about 1%, as suggested in Figure 54 by the curves for c of 0 and 1. At the bottom, elasticity is negative, and increasing c slows down the slow photosynthesis in the shade. Figure 54 shows that changing c below zero affects the profile of photosynthesis similarly.

For change in L, the elasticity of P is positive at all depths because more foliage means that more disease near the bottom of a deeper canopy is balanced by more health in the sunshine at the top. For changes in the K_I that determines interception of sun, the elasticity of P is fully 2 at the top of deep canopies and 1 at the top of shallow ones.

Through the entire canopy, the photosynthesis $P(r)$ is

$$P = \varepsilon\, I(0)\, h_{bar}\, c\, K_I\, L\, [1 - 0\,(I,h,L)]\, \{[1 - 0\,(h,L)]\, [1 + c]\}^{-1} \qquad \text{Equation 35}$$

When c approaches 0, Equation 35 approaches the summary model for P without depth or horizontal extent. In Figure 55, the photosynthesis P through the canopy when average health h_{bar} is constant is related to shade $(K_I\ L)$ and to c. For the h_{bar} of 0.25 chosen for the figure, $(c\ K_I\ L)$ cannot exceed 4 because no h can exceed 1.

The important thing is the change in photosynthesis when c, K_I and L change. (The elasticities of $P(r)$ with changes in h_{bar}, ε and $I(0)$ are 1.) When the canopy is thin and $(K_I\ L)$ small, the distribution of disease in the canopy specified by c

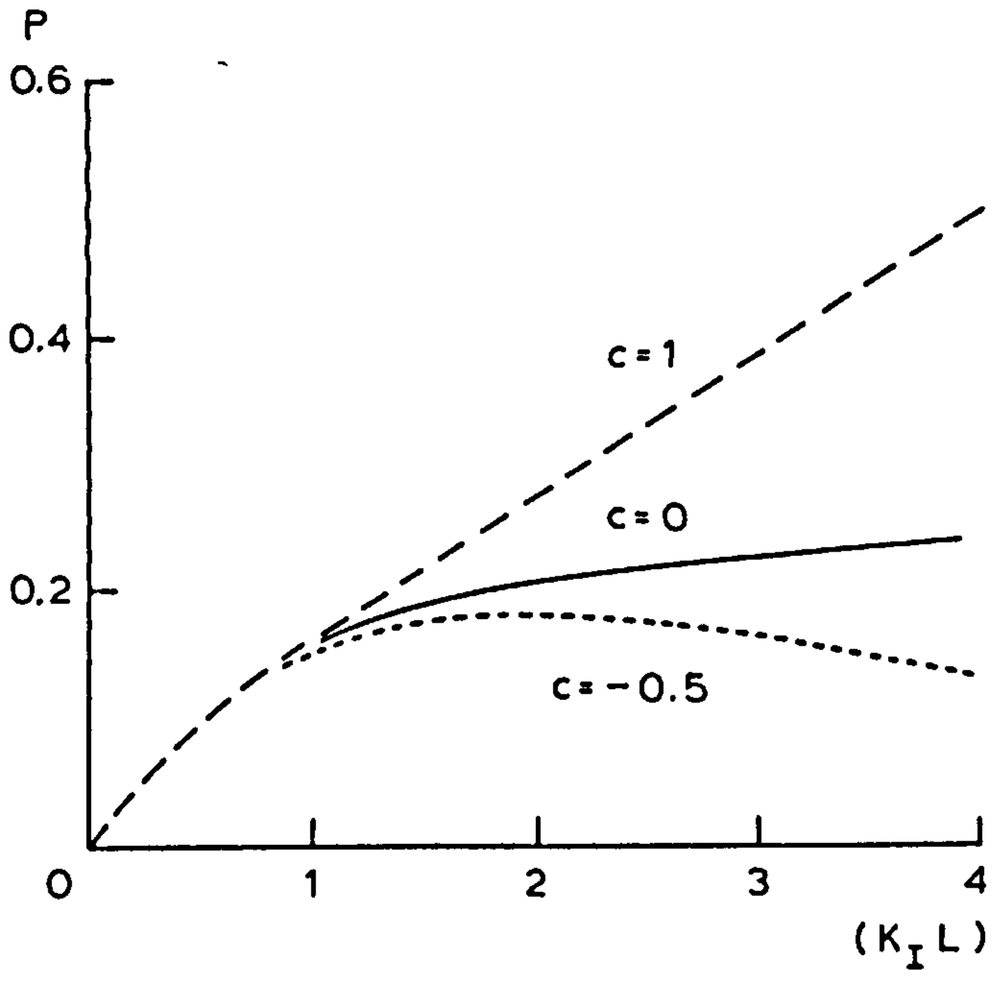

Figure 55. When the average health is 0.25 through the canopy, the photosynthesis P of an entire canopy of foliage with deepening shade (K_I L). (– – –) is photosynthesis P when h worsens with depth because c is 1, (——) is P when h is uniformly the average because c is 0, and (- - -) is P when h improves in the canopy because c is -0.5. The P are calculated for $\varepsilon = 1$ and $I(0) = 1$.

matters little as shown in Figure 55 by the convergence of the curves at small (K_I L). On the other hand, when the canopy is deep and (K_I L) large, c and the consequent distribution does matter.

When c is 1 and healthy leaves are concentrated near the top, deepening the shade (K_I L) intercepts more sunlight and speeds the photosynthesis in the column. When (K_I L) is large, the photosynthesis is about $[\varepsilon\, I(0)\, h_{\text{bar}}\, (K_I\, L)/2]$. On the other hand, when c is -0.5 and healthy leaves are concentrated well down in the canopy, deeper shade decreases the sun on the healthy leaves and thus slows photosynthesis. For c greater than 0, the elasticity of $P(r)$ for change in c can be calculated. It increases from zero at the small (K_I L) where the curves for different c converge in Figure 55 to about $(1 + c)^{-1}$ at large (K_I L). For the same average disease, the profile of disease in a shady canopy matters.

If the profile matters even when the average is unchanged, then photosynthesis reckoned from the average health can be wrong. So I calculated the ratio Φ of the photosynthesis integrated with an h varying through the canopy divided by the photosynthesis simply reckoned from average health. The error of reckoning photosynthesis from the average health is thus $(1 - \Phi)$. The photosynthesis for varying h is calculated by Equation 35. For constant h_{bar}, photosynthesis is $\{\varepsilon\, I(0)\, h_{\text{bar}}\, [1 - 0(I,L)]\}$, which can be derived from Equation 34 with c approaching zero or from Equation 29 with h_{bar} substituted for h. The ratio is then

$$\Phi = c\, K_I\, L\, [1 - 0(I,h,L)]\, \{(1 + c)[1 - 0(h,L)]\, [1 - 0(I,L)]\}^{-1} \qquad \text{Equation 36}$$

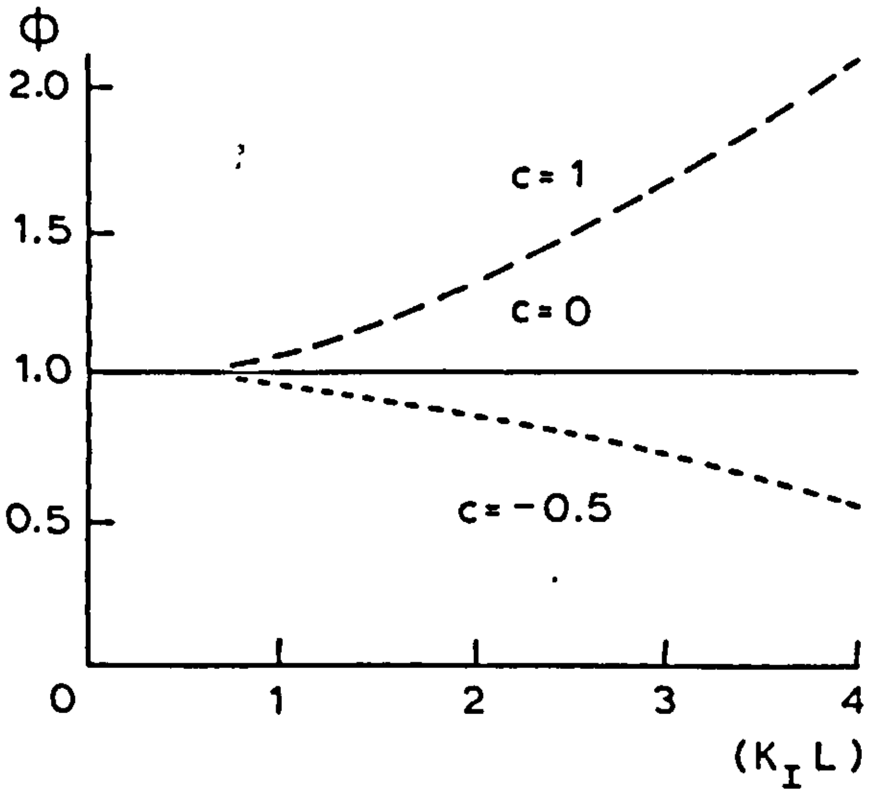

Figure 56. The ratio Φ of photosynthesis in a column of a canopy, calculated from *h* varying in the canopy divided by the photosynthesis reckoned from the average. (– – –) when *c* is 1; (——) when *c* is 0; (- - -) is Φ when *c* is -0.5.

If the canopy is very thin or if *c* is 0 and health uniform from top to bottom, the ratio in Figure 56 is 1. Average and integration give the same answer.

A shady canopy with health worsening from top to bottom because *c* is greater than zero, however, produces different answers. Figure 56 shows that a *c* of 1 causes a Φ of 1.3 when shade (K_I L) is 2 and Φ of 2 when shade is 4. That is, the integrated photosynthesis is 30% greater than that reckoned from the average when shade is 2, and it is 100% greater when shade becomes 4. When shade is deep, Φ is about $[c\ K_I\ L\ (1 + c)^{-1}]$. The elasticity for change in *c* of this approximate Φ is $(1 + c)^{-1}$: when *c* is 1 and (K_I L) is 4, photosynthesis integrated from the varying health in twice that reckoned from its average, and the multiple rises about 5% for each 10% rise in *c*.

Reverse the profile of health to specify health in the shade by the label $-$ 0.5 in Figure 56. Then the photosynthesis calculated from the varying *h* is less than that reckoned from the average.

The conclusion: when disease varies in the depth of a shady canopy, calculating photosynthesis from the average health rather than from health, depth by depth, causes large errors. The error grows with shade, and it may be either an under or over estimate, depending on the profile of health.

9.7.3 *A circular field with variation of h(0)*

When I began to examine variation, I promised to examine heterogeneity with distance *r* from the infected centre of a circular field to its periphery at *R*. Equation 30 specifying *h* at a depth *f* has ways for varying *h* horizontally as well as with *f*. First, let health *h*(0) at the canopy top be a function of *r*, improving from a focus of disease at the centre of the field as depicted at the top of Figure 47. Or, let leaf area index *L* that limits *f* or the extinction coefficient (c K_I) of *h* be functions of

r. For the present, I shall vary $h(r,0)$ with r but keep c, K_l and L constant. Later I shall vary L and c.

Varying $h(r,0)$ while keeping $(c\ K_l)$ constant made the isolines of health h in Figure 57. On the left margin of Figure 57 representing the centre of the field, $h(0)$ is zero. At an r of 1, $h(0)$ has already improved to 0.6, but at the bottom of the canopy at the same r, h is still only 0.1. At the right margin where r is 4, the health at the bottom of the canopy is still poor, but at the top $h(0)$ has improved to nearly 1. Since the health is extinguished according to Equation 30 with $(c\ K_l)$ equal to 0.5, $h(f)$ at a depth f is the same fraction of the $h(0)$ at the top of a column, whether it is near or far from the diseased centre.

In a column of foliage at distance r, the ratio $H(r,0)/h(r,0)$ of all the healthy area to the health at the top is constant. This is evident from Equations 30, 31a, and 31b with c, K_l and L constant. Further, the ratio Φ of the photosynthesis calculated by integration of an h varying through the column to that reckoned from the average is Equation 36; it is not a function of $h(0)$, and it is unchanged by changing $h(0)$.

Two laws for the extinction of disease $h(0)$ with distance from the source are the exponential and the power law. The exponential could reflect the depletion of dispersing spores by the trapping of the fraction K_r per travel r through foliage.

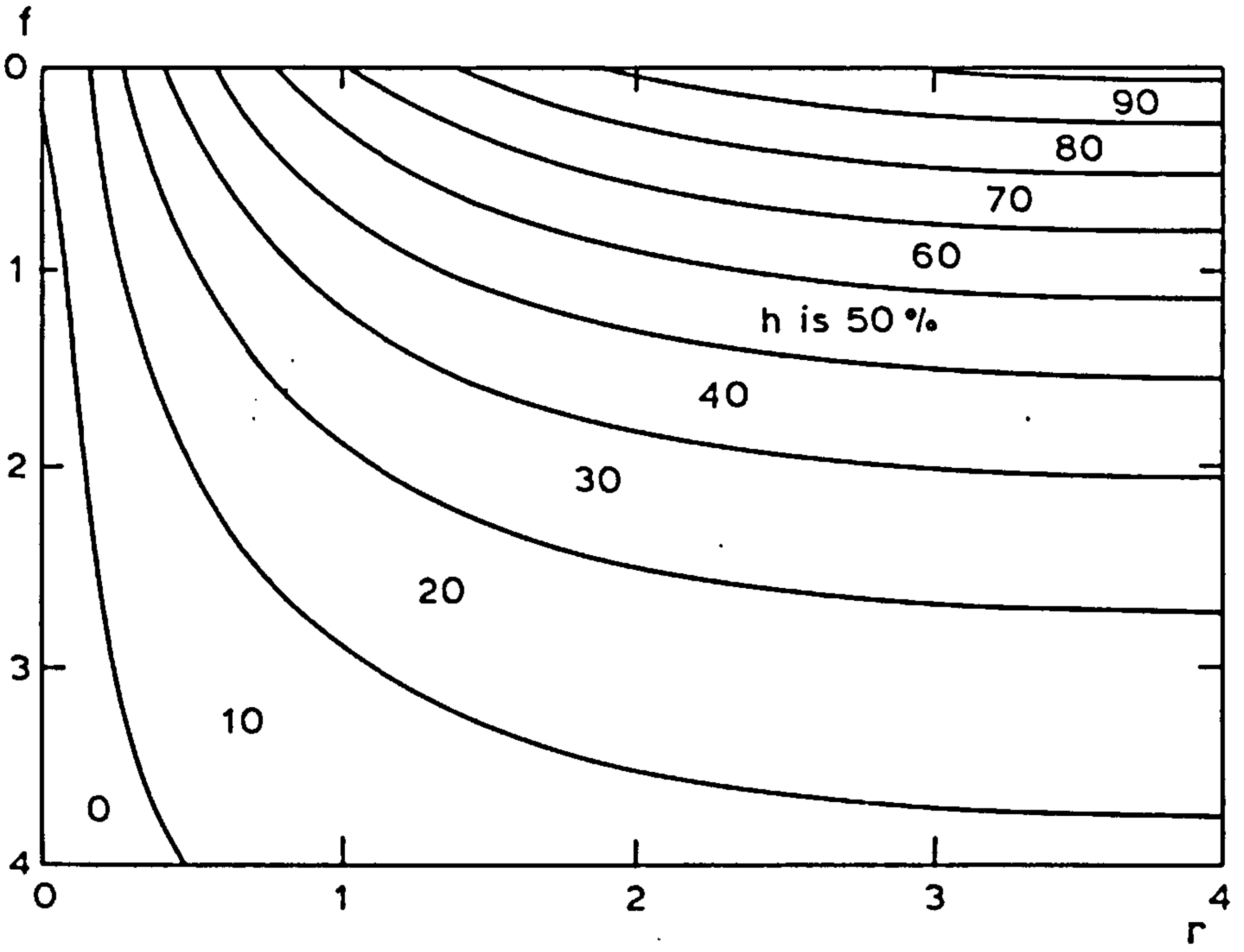

Figure 57. Isolines of health through a canopy when $h(0)$ improves with distance r from the infected centre of a circular field, when the extinction of disease in the canopy is constant. The $h(0)$ at canopy top improves according to the exponential law, Equation 37 with K_r equals 1. In the canopy h worsens exponentially because $(c\ K_l)$ is 0.5. The isolines of h are drawn from a minimum of 0.05 or 5% at the lower left to a maximum of 95% at the upper right, and the h between are shown as percentages.

The power law could reflect the expansion of a spore cloud with the n^{th} power of r and the accompanying dilution of spore concentration.

The exponential fall with an extinction coefficient K_r,

$$h(r,0) = 1 - \exp(-K_r r), \qquad r \geq 0 \qquad \text{Equation 37}$$

specifies $h(0)$ is zero at the diseased centre and approaches 1 at a great distance r. The changing $h(0)$ at canopy top in Figure 58 was calculated by Equation 37.

The power law decreases disease as the reciprocal of the power n of r.

$$h(r,0) = 0, \qquad 0 \leq r \leq 1$$

$$h(r,0) = 1 - r^{-n}, \qquad r > 1 \qquad \text{Equation 38}$$

In the central column of radius 1, the foliage is completely diseased, with health zero. Beyond, $h(0)$ improves, producing profiles of h in the canopy like those of Figure 57 wherever Equations 37 and 38 produce the same $h(0)$. Where r is $[n \log(r) K_r^{-1}]$, the $h(0)$ are equal for the two laws or equations, and the profiles are identical.

To depict the change in health and disease with distance in Figure 59, the disease $x(r,0)$ at the top of the canopy specified by the two laws is related to

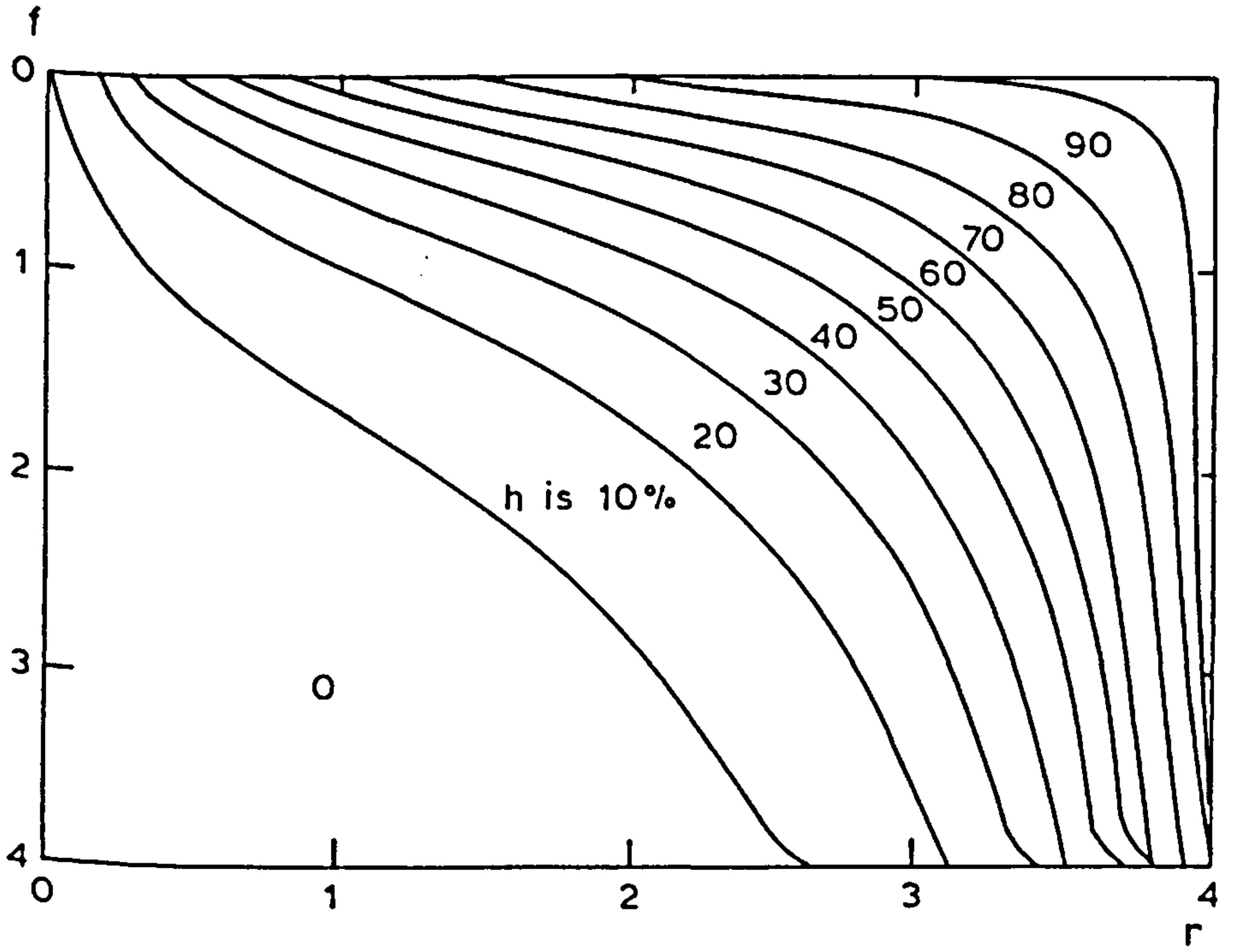

Figure 58. When the extinction of disease in the canopy varies, isolines of h through a canopy when $h(0)$ improves with distance r from the infected centre of a circular field. The $h(0)$ at canopy top improves according to the exponential law, Equation 37 with K_r equals 1. In the canopy h worsens exponentially with a c decreasing with r from 2 at the centre to 0 where r is 4. The isolines of h are drawn from a minimum of 0.05 or 5% at the lower left to a maximum of 95% at the upper right, and the h between are shown as percentages.

distance. The logarithm of disease is related to the logarithm of the distance. The coefficient K_r that extinguishes $x(r,0)$ exponentially with r is 0.25, and n was chosen to make the $x(r,0)$ equal for the two laws where r is 4.

Where r is 1, the disease $x(r,0)$ calculated from the exponential law has already decreased to $\exp(-K_r\,1)$ or about 80%, whereas according to the power law it is 100%. Then for a short way with the exponential law disease decreases more slowly than with the power law. Soon, however, disease declines more slowly according to the power law. The disease curves for the two laws cross where r is 4 because they were forced to be equal. Beyond, the disease according to the exponential law rapidly falls behind.

Turning from Figure 59 to Figure 60 is turning from disease to health at the canopy top. The $h(r,0)$ according to both laws are equal where r is 2 or 4, but between 2 and 4 the health according to the power law is better than that according to the exponential. Beyond the forced equality where r is 4, however, the $h(r,0)$ of the exponential is better than that of the power law. Whereas Figure 59 shows that the ratio of the diseases $x(r,0)$ according to the two laws diverges beyond the r of 4, Figure 60 shows that the healths $h(r,0)$ converge. According to both laws, $h(r,0)$ approaches 1 at long distance.

At far distances, the little disease specified by either law scarcely affects health at canopy top and matters little to photosynthesis. On the other hand, if one is concerned with disease x and inoculum rather than with health h and photosyn-

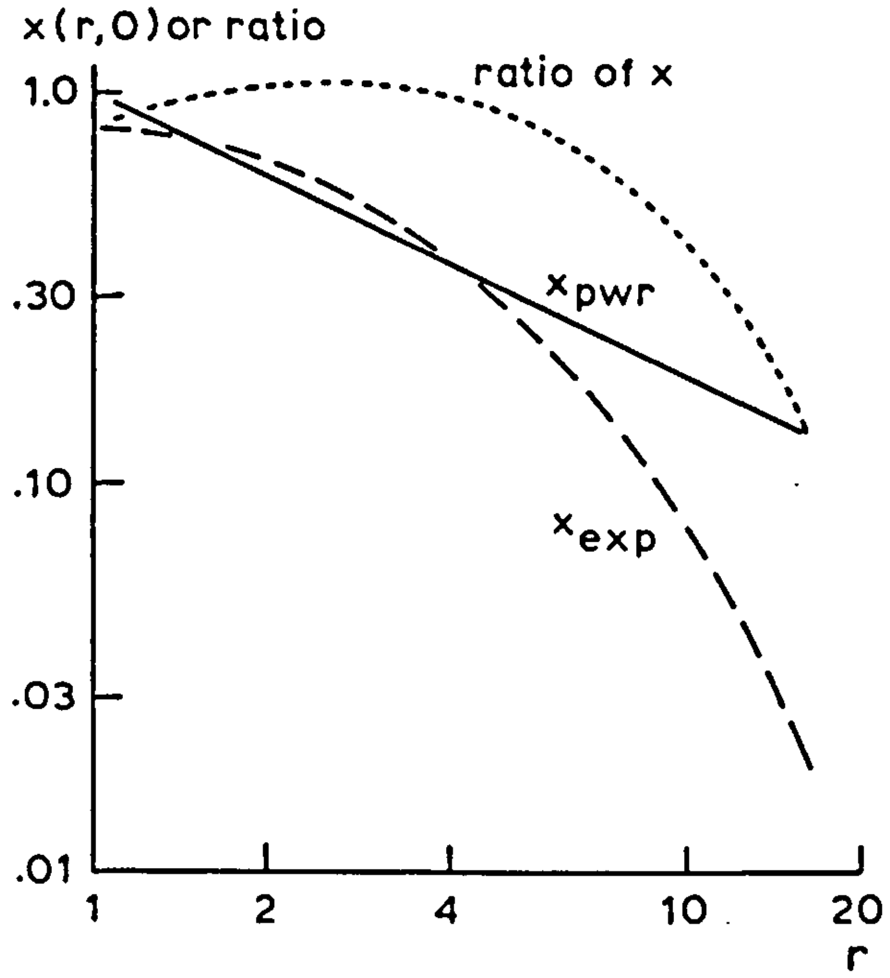

Figure 59. Disease $x(r,0)$ at canopy top decreasing with distance r according to the exponential (*exp*) and to the power (*pwr*) law and their ratio. (– – –) is the exponential fall when K_r is 0.25; (——) is the fall according to the power law when n is chosen to make the disease equal for both laws where r is 4; (- - -) is the ratio of the x according to the exponential law divided by x according to the power law. The coordinates are logarithmic.

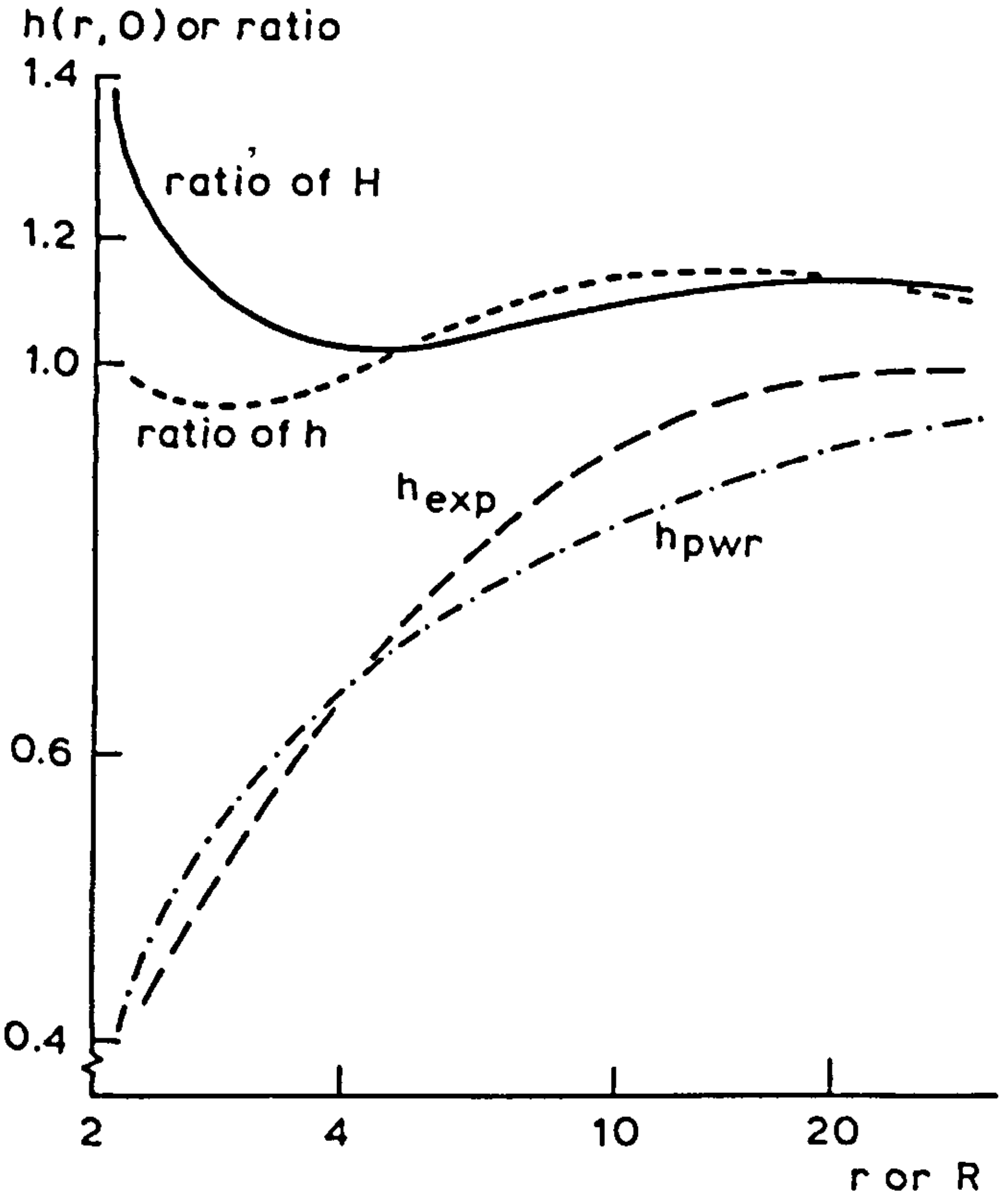

Figure 60. The improvement with distance r of the health $h(r,0)$ at canopy top, and the expansion of the healthy area H in a field with increasing radius R. (– – –) is the improvement of h with r according to the exponential law (*exp*) when K_r is 0.25; (–·–) is the improvement with r according to the power law (*pwr*) when n is chosen to make the disease equal for both laws where r is 4; (---) is the ratio of the h according to the exponential law divided by h according to the power law; (——) is the ratio of the healthy area H calculated by the exponential law to that calculated by the power law in fields of increasing radius R. The ratio of the H is S_e/S_p.

thesis, it matters. Although the disease specified by the power law is slight, its excess over that specified by the exponential law is crucial to the spread of the pathogen (Aylor, 1987). The many-fold difference in disease is emphasized in Figure 59 by a curve for the plummeting ratio of power to exponential law. In contrast, in Figure 60 the ratio of healthy areas approaches 1 at far distances.

The next subject is healthy area H rather than healthy fraction h. The healthy area H in the entire field is calculated by integrating the $H(r)$ of Equation 31b for $0 \leq r \leq R$. So H is only an integral of $h(0)$ times two terms of Equation 31b, $(c\ K_l)^{-1}$ and $[1 - 0\ (h,L)]$. Since the two terms are not functions of r, they are unaffected by the law relating $h(r,0)$ and thus H to r. Consequently, the ratio of the H for one law to H for another is merely the ratio of two integrals of $h(r,0)$. The integrals are S_e for the exponential law from $0 \leq r \leq R$ and S_p for the power law from $1 \leq r \leq R$

$$S_e = 2\pi\,\{R^2/2 - K_r^{-2}\,[1 - \exp(-K_r R)\,(K_r R + 1)]\}$$

$S_p = 2\pi\{[R^2 - 1]/2 - [R^{(2-n)} - 1]/[2 - n]\}$

The equation for S_e can be written briefly if I define the integral $S(a)$

$S(a) = {}_0\int^R r\exp(-ar)dr = a^{-2}[1 - \exp(-aR)(aR + 1)]$

Then the equation for S_e becomes

$S_e = 2\pi\{R^2/2 - S(K_r)\}$

For the exponential law, H is $\{S_e[1 - 0(h,L)][c K_l]^{-1}\}$, and for the power law it is the same except S_e is replaced by S_p.

The ratio of the healthy areas is the ratio of the integrals, S_e/S_p. Since at short r the disease specified by the exponential law is less than disease by the power law, in Figure 60 the ratio of healthy areas begins on the left greater than 1. In large fields, however, the focus of disease is a small portion of the field, H approaches πR^2, and the two laws specify about the same healthy area, making the ratio about 1. At intermediate distances, however, the exponential law specifies a greater health than the power law, and the ratio passes through a maximum before declining toward 1. In Figure 60, the K_r of the exponential law is 0.25, and the n of the power law is set to make the two $h(r,0)$ equal where r is 4. Unlike the small amounts of disease $x(r,0)$ at great distances, which grow relatively more and more different according to the two laws, and like the $h(r,0)$, which both approach 1, the sums H of the healthy area in the field grow more and more similar. In fact, the healthy area is eventually overwhelming, and both integrals approach πR^2 as R approaches infinity. When K_r is 0.25, their ratio passes through a minimum near $R = 4$ before increasing and then starting the slow decline toward 1. When K_r is 1, which is not shown in Figure 60, the ratio of the H calculated by the two laws declines steadily toward 1. Whether disease diminishes as the exponential or power law matters in the spread of disease. But it matters little in the healthy area of a large circular field with a focus of disease.

The photosynthesis P in the entire field is calculated by integrating the P of Equation 34 for $0 \leq r \leq R$. P is simply the integral S_e or S_p of $h(r,0)$ times the terms $\{\varepsilon I(0)[1 + c]^{-1}[1 - 0(I,h,L)]\}$ from Equation 34. Since these terms are not functions of r, the ratio of the P for one law to P for another is merely the ratio S_e/S_p of the two integrals (Figure 60).

Because so much hangs on S_e and S_p, their elasticities are worth knowing. In a small field, the elasticity for lengthening radius is high because adding radius adds fairly healthy area to the diseased centre, but the elasticity soon approaches 2 because area expands as the power 2 of the radius. The limit would have been 1 instead of 2 had I analysed disease diminishing from a linear source at the edge of a rectangular field rather than from the centre of a circular one.

In a field with a radius R of 4, the elasticity for change in the extinction K_r and the power n decline similarly. They both decline from nearly 1 for very small K_r or n to about 0.2 when K_r is 1 and n is the equivalent 2.88. In a field with a radius of fully 16, the elasticity for change in K_r is somewhat less than for change in n. Briefly, consider a field with disease severe in a focus at the centre and diminishing outward roughly with the inverse of a power of the distance. Or diminishing by a similar exponential fall. A 10% increase in the power or extinction coefficient that diminishes disease with distance will enhance photosynthesis 2 to 5%. Faster fall of disease with distance increases healthy area and photosynthesis – but with elasticity less than 1.

The ratio Φ of Equation 36 shows that the photosynthesis integrated through a column with health changing with depth differs from that reckoned from the average. What of photosynthesis in an entire field reckoned from its average health? Because the Φ of Equation 36 is not a function of $h(0)$, it is unchanged by changing $h(0)$. Since the photosynthesis of the entire field is simply the integral of columns of foliage with a constant Φ times the photosynthesis calculated from the average health, the photosynthesis of the whole field is simply Φ times that reckoned from the average health. The ratio Φ is unchanged by variations in $h(0)$ so long as c, K_I and L are constant. The errors of the field are the errors of the column.

9.7.4 *A circular field with variation of h(0) and L*

I keep my promise to explore the variation of L as well as $h(0)$. Let L be $(K_L\, r)$. Then defoliation is concentrated in the centre. It would be represented by a diagonal line in Figure 47 beginning at an f and L of zero at the upper left or top of the canopy and centre of the field. It would slope down to 4 at the right or periphery of the circular field. If K_L is the maximum L divided by the radius R of the field, then L expands linearly from zero at the diseased centre to the maximum L, say, 4 at the healthier periphery. The stippled areas L denoting foliage now grow from zero at the centre to 4 at the periphery.

The total leaf area in the circular field, diseased or healthy, is the integral of $[2\pi\, r\, L]$ or $[2\pi\, r\, K_L\, r]$ from $0 \leq r \leq R$, which equals $(2\pi\, K_L\, R^3/3)$. When divided by the area of the field, this becomes the average L, $(2\, K_L\, R/3)$.

With the limit on f being L equal to $(K_L\, r)$, the integral for H seems daunting.

$$H = 2\pi\, {}_0\!\int^R {}_0\!\int^L r[1 - \exp(-K_r\, r)] \exp(-c\, K_I f)\, \mathrm{d}f\, \mathrm{d}r$$

It becomes manageable if I recall defining the integral $S(a)$. Then,

$$H = 2\pi\, (c\, K_I)^{-1}\, [R^2/2 - S(K_r) - S(c\, K_I\, K_L) + S(K_r + c\, K_I\, K_L)]$$

When c approaches 0 and K_r is large, h is nearly 1 from top to bottom and centre to periphery. Then H is nearly the total of healthy plus diseased leaf area.

The photosynthesis in the field is an integral resembling that above for H. The health h at a depth f and distance r is calculated from the $h(0)$ set by r. The h times the interception of sun is integrated from $0 \leq f \leq [L = (K_L\, r)]$. The integral times $2\pi\, r$ is integrated $0 \leq r \leq R$. The result is

$$P = 2\pi\, I(0)\, (1 + c)^{-1}\, \{R^2/2 - S(K_r) - S[(1 + c)\, K_I\, K_L] + S[K_r + (1 + c)\, K_I\, K_L]\} \qquad \text{Equation 39}$$

When c is 0 and K_r is large, the P of the healthy field is about $\{\varepsilon\ I(0)\ 2\pi\ [R^2/2 - S(K_l\ K_L)]\}$.

The behaviour of photosynthesis in a field with $h(0)$ improving exponentially at canopy top while the leaf area index expands along the radius r from the focus of disease is exemplified in Table 11 by a field with a radius R of 4. The photosynthesis P is calculated for unit ε and $I(0)$.

When K_r has the large value of 100, $h(0)$ is about 1 everywhere. Then when c is 0, the average h is simply 1 as one reads in the right column of the first block in the table. Further, the photosynthesis for the entire field is 49.54, about the area times the fraction $[1 - \exp(-K_l\ 4)]$ of sun intercepted in the uniform L of 4. The photosynthesis calculated by integration through the canopy is the same as that reckoned from the average because disease is homogeneous through the canopy and across the field, and thus the ratio Φ is 1.

When K_r is smaller, first 1.00 and then 0.25 in Table 11, the disease spreads farther along the canopy top, making $h(0)$ less than 1, farther and farther from the centre. Average health worsens, and photosynthesis slows. Since c is 0, however, disease is still homogeneous vertically, and the ratio Φ remains 1.

The second block of Table 11 still pertains to a constant leaf area L. But now c is a constant 1, and health worsens with depth while it improves with distance. Average health worsens and photosynthesis slows. The Φ in Table 11 for the field is the same 2.07 shown in Figure 56 for a column with c of 1 and $(K_l\ L)$ of 4. They are the same because c and L are the same in every column of foliage in the field.

The above three paragraphs are reviews, and now we come to the effect of leaf area expanding with r at the rate K_L (from zero at the centre to 4 at the periphery) which is shown in the third block of Table 11. I compare it with the second block, which has the same extinction of health in the canopy at $(c\ K_l)$. A third of the foliage is lost. Since more leaves are lost from the unhealthy regions near the centre and low in the canopy, average health is improved. For the same reason, photosynthesis is slowed little by the defoliation. The combined effects of improved average health and somewhat less photosynthesis cause the estimate of photosynthesis from average health to be nearer that from integration, which makes the ratio Φ less. Although the ratio varies slightly with different K_r, it never departs much from the 1.53 in a column with $c = 1$ and an L equal to the average in the field. The loss of shaded, diseased foliage does not matter much.

A glance at Equation 39 shows that deriving elasticities analytically will be difficult. Instead, I calculated elasticities numerically for 10% changes near $c = 1$, $K_r = 1$ and $K_L = 1$. Expanding leaf area by increasing K_L 10% speeds photosynthesis less than 1%. Again, the loss of shaded, diseased foliage matters little.

Table 11 shows that the ratios Φ of photosynthesis calculated from integrations are 1.5 to 2.0 times that reckoned from average health. Averaging underestimates photosynthesis and, presumably, yield. The error worsens with improving health, because of faster extinction K_r of disease with distance. It remains, however, much the same as already expected from the c and a column with the mean leaf area. Averaging leaf area after averaging through the column affects the third block in

Table 11. The average health h_{bar}, photosynthesis P and the ratio Φ of (photosynthesis calculated by integration) divided by (photosynthesis reckoned from average) in fields of radius 4 when sun is intercepted with K_l of 1. The disease $x(r,0)$ at canopy top decreases exponentially with distance r from the centre at rate K_r. The photosynthesis is calculated for unit c and $I(0)$. When h is homogeneous in the canopy because c is 0 and $h(0)$ is 1 and because L is 4, P is the area of 50 multiplied by the interception of sun $[1 - \exp(-4\ K_l)]$.

K_L	c_0	K_c		K_r		
				0.25	1.00	100.00
Disease homogeneous with depth						
–	~0	0	h_{bar}	0.47	0.89	1.00
			P	23.41	43.90	49.54
			Φ*	1.00	1.00	1.00
Constant c and L						
–	1	0	h_{bar}	0.12	0.22	0.25
			P	11.93	22.39	25.25
			Φ**	2.07	2.07	2.07
L expanding with r but c constant						
1	1	0	h_{bar}	0.16	0.30	0.33
			P	11.68	21.83	24.34
			Φ^{+}	1.53	1.53	1.57
Decreasing c from c_0 at centre of field but L constant						
–	2	0.50	h_{bar}	0.24	0.42	0.45
			P	16.50	29.84	32.65
			Φ^{++}	1.39	1.44	1.46

The Φ in the table are for the entire field. The Φ for a column (Equation 36) for the several cases are: * for c is 0, 1; ** for c is 1 and L is 4, 2.07; + for c is 1 and average L is 2.67, 1.53; ++ for average c is 0.67 and L is 4, 1.75.

Table 11, but not much, because the lost foliage contributed little photosynthesis.

9.7.5 *A circular field with variation of h(0) and the profile of health in the canopy*

The isolines show the consequences of constant c and K_l extinguishing the health in the canopy to a constant fraction of the $h(r,0)$ all along the radius depicted in Figure 57. Figure 58 shows another pattern. The health $h(r,0)$ at the top still worsens with distance in the same way, and L is constant. In the new pattern, however, health is extinguished rapidly with depth near the source where health is poor. At the right margin where r is 4, however, the canopy is healthy throughout its depth. Making c a function of r changed the pattern. That is, I let c be $(c_0 - K_c r)$. I let c_0 and thus the c in the centre be 2; and I let K_c be 0.5, reducing c to zero at the periphery where r is 4.

Following a now familiar course, I obtained the healthy area H in the entire field by integrating the product of the health $h(r,0)$ at the top times the extinction in the canopy, first through the depth L and then over the area of the field of radius R. This time, however, the extinction coefficient of h is the function of r, $[(c_0 - K_c r) K_l]$. Integration through f is easy but over r is hard, leaving me to integrate the following by the method of Runge-Kutta:

$$H = 2\pi\, {}_0\!\int^R \{r[1 - \exp(-K_r r)][1 - \exp(-(c_0 - K_c r)K_l L)][K_l(c_0 - K_c r)]^{-1}\}\,\mathrm{d}r$$

Equation 40

The average health h_{bar} in the field is H divided by $(\pi R^2 L)$.

The photosynthesis P in the field is $\varepsilon I(0)$ times an integral like Equation 40, but $(c_0 - K_c r)$ is replaced by $(1 + c_0 - K_c r)$. Numerical integration made the quantities in the last block in Table 11. The accuracy is demonstrated by the numerical integral of 49.54 in the upper block of the table versus the analytical answer of 49.34, area times interception of sun.

The effect of varying c rather than keeping it constant is illustrated by two blocks in Table 11. In the second block c is 1 everywhere, whereas in the bottom block the c is $(c_0 - K_c r)$, which decreases linearly with distance r beginning at c_0 at the centre of the field (i.e. c falls from 2 to 0). The second block has profiles of health decreasing to constant fractions of $h(0)$ at constant depths, like those in Figure 57. The bottom block has the changing profiles shown in Figure 58. The changing c in Figure 58 improves health through the large volume of foliage far from the centre. This improves average health despite the faster extinction of health in the canopy near the centre. Photosynthesis is also speeded, but not as much as average health.

Changing the parameters 10% near $K_c = 0.25$, $c_0 = 1$ and $K_r = 1$, I found the following elasticities. Flattening all profiles 10% by decreasing c_0 boosts photosynthesis by 8%. Hastening the flattening with distance by increasing K_c 10%, boosts photosynthesis by 5%.

The photosynthesis integrated throughout the field is finally compared with the photosynthesis reckoned from the average health and from the average c of 0.67. Their ratio is about 1.4 as shown in the last line of Table 11. For a column with c of 0.67 rather than the whole field, the ratio is 1.75. Thus, unlike defoliation near the focus of disease, the flattening of profiles with distance affects the error of using an average health. In the example, it lessens the error below 75% but leaves it about 40%.

9.8 The summing up

So far, we see that C.T. de Wit's career has progressed from 1949 and IJssel water, and 1953 and a theoretical treatment of practical fertilizers. In 1958, it progressed through entrammelling complications to the summary model of assimilation proportional to sun. During intervening years his career gave us a school of theoretical ecologists, and it gave us comprehensive simulators.

Coming full circle, his career arrived in the 1980s at summary models that are simple because of conscious and guided reductions of comprehensive ones. It arrived at summary models that are theoretical in embodying principles but practical in their simplicity. De Wit became the eponym of models of crops.

Optimists see the half left in the bottle. Pathologists should see the healthy leaves still on the crop. Using a summary model, they can often calculate yields from the remaining leaf area and its health. What matters is the Healthy Area Absorption, the *HAA* of sun by leaves.

The theoretical foundation is simply that plants grow by absorbing sun in their leaves, which energizes photosynthesis in the healthy ones with an efficiency undiminished by pests.

The simple summary model built on this transparent and theoretical base organizes thinking about the possible. One can reason, for example, about approximations by still simpler models. Since yield is an integration of a season, a correlation between the yield lost to disease and the simple integral of disease severity alone can be destroyed by changing sun and leaf area. Similarly, the correlation between the yield and the product of leaf area and disease can be destroyed by changing sun and leaf area or by a large leaf area.

One can also think about estimating yields from averages. If health is extinguished like sun in the canopy, making a profile of health, the photosynthesis of an entire shady canopy is underestimated from average health. The flattening of the profile in part of a field, of course, diminishes the underestimation. Defoliation in the least healthy part of the field has little effect on the underestimation.

Concentrating on disease severity rather than the remaining healthy foliage, neglecting the change in sun and calculating the effect of disease from averages may sometimes be wrong. Summary models that are theoretical in embodying principles but practical in their simplicity seem generally right. They seem right whether they are de Wit's proportionality between sun and assimilation or the related summary model of healthy area absorption. They are organized thinking about the possible.

9.9 Symbols used

Symbol	*Units*	*Definition*
Field	m^2	Area of field
Land	m^2	Land area
Leaf	m^2	Leaf area
c	1	Ratio (extinction of healthy area in the canopy) to (extinction of sun)

d	1	Fraction defoliated
f	m^2m^{-2}	Depth in the canopy measured as leaf area index from zero at the top to L at the bottom (Leaf/Land)
h	1	Health, the fraction of healthy leaf area
h_{bar}	1	Average health h in column or field
r	m	Distance from centre of circular field
x	1	Disease severity as fraction (1-h) of diseased leaf area
t	d	Time (in days)
E	1	Elasticity or relative change in one factor with change in another
H	m^2m^{-2}	Healthy leaf area in a column of foliage (Leaf/Land)
H	m^2m^{-2}	Healthy leaf area in a field (Leaf/Field)
I	$MJ\ m^{-2}\ d^{-1}$	Insolation or simply Sun (MJ/Land/time)
L	m^2m^{-2}	Leaf area index through canopy (Leaf/Land)
P	$(g\ m^{-2}d^{-1})/f$	Photosynthesis per depth f in a column (g/Land/time/f)
P	$g\ m^{-2}d^{-1}$	Photosynthesis integrated through a column of foliage (g/Land/time)
P	$g\ d^{-1}$	Photosynthesis integrated throughout a field (g/time)
R	m	Radius of field
$S(a)$	m^2	An integral of a in a field (Land)
S_e	m^2	An integral of h at canopy top varying as the exponential law (Land)
S_p	m^2	An integral of h at canopy top varying as the power law (Land)
W	$g\ m^{-2}$	Yield (g/Land)
ε	$g\ MJ^{-1}$	Efficiency of photosynthesis
θ	1	Transmission of I or h to depth f or L
Φ	1	Ratio (photosynthesis calculated by integration over the variation) to (photosynthesis reckoned from an average)

Coefficients

c_o	1	c at the centre of the field
K_I	m^2m^{-2}	Extinction of sun by f (Land/Leaf)
K_c	m^{-1}	Increase of c per distance from the centre of the field (1/Length)
K_L	m^{-1}	Increase of L per distance from centre of the field (1/Length)
K_r	m^{-1}	Extinction of disease at canopy top by distance from centre of the field (1/Length)

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10 The bridge function of production ecology in pest and disease management

R. Rabbinge, W.A.H. Rossing and W. van der Werf

10.1 Introduction

There are several ways which pests or diseases affect physiological processes in plants and cause yield loss and damage. They may for example, reduce crop stands by elimination of plants, reduce inputs such as light, carbon dioxide and water, interfere with transportation of assimilates or nutrients and remove or consume previously produced structural material. These effects can be quantified in the laboratory under well defined conditions. The quantified relations at process level may be integrated in simulation models that are used to provide insight in yield loss at the field level. Eventually, these simulation models enable quantification of growth and yield reduction under various circumstances. This may help to define damage thresholds that depend on yield expectation and change in time. This chapter shows how such a process may take place.

10.2 Factors that define, limit and reduce crop growth

Crop growth, the accumulation of dry matter and its distribution among various crop organs, is determined by irradiation, temperature and the physiological, phenological, optical and geometrical characteristics of the crop, provided that water and nutrients are abundantly available and pests, diseases, weeds and any other factors that reduce crop growth are absent. Under these conditions, the growth of the crop is entirely governed by these characteristics and by the prevailing weather (mainly incoming radiation and temperature). Such a situation is, however, rare since the great majority of agricultural crops (> 99%) suffers from water and/or nutrient shortage and by pests, diseases and weeds.

The distinction in crop growth situations proposed by de Wit & Penning de Vries (1982) may be helpful to illustrate this. When water and nutrients are abundantly available, crop growth is fully determined by factors that define crop growth and by the prevailing weather. According to the calculations de Wit presented more than 20 years ago, crop growth may reach values between 150–350 kg dry matter per ha per day under Dutch conditions. The rule of thumb of 200 kg ha^{-1} day^{-1} is the simplest and in very many cases most adequate model of crop growth.

When water is limiting or nutrients are not abundantly available, other production situations are reached. Table 12 gives the four Production Situations, together with some characteristic yield levels. For computation of these values, a typical transpiration coefficient of 300 kg transpired water per kg dry matter

Table 12. The four Production Situations proposed by de Wit & Penning de Vries (1982).

Production Situation	Limiting factor	Growth rate × period	Total dry matter production in a growing season, under Dutch conditions (kg ha^{-1})
1	radiation (growth rate), temperature (length of growing period)	200 kg $ha^{-1}d^{-1}$ × 100 d =	20000
2	water, e.g. 300 mm available; transpiration coefficient 300 kg H_2O per kg dry matter	ca. 200 kg $ha^{-1}d^{-1}$ × 50 d =	10000
3	nitrogen, e.g. 50 kg N ha^{-1} available; lower limit 1 % N in total dry matter		5000
4	phosphorus, e.g. 1.5 kg P ha^{-1} available; lower limit 0.05 % P in total dry matter		3000

produced was used, in combination with minimum concentrations of nitrogen and phosphorus of 1 % and 0.05% on dry weight basis. The situations indicated in Table 12 seldom occur in this schematic form. Water may be so limiting that total dry matter production is lower than in Production Situation 4, so the indicated situations are merely guidelines. In practice many other sets of conditions may be encountered.

Crop growth is usually limited by various factors during part or all the growing season. On top of that, growth-reducing factors may be present. The consequences of pests and diseases may differ considerably in various Production Situations. For example, cereal aphids cause a yield loss of circa 300 kg grain ha^{-1} when yields are circa 5000 kg grain ha^{-1} and aphid density is 15 aphids $tiller^{-1}$ at flowering, whereas the same aphid density results in a yield loss of circa 1000 kg grain ha^{-1} at a yield of 8000 kg grain ha^{-1}. The explanation for this phenomenon is given below. Other diseases do not cause such a superproportional effect but have a proportional or even subproportional effect on yield loss with increasing yield (Rabbinge, 1986).

In order to explain this, growth reduction and yield loss must be analysed in detail.

10.3 Crop condition and pests and diseases

Many studies in crop protection consider the effect of crop condition on various components of the population dynamics or dispersion of pests and diseases, but ignore yield losses.

Crop condition, often expressed in nitrogen content, affects various epidemiological parameters; for example, the latency period, infectious period and intrinsic rate of increase (number of daughter lesions per mother lesion per day) of powdery mildew on wheat. As a result, the upsurge of an epidemic may be accelerated in well fertilized wheat fields, whereas at low nitrogen contents, which usually result in very low yields, the disease hardly develops.

In many pests similar reactions to growth circumstances are found, e.g. yellow rust (stripe rust), leaf rust, cereal aphids in wheat, and spider mite, apple scab and mildew in apple. The presence of such a reaction to crop condition should be taken into account in decision-support systems for crop protection. For example, epidemiological parameters dependent on crop conditions were introduced in the EPIPRE system which was developed and implemented in cereal production in the Netherlands and other European countries in the 1980s. Thus the model calculations on population dynamics in EPIPRE are tailored to the specific characteristics of the individual field as expressed in expected yield.

The dispersion of pathogens may vary, depending on crop condition. A crop that is dense because water and nutrients are readily available has a geometrical structure that prevents an intensive diffusion of spores. Studies have been done to quantify the consequences of crop condition on pest and disease development. Their results are rarely used in pest and disease management. However, our quantitative understanding of these aspects of pest and disease development is very limited at present.

10.4 Yield loss and yield levels

Factors that reduce crop growth have always played a role in agriculture, but the way they are approached has changed considerably in the last 20 years. Technological advances have produced various preventive and curative measures to eliminate the effects of factors that reduce crop growth. The concept of economic injury level was introduced in the late 1950s. Until then, pest and disease control was carried out whenever symptoms were present or when farmers intuitively decided that it was necessary. Preventive control by breeding and by agronomical hygiene was promoted and generally accepted.

The emphasis on preventive measures was continued and in addition other control measures were developed, using fixed economic injury levels. These economic injury levels presume fixed relations between density of the pathogen and yield loss or damage. It is assumed that the production situation does not affect the level of damage, in other words that there is a fixed proportional relation between yield and damage (fixed percentage damage).

Whereas this assumption may hold for many leaf pathogens that affect crop growth only through reduction of leaf area it may be too simple when other processes are affected. The fact that damage caused by cereal aphids increases disproportionately with yield may illustrate this. Therefore, when in the early 1980s appropriate agronomical measures enabled yields (especially in well-endowed regions) to approach potential levels, it was necessary to introduce flexible economic injury levels for pests and diseases taking into account crop growth rate and yield level. It was possible to develop these flexible economic injury levels as more knowledge and understanding of the nature of crop growth reduction and damage became available. Thus, no fixed relations between disease/pest intensity and yield loss need to be used in pest and disease management. Pest and disease management can now be tailored to the specific circumstances of individual fields and can vary in time. Thus, pesticide use can be limited and efficiency of inputs per unit of output can increase considerably. Such an objective is attractive both from an agricultural point of view and for environmental reasons.

10.5 Effects of pests and diseases on crop growth

Various pests or diseases may affect different basic processes that govern growth, as illustrated in Table 13 (an amended version of the diagram presented by Boote et al., 1983). They may, for example, reduce crop stands by elimination of plants, reduce inputs such as light, carbon dioxide and water, interfere with transportation of assimilates or nutrients and remove or consume previously produced material. Different crop growth components may be affected. The rate of biomass increase is affected by tissue consumers such as lepidopteran larvae or leaf beetles. Assimilation rate may be affected via a reduction of leaf area or light absorption or via effects on water and nutrient relations.

Leaf consumption and leaf senescence caused by leaf miners, spider mites, aphids, leaf pathogens or air pollutants affect leaf area and thus the assimilation rate. Weeds, other competing plants, perthotrophic and saprophytic fungi steal light and thereby affect absorbed light, thus reducing the assimilation rate. Aphids, root-feeding coleopterans and various bacteria affect the turgor of plants, by reducing the availability of water, hence causing stomatal closure and a decrease in assimilation rate.

Many aphids and other phloem sap feeders affect the ratio of various elements such as N, P and K. This influences assimilation rate because the functioning of chloroplasts or various steps in the photosynthesis process are affected.

The growth rate per organ may be affected by changes in partitioning coefficients caused by disrupted functional balances in the plant as a result of infestation by nematodes. The conversion of assimilates into structural crop components may be affected by selective consumption of assimilates, for example by aphids. Finally, the leaf area index may be affected by influences on the specific leaf area because the presence of viruses or other leaf pathogens induces suberization or extra parenchymal cell layers.

Table 13. The effects of pests and diseases on crop growth.

Crop growth component	Damage mechanism	Agent of damage
a. rate of biomass increase	tissue consumption	lepidopteran larvae, leaf beetles.
b. assimilation rate: effects via		
• leaf area	leaf consumption, senescence promotion	leaf miners, spider mites; aphids, many leaf pathogens, air pollutants;
• incident light	light stealing	weeds, competitors, perthotrophic and saprophytic fungi;
• water	turgor reduction	aphids, root-feeding coleopterans, bacteria;
• N/P/K	phloem sap uptake	aphids.
c. growth rate per organ:		
• assimilate partitioning	functional balance disruption	nematodes;
• assimilate conversion	assimilate consumption	aphids.
d. leaf area index	reduction of specific leaf area	viruses, various leaf pathogens.

Table 13 is not comprehensive, it merely illustrates how damage mechanisms induced by various pests and diseases affect different crop growth components. The consequences for crop growth may differ considerably, depending on the stage of crop development during which the disease is present, or on the conditions for crop growth, which are dictated by the factors that define and limit crop growth. The examples discussed below will illustrate this.

10.6 Beet yellows virus

Beet yellows virus was a major leaf disease in the 1950s in virtually all sugar beet growing areas. Since then the disease has declined in importance because of improved plant hygiene and agronomical measures and the reduced importance of fodder beet. Virus yellows can be caused by two different viruses: beet yellows virus (BYV), which belongs to the closterovirus group, and beet mild yellowing virus (BMYV), which belongs to the luteovirus group. The epidemiology of the disease has been studied since the early 1950s. Recently, van der Werf (1988) showed that the rate of within-field spread of these viruses depends on crop growth stage at time of infection and environmental conditions. The complement to this epidemiological research is research on the relations between damage and crop growth and environmental conditions (van der Werf et al., in prep.).

BYV reduces crop growth through four components:

- reduced leaf area index
- reduced light absorption
- reduced photosynthesis (both light use efficiency and photosynthesis at light saturation are affected)
- increased respiration.

In Figure 61 it is shown how the leaf area index of an early infected sugar beet crop (5 June) is strongly reduced whereas the leaf area index of a late infected sugar beet crop (14 July) is scarcely affected. Leaf area index is reduced by virus infection because specific leaf weight increases as a result of the accumulation of sugars and starch and of changes in the morphological structure of the leaves. The later the infection the smaller the effect as leaves which have appeared before the plant contracts infection are not invaded by the virus via the phloem pathway.

The leaves of the sugar beet already show a slight change in light absorption at relatively low infection levels and before clear symptoms are visible. Both reflection and transmission of radiation are affected. More light is reflected and

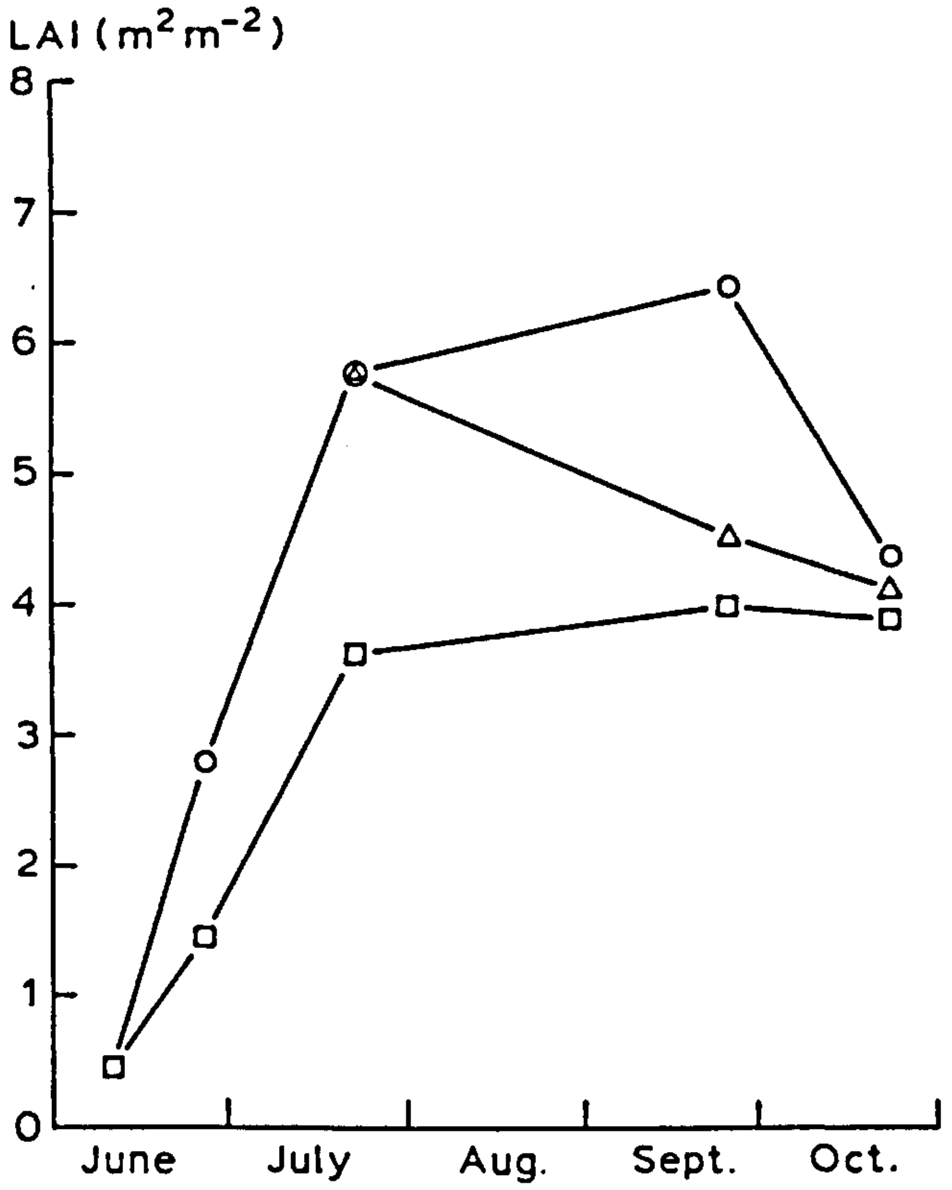

Figure 61. Leaf area index of healthy sugar beet (o) and beet infected with BYV on 5 June (□) or 14 July (△). Ten representative plants were examined on 11 and 27 June and 23 July, five on 18 September and seven on 24 October, respectively.

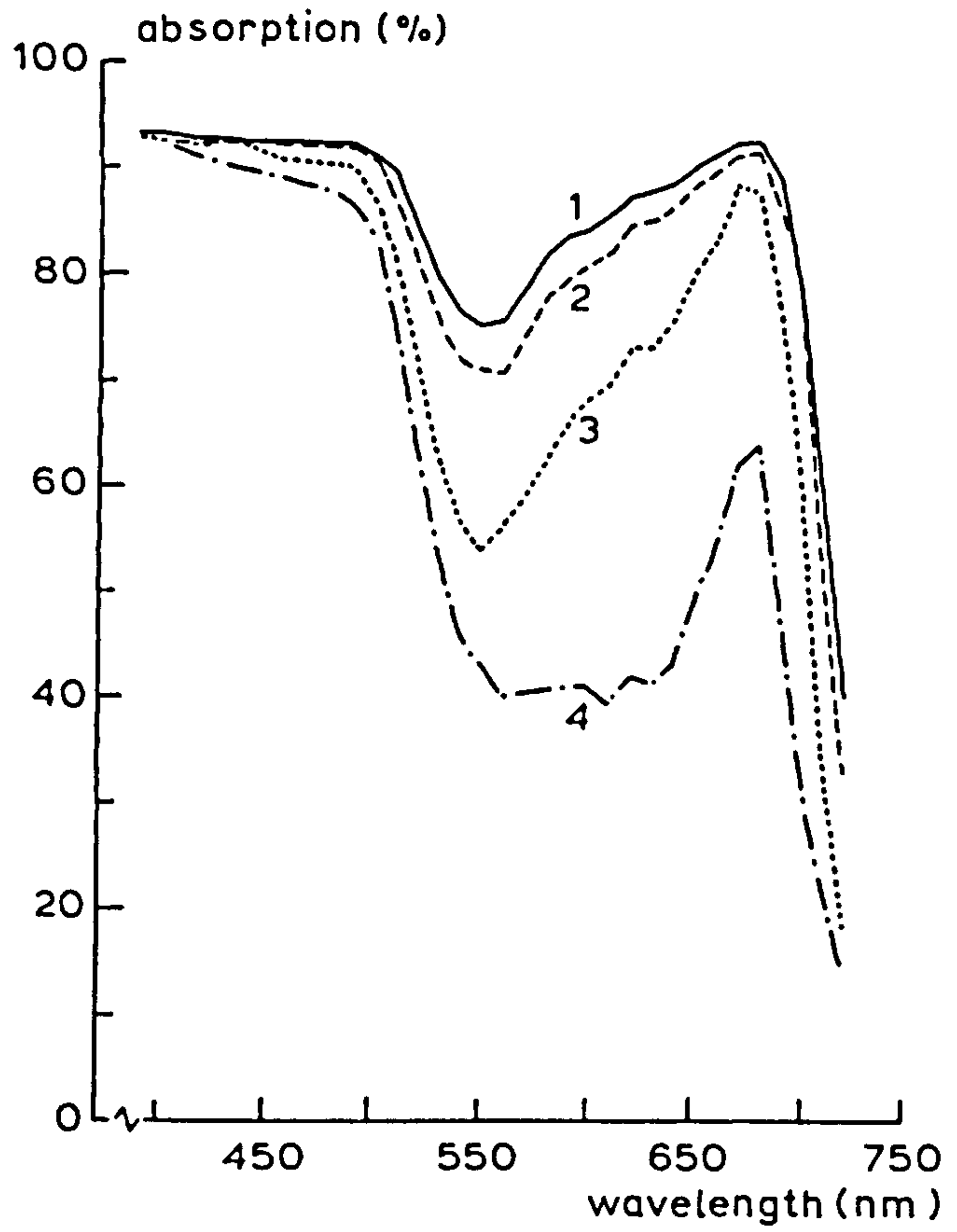

Figure 62. Absorption spectra of healthy (1) and BYV-infected green (2), greenish yellow (3) or bright yellow (4) beet leaves.

more light is transmitted, and as a result much less photosynthetically active radiation is absorbed (Figure 62). When symptoms are clear, as in infected bright yellow leaves, the effect is considerable.

The third component of crop growth reduction concerns a physiological change in the leaves. Photosynthesis initial light use efficiency and photosynthesis at light saturation are affected (Figure 63).

Light use efficiency is affected by the reduced light absorption indirectly, but also directly, probably through an effect on the photochemical process in the CO_2 assimilation.

Photosynthesis at light saturation is probably affected via the carboxylation process. Again there is a very clear effect in bright yellow leaves and the effect is already considerable when only vein clearing is present. These effects, measured under field conditions by van der Werf (1988) confirm earlier observations by Hall & Loomis (1972a, b).

The effect of virus beet yellows on leaf respiration is also shown in Figure 63.

We incorporated the various components of damage measured at leaf level in a crop growth model to study the consequences at crop level. An amended version of the basic summary model of crop growth SUCROS87 was used (van der Werf, 1988; Spitters et al., 1989).

Each component was introduced on the basis of the relations described above.

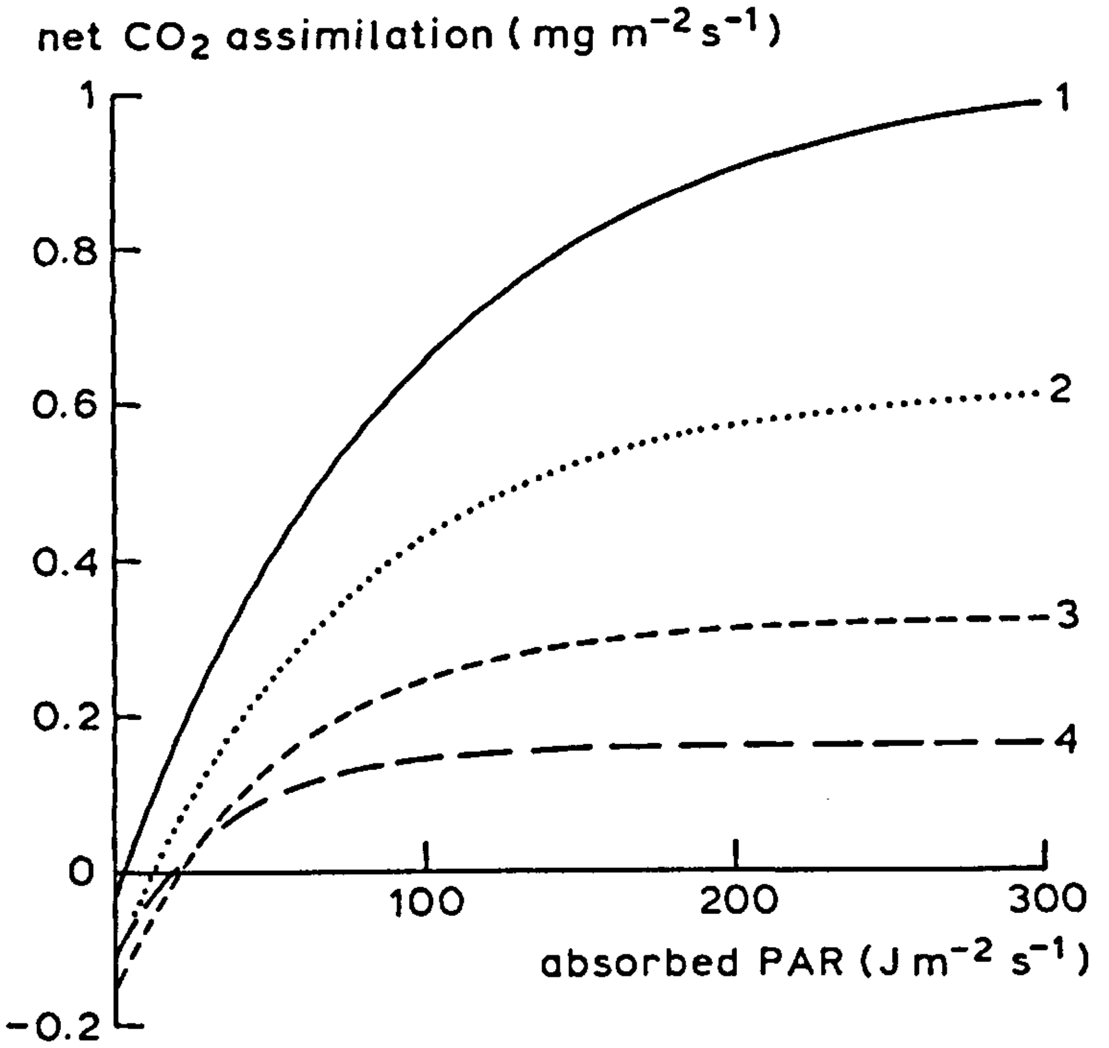

Figure 63. Characteristic photosynthesis–light response curves of healthy and BYV-infected beet leaves, fitted to experimental data. Numbers 1–4 represent healthy leaves, and infected leaves with vein-clearing, greenish yellow and bright yellow symptoms, respectively.

The course of the green and yellow leaf area index was introduced in the model through a forcing function derived from field observations. The outcome of the crop growth model was compared with the results of periodic crop growth analysis. Figure 64 shows the results of simulation runs using the environmental conditions as inputs, for two treatments and a disease-free control. Control and treatments are simulated satisfactorily. The various components of crop growth reduction measured at leaf level seem to be sufficient to explain the behaviour of an infected crop under field conditions. Results of the simulation model were then compared with yield loss, expressed as sugar yield, in various field experiments (Figure 65).

The simulated curve corresponds more or less with data from various field experiments. The absence of field-specific *LAI* data as forcing functions may partly explain the differences between measured and simulated data. It is very clear that infection date is most decisive for the explanation of yield reduction. The simulation model predicts that the relation between yield loss and infection date depends on the leaf area development of the crop. For a given infection date, early sown crops incur smaller yield loss than late crops.

Thus it is pointless to attempt to achieve late control of virus by spraying against aphids late in the season. Only an early control may prevent substantial damage. Tolerable densities of aphids in the course of time should also be ascertained by analysing the population dynamics and dispersal of aphids.

The simulation model was run several times for two infection dates, to evaluate

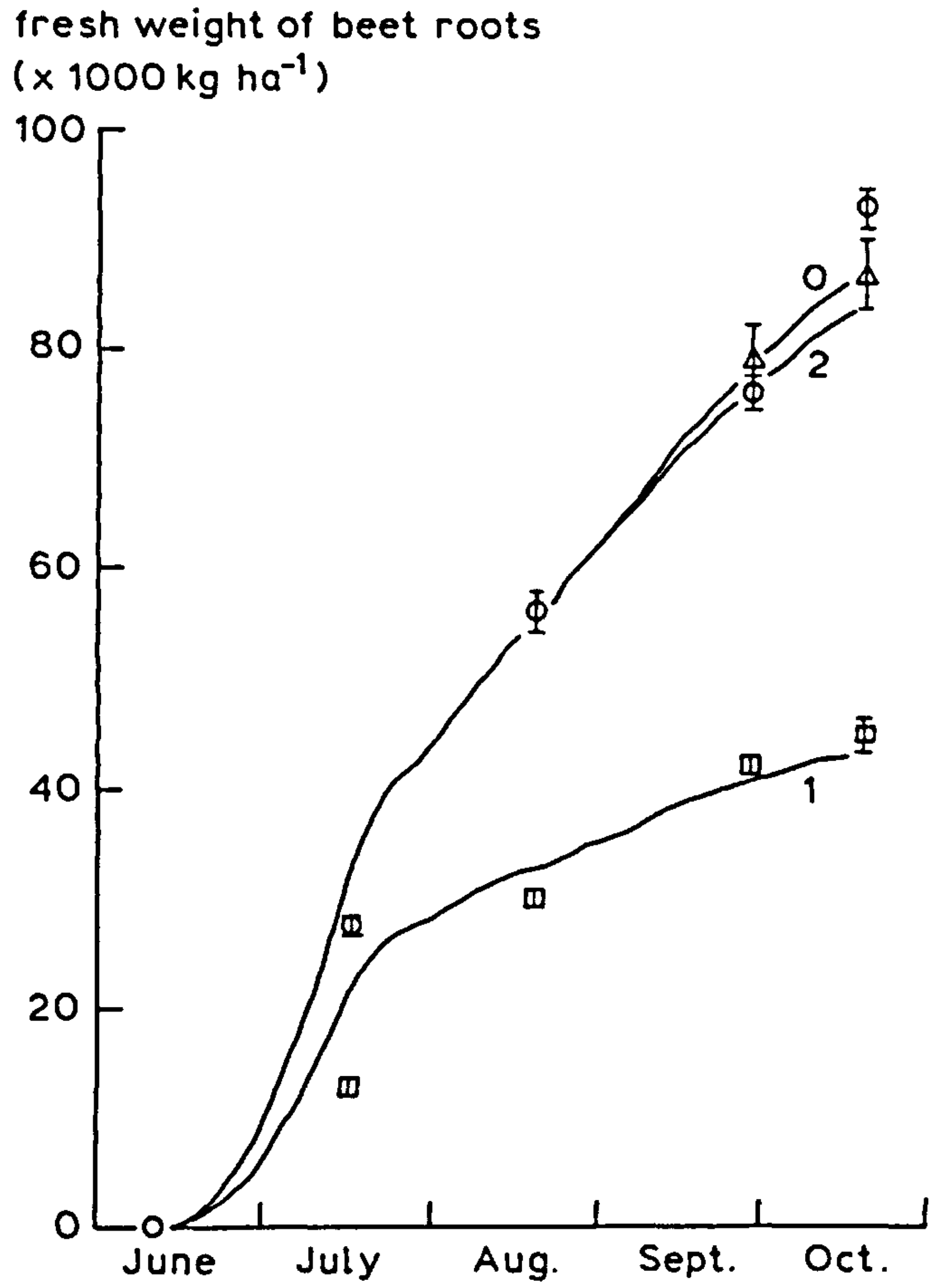

Figure 64. Experimental (symbols) and simulated (solid lines) growth patterns of sugar beet infected with BYV on 5 June (□ = line 1) or 14 July (△ = line 2), compared with that of healthy plants (o = line 0).

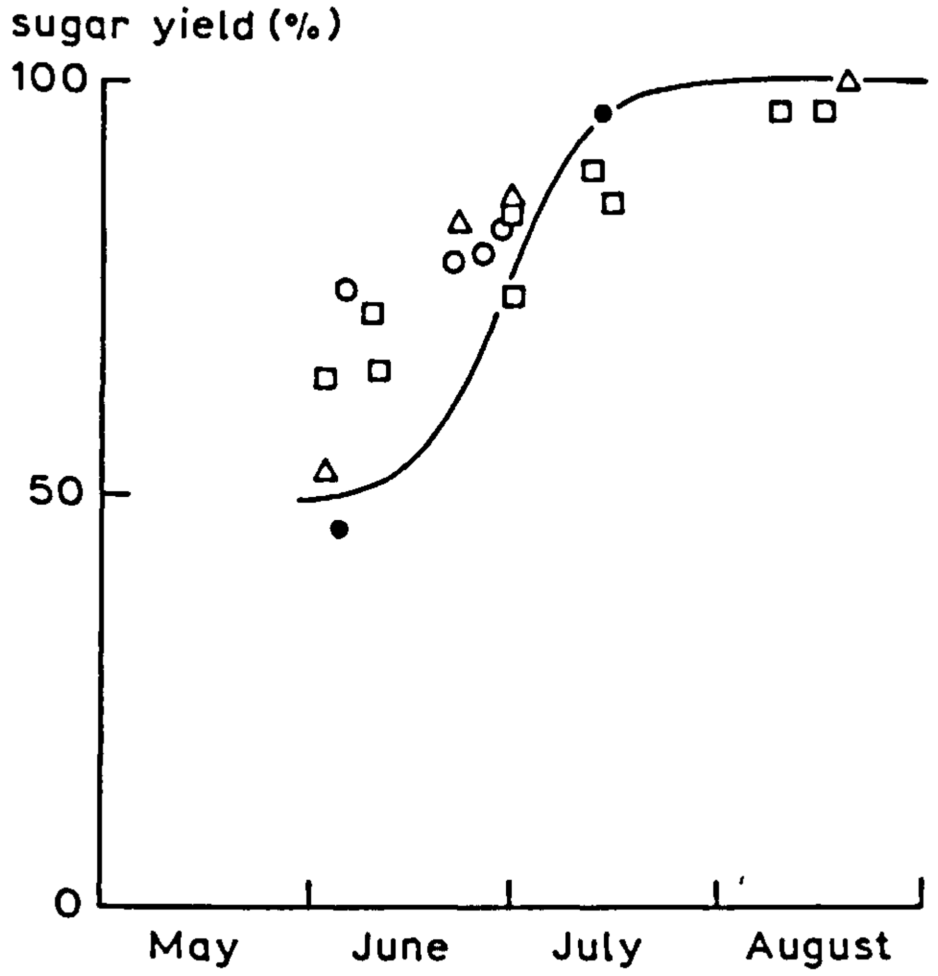

Figure 65. Simulated sugar yield (as % of control) as a function of infection date (——) in comparison with field experiments done by various authors: (□) Heijbroek, 1988; (△) Smith, 1986; (o) Russell, 1963; (●) van der Werf, 1988.

Table 14. Simulated contribution to total yield loss of four components of damage by BYV, inoculated in two stages of crop growth (ε is the initial light use efficiency, A_m is the photosynthesis at light saturation).

Damage component	Early infection*		Late infection**	
	% yield	added % loss	% yield	added % loss
no disease	100		100	
		7.1		1.5
1 (reduced leaf area index)	92.9		98.5	
		5.2		1.5
1 + 2 (reduced light absorption)	88.0		98.2	
		36.4		1.7
1 + 2 + 3 (reduced photosynthesis, ε and A_m)	56.0		96.6	
		11.7		0.5
1 + 2 + 3 + 4 (increased respiration)	49.4		96.1	
measured	48.2 ± 2.5		93.4 ± 5.1	

* Early infection: 5 June, 7 leaves, LAI = 0.1; ** Late infection: 17 June, 21 leaves, LAI = 5.1

the various damage components (Table 14). This demonstrated that most of the yield reduction can be attributed to the effect of the virus on light use efficiency and photosynthesis at light saturation. The other components have much less impact. There is no clear difference in relative importance of the damage components between infection dates.

The relative effect of beet yellows virus changes considerably in the course of time and this is apparently the result of a decrease in all damage mechanisms.

10.7 Cereal aphids in winter wheat

Another well studied example of yield reduction concerns cereal aphids. Since the early 1970s cereal aphids have increased considerably in economic importance and are now a yearly target of chemical control in many Western European countries. Their increase in pest status is most probably related to the increase in wheat yields. In a simulation study the effects of *Sitobion avenae*, the most abundant species in the Netherlands, were studied. To do this the various effects of the aphids were incorporated in a crop growth simulator (Rossing & van de Wiel, 1990; Rossing, 1990a, b), so that the effects observed by various authors (Wratten, 1978; Vereijken, 1979; Rabbinge & Mantel, 1981; Watt et al., 1984;

Entwistle & Dixon, 1987) could be reduced to a common denominator.

Winter wheat is affected directly or indirectly by the presence of cereal aphids. Direct effects result from the aphids' uptake of carbohydrates and amino-nitrogen by feeding, and the active substances they inject via their saliva. Active substances have not been observed in the saliva of summer populations of cereal aphids and are not considered here. Indirect effects are produced by virus transmission, honeydew excretion and changes in the phyllosphere microflora which may influence crop physiology. In this study only the effects of honeydew excretion onto leaf surfaces were considered. Both the direct and indirect effects of cereal aphids have been quantified in detailed studies. Rates of phloem sap uptake have been measured in energy budget studies (Vereijken, 1979; Rabbinge & Coster, 1984). The indirect effects studied are the effects of honeydew on photosynthesis of leaves of wheat. Rabbinge et al. (1981) observed that both the maximum rate of photosynthesis and light use efficiency fell immediately after the application of honeydew to wheat leaves. Rossing & van de Wiel (1990) found no significant effects after one day, but after 15 days they measured both a reduction of photosynthesis at light saturation and an increase in respiration. The processes resulting in what appears to be accelerated senescence remain to be identified.

In a modelling approach by Rossing (1990a), *S. avenae* is assumed to share the phloem sap supply with the grains. The aphids may be the first to obtain their share because of their feeding site, thus outcompeting the grains. Alternatively, the aphids and the grains share the supply with the grains in proportion to their respective demands. On the supply side the rate of phloem sap transport may or may not be increased because less phloem sap reaches the grains. An increase will result in enhanced depletion of reserves of assimilates and nitrogen in the leaves and thus accelerated senescence. Rossing (1990a) formulated four hypotheses concerning the partitioning of phloem sap between aphids and grains. Two of these will be discussed here:

–Hypothesis I

Aphid–grain competition: the phloem sap supply is partitioned in proportion to the respective demands of aphids and grains. There is demand-supply feedback, i.e. the total demand equals the sum of demands of grains and aphids.

–Hypothesis II

Aphid dominance: the phloem sap supply is first utilized by the aphids. There is no demand-supply feedback, i.e. the total demand equals the demand of grains.

Direct and indirect effects were introduced in a version of the SUCROS87 crop growth simulator modified to account for the nitrogen balance in the crop. The results of the model were compared with data collected in a field experiment. Aphid density in course of time was introduced in the model as measured in the field. Simulation runs were done for the two hypotheses mentioned above.

The aphid population reached a peak density of approximately 45 tiller^{-1} (Figure 66). The control was not completely free of aphids and a peak density of

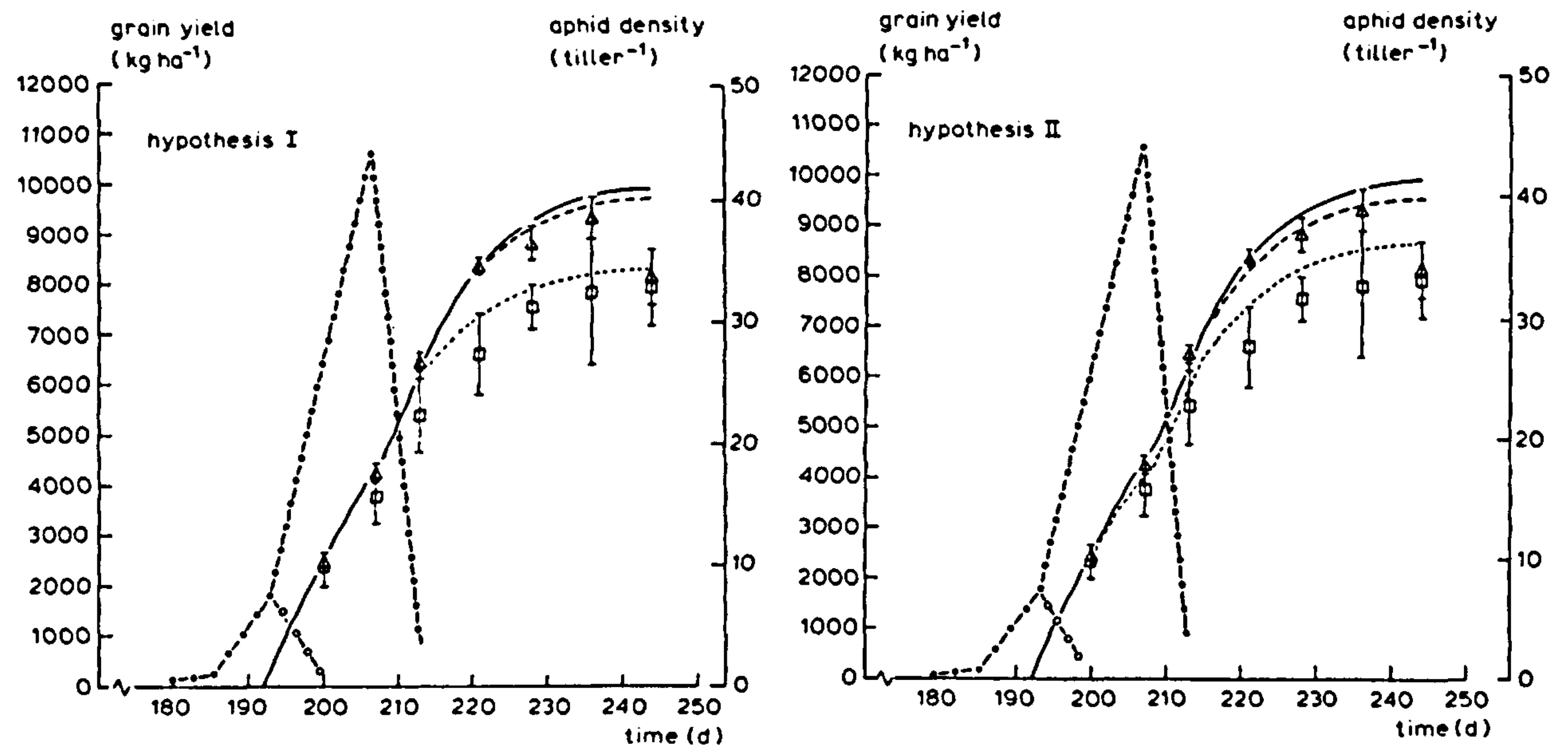

Figure 66. Actual and simulated grain yield of data set EEST84 at two aphid infestations using two hypotheses (I and II) on direct damage by *S. avenae*. Vertical bars represent standard errors of the mean. Grain yield without aphids (simulated: ——), aphid infestation as in control treatment (simulated: ---; measured: △) and high aphid infestation (simulated: ···; measured: □). The size of the aphid infestations is shown for the control (-o-o-) and the high infestation (-●-●-).

about 5 aphids tiller^{-1} was reached. In the control, simulated and observed grain yield agree well during the first part of grain filling. Later, the model overestimates yield, because leaf senescence is underestimated. In the aphid treatment the two hypotheses result in a different time course of damage, but no major difference in final damage. In the model based on Hypothesis I damage occurs only when grain filling is source-limited. In the field experiment, however reduction of yield was measurable from the onset of grain filling when grain-growth is sink-limited. This pattern is reproduced correctly by Hypothesis II. However, the latter hypothesis does not account for the observed depletion of reserve carbohydrates nor the accelerated leaf senescence, as Rossing (1990a) showed in a detailed analysis. These phenomena are accounted for by Hypothesis I.

The contribution of various damage components to total damage is shown in Figure 67. As mentioned above, the time course of damage is different for the two hypotheses. Moreover, with Hypothesis I damage resulting from uptake of nitrogen in the phloem sap continues to increase after the aphids have left the crop (Day 221). Aphids accelerate depletion of the nitrogen pool and thus leaf senescence. For the conditions used in the simulation, direct effects account for approximately 50 % of the total damage.

The model was used to evaluate the damage caused by an aphid population under various crop growth conditions (Rossing, 1990b). For this purpose the model was initialized with crop data from a number of field experiments in which nitrogen input was varied. Temperature and radiation data were 33-year averages

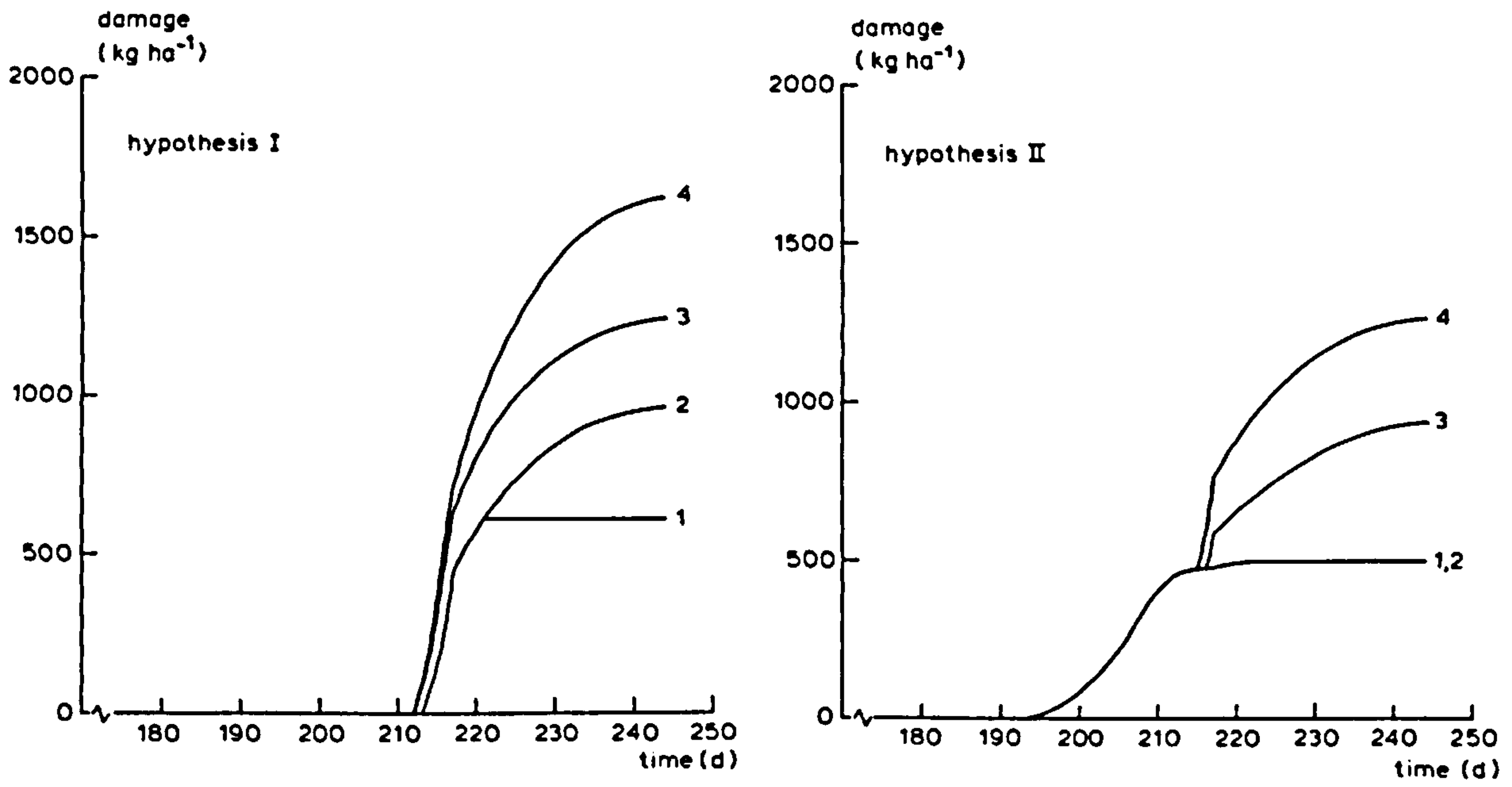

Figure 67. Simulated total damage (grain yield reduction, kg ha^{-1}) and damage components using two alternative hypotheses on the direct effects of *Sitobion avenae*. Data from EEST84, the high aphid infestation. 1: carbohydrate uptake. 2: carbohydrate and nitrogen uptake. 3: carbohydrate and nitrogen uptake + increased maintenance respiration. 4: carbohydrate and nitrogen uptake + increased maintenance respiration + decreased photosynthesis at light saturation.

for Wageningen, the Netherlands. An exponentially growing aphid population was introduced, with a peak density of 17 aphids $tiller^{-1}$ at development stage DC 77 (Decimal Code, Zadoks et al., 1974). In Figure 68, the results of runs with the crop model and the damage model are combined in three graphs representing three development periods after flowering. The results show that at low and moderate yields aphid damage increases approximately linearly with yield of the control. At high yields damage exceeds the linear trend. High yields are attained only when green leaf area duration is large, resulting in more damage by honeydew. Later during the development of the crop the effects of honeydew are dominated by the direct effects, because honeydew effects take some time to develop.

10.8 Concluding remarks

The examples discussed above demonstrate how crop growth models may be used to bridge the gap between detailed laboratory experiments and the interpretation of field data. Thus, simulation studies help to elucidate the quantitative meaning of various components of crop growth reduction. This insight is used in further simulation experiments to derive economic injury levels that are flexible, dynamic and specific and depend on the production situation, taking into account the availability of water and nutrients. These economic injury levels are also dynamic because they may change in the course of time. An early infection or late

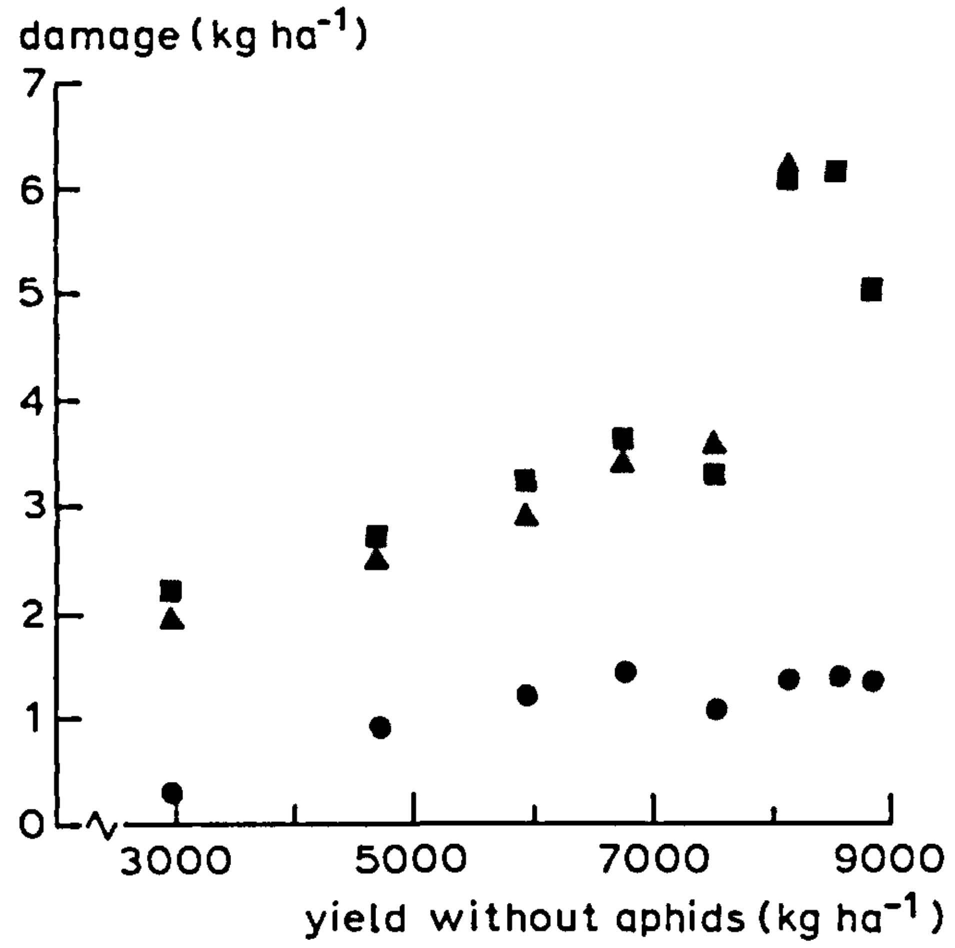

Figure 68. Simulated damage (kg ha^{-1} (aphid-day)$^{-1}$) for three periods of crop development (■ DC60-69; ▲ DC69-73; ● DC73-83), calculated with Hypothesis I on aphid–crop interaction.

infection may have considerably different consequences, depending on crop development stage. Finally, the economic injury levels may be tailored to the specific circumstances of individual fields.

The comprehensive simulation models used in this study are not adequate for pest and disease management. They help increase our understanding and may be used to derive economic injury levels that may be implemented in computerized pest and disease management systems. This clearly demonstrates the bridge function of production ecology.

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11 Agronomical measures to control growth and yield reduction by weeds

K. Baeumer

11.1 Introduction

The farming systems in use today in Western Europe contain fewer cereals and more high-yielding row crops, such as maize, sugar beet or potatoes. Consequently, not only the intensity of soil cultivation, fertilization and plant protection, but also the impact of mechanization on the productivity of the farming system has been increased. Frequently, the need to use heavy farm machinery causes soil structure to deteriorate and increases the risks of water erosion. In an attempt to repair the damage, farmers intensify soil cultivation, with the result that the loosened soil becomes even more liable to recompaction by heavy traffic.

De Wit recognized this drawback of loose-soil husbandry. During the early 1960s he initiated research on the feasibility of crop husbandry on naturally compacted soils (Bakermans & de Wit, 1970). If crops can be grown with the least possible soil disturbance, a permanent cover of living or dead vegetation protects the soil from erosion throughout the year. The changes in soil structure that result from firm-soil mulch-husbandry alleviate the negative impact of heavy traffic on soil structure. Labour and energy costs can be minimized by omitting deep ploughing or other intense soil cultivation.

Reducing tillage intensity to the sowing operation only, however, means that unwanted vegetation has to be controlled by other than mechanical means. In conventional farming yield reductions are avoided by the combined effect of the following measures:

- intense cultivation, especially deep ploughing during fallow periods
- chemical and mechanical weeding during crop growth
- crop competition as regulated by crop species in rotation, cultivar, planting time, fertilization, irrigation, plant protection and harvest time.

In firm-soil mulch-husbandry the direct effect of soil cultivation has to be replaced by using herbicides that can completely destroy existing vegetation without any residual effects on the following crop. Hence, the dependence on soil cultivation to control weeds shifts to almost total dependence on herbicides, a change that is open to criticism concerning its practical and ecological implications.

Initially, the availability of suitable herbicides stimulated research. It not only permitted the development of non-inversion tillage systems but also opened novel ways to re-examine a central theme of agronomy, i.e. the objectives and benefits of soil tillage. Is soil cultivation indispensable for improving the soil structure for crop growth or for controlling weeds? The answers given depend on the cropping system, soil and climate conditions and are not overwhelmingly in favour of one alternative. But by comparing contrasting tillage systems much has been learned about the interactions between soil structure, aeration, water and nutrient regime on the one side, and soil and fauna, microorganism and crop growth on the other.

In terms of practical application, the results of numerous experiments with reduced tillage intensity favour zero tillage on structurally stable and well drained soils and in farming systems dominated by grain and fodder crops. Yet because of the costs and risks of weed control only a minority of farmers have adopted zero tillage. Additional herbicides with a more satisfactory selectivity are needed. Some weeds are favoured by zero or shallow non-inversion tillage. If these weeds are difficult to kill with herbicides, changes in composition and abundance of the weed flora will in time render the farming system unmanageable and unprofitable.

Therefore, if alternative no-plough farming systems are to be developed a solution needs to be found for the weed problem. Research aimed at solving this problem is proceeding along two avenues: the main body of experimentation consists of field experiments exploring the effect of various agronomical measures on weed population dynamics; the second approach, which is still being developed, uses data obtained in field research to model the effect of tillage on weed population dynamics.

The research group at Göttingen has contributed to this second line of research. In conjunction with other findings our results may illustrate which weed problems are caused by non-inversion tillage and how concepts have been changed to solve these problems. Since graminaceous weeds cause the greatest problems in no-plough farming systems, the following discussion is largely restricted to these weed species.

11.2 Experimental work on the effect of tillage on weed population dynamics

11.2.1 Perennial grasses

In West Germany several long-term zero tillage experiments had to be discontinued because of the increase in grass weeds. Couch grass (*Agropyron repens*) was the most difficult and intractable weed if

- cereals were grown continuously without a 'break' crop
- fallow periods between cropping were not used for shallow stubble cultivation and growth of competitive green manure crops
- paraquat – even with repeated application – was used as the only herbicide for couch grass control.

Paraquat only kills the photosynthesizing plant organs and does not kill reproductive underground organs. Though complete eradication of couch grass cannot be achieved by paraquat, it used to be the preferred herbicide for presowing applications, because of its quick action in killing existing vegetation and its immediate and complete inactivation on soil contact. Recently, the use of paraquat has been banned because of its high toxicity and its persistence in the soil.

Yield reductions of wheat caused by couch grass are density-dependent (Figure 69A), but often insignificant when the density of the couch grass population does

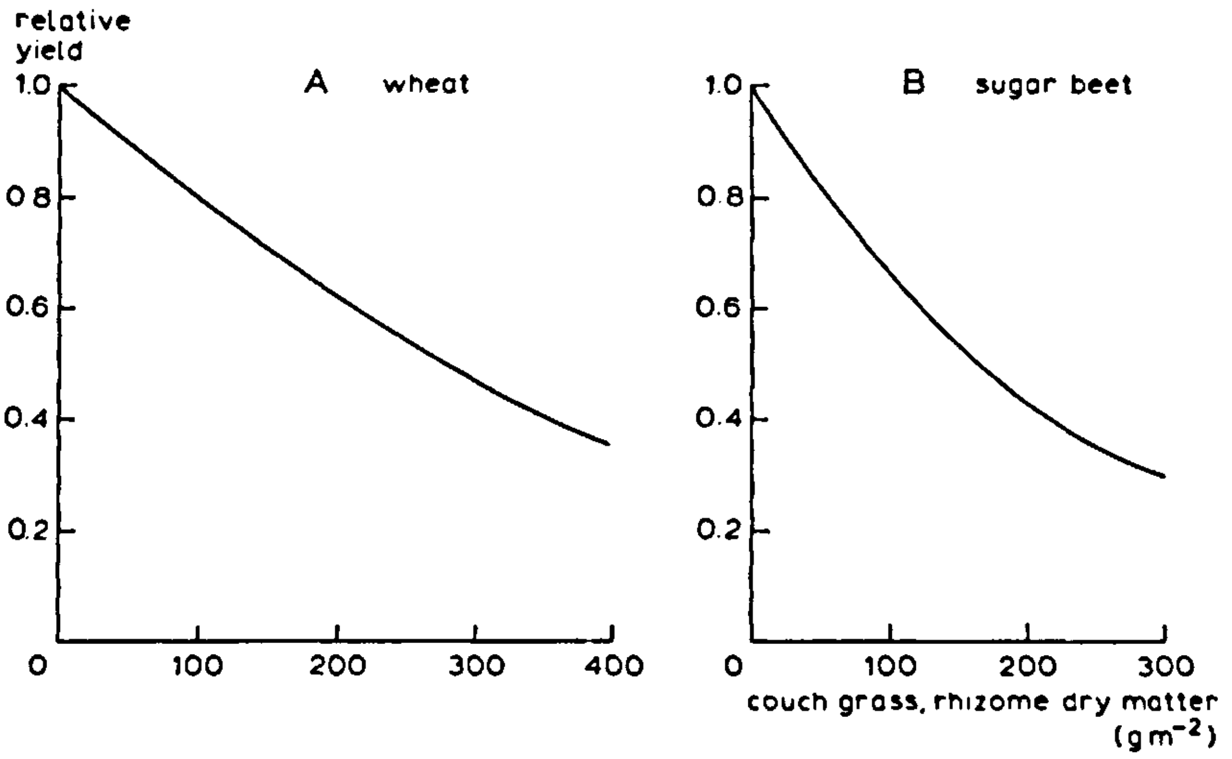

Figure 69. Density-dependent yield reductions caused by couch grass. A: winter wheat (Nuyken, 1975). B: sugar beet (Böttger, 1978).

not exceed 20 spikes m^{-2}. Sugar beet crops suffer more from similar couch grass density (Figure 69B), because they are more affected by the shading of the grass. Since couch grass is able to build up high populations during the course of one year – even with intensive tillage and competitive crops (Cussans, 1968; Schwerdtle, 1975) – the real object of control should be the population capable of reproduction.

Couch grass can propagate by seeds (Nuyken, 1975), but with common crop husbandry practices the chance of seedlings of couch grass surviving is only small (Böttger et al., 1982). The main source for reproduction is rhizome buds. Growth of new rhizome matter starts when shoots have developed at least three aerial leaves. Rhizome production is greatest when competition by crops for light and other sources is weak or has ceased during senescence of the crop.

In cereal cropping systems where no direct measures are taken to control couch grass, rhizome dry matter has been observed to increase by a factor of 2 to 3 during one year; in combination with maize without the application of atrazine it increased by 1.5, and in combination with sugar beet without mechanical or chemical weeding it increased by 5.5 (Table 15). These figures for rhizome propagation not only reflect the differences in competitive strength of the three crops. Maize has a longer growing period than sugar beet.

The explosive increase in reproduction potential of couch grass calls for measures directed to eradicating any existing couch grass infestations. As shown by the observed propagation rates (Table 15) this goal can be approached only by the application of glyphosate, a foliar-acting systemic herbicide. Sprayed on a vigorously growing couch grass stand about three weeks before sowing, it kills up to 95 % of the existing rhizomes. If a late sown spring crop (e.g. of maize) follows and the glyphosate application is repeated in spring, complete eradication can be achieved (Tiedau et al., 1974). Repeated application of this herbicide during a single crop sequence is too costly compared with other means of control. To avoid a situation with high levels of couch grass infestation, alternative farming systems that keep couch grass populations at tolerable densities have to be employed.

Table 15. Effect of cropping, soil cultivation and herbicide application on rhizome propagation of couch grass. Propagation rate: $P_{final}/P_{initial}$, rhizome d.m. per unit area and year.

Treatment	P_f/P_i	Author(s)
Conventional tillage without control measures		
• winter wheat	1.9–2.7	Hacker & Hess, 1986
• spring barley	1.4	
• maize (without atrazine)	1.5	
• sugar beet	5.5	Böttger, 1978
Conventional tillage with special control measures		
• spring wheat		
+stubble cultivation once (st × c)	2.0	
+st × c + green manure	1.5	Hacker & Hess, 1986
+stubble cultivation 3 times	0.8	
+glyphosate	0.05	
• sugar beet		
+mechanical weeding	0.4	Böttger, 1978
+grass-herbicide post-emergence	0.3	
Zero tillage without control measures		
• winter wheat	2.3–3.0	Nuyken, 1975
Zero tillage with special control measures		
• spring barley		
+paraquat + green manure	1.9	Tiedau et al., 1974
+paraquat + green manure + dalapone	1.3	
• winter wheat		
+ glyphosate	0.05	Nuyken, 1975

11.2.2 Annual grasses

In no-plough tillage systems perennial weeds that reproduce vegetatively can be successfully controlled by foliar-acting systemic herbicides. Only annual weeds that propagate by seeds remain a problem. This is especially true for black grass (*Alopecurus myosuroides*) and barren brome (*Bromus sterilis*). Both are greatly encouraged by shallow non-inversion tillage in farming systems dominated by winter cereals. This is mainly because the seeds are not buried to depths from which emergence is unlikely but are retained close to the soil surface from where seedlings can readily emerge (Figure 70). Therefore, better weed control is required from herbicides than in conventional tillage systems. Based on field experiments a population model has been developed from which it is possible to determine the effectivity of control to maintain a static population of black grass.

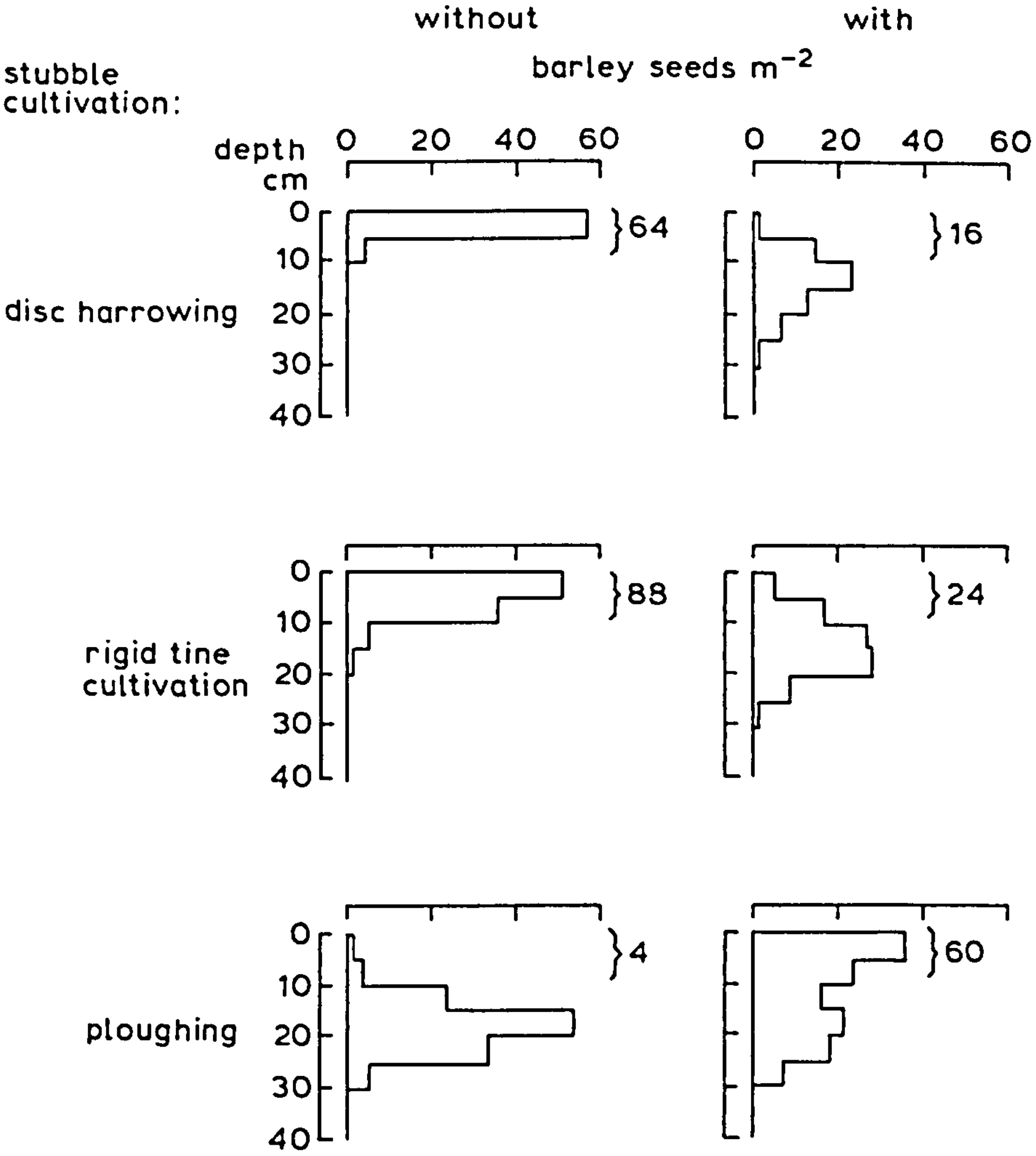

Figure 70. Effect of soil cultivation on the vertical distribution of volunteer barley seeds in soil without (left-hand column of graphs) and with (right-hand colums of graphs) ploughing before winter (Rauber, 1985).

Results from field experiments (Table 16) show that soil-acting herbicides were less effective in reducing black grass on plots untilled for a number of years where the straw had been burnt than on ploughed land (Moss, 1979). This is because of the increased adsorption of herbicides onto organic matter accumulated near the soil surface. Burnt straw residues have been found to be especially highly adsorptive to herbicides (Moss, 1984). The effectiveness of herbicides can be improved by incorporating the straw or ash residue into the soil by deep tine cultivation or ploughing.

This measure has the additional effect of burying freshly shed grass seeds in deeper soil layers. As shown by the example of volunteer barley seeds (Figure 70), ploughing leaves only few seeds in the 0–10 cm soil layer, from which new plants can be successfully established. Therefore, the population of growing black grass is reduced by ploughing during the subsequent year. However, when the land is reploughed, viable old seeds are brought back towards the soil surface, with the result that the growing population increases again during the third year. The amplitude of this cycle diminishes in tillage systems with repeated deep ploughing. As a consequence, conventional tillage systems do not prevent an increase in annual grass weed populations. On the other hand, compared with non-inversion tillage, ploughing results in far better control of weed species whose seeds have a short life-span in the soil (Knab & Hurle, 1986; 1988).

Alopecurus myosuroides, Avena fatua, Apera spica venti and *Bromus sterilis* are favoured by growing cereal crops continuously. Therefore, 'break' crops, especially dicots sown in spring, offer an effective means of containing weed grass populations within tolerable densities.

In West Germany the crop rotation of sugar beet, winter wheat and winter barley is widely used on loess soils prone to slaking and water erosion when situated on slopes. To prevent soil erosion a system of loose-soil mulch-husbandry has been developed (Baeumer & Pape, 1972) consisting of the following steps:

- incorporating straw into the soil by two tine cultivations following barley harvest
- growing a green manure crop (*Phacelia tanacetifolia, Raphanus sativus* or *Sinapis alba*) that is killed by low temperatures during winter

Table 16. The calculated annual percentage kill by herbicides needed to maintain a static population of black grass (Cussans & Moss, 1982).

	Straw burnt (%)	Not burnt (%)
Ploughed	50	65
Direct drilled	88	92

- preparing the seed bed for sugar beet in spring by shallow non-inversion cultivation.

The plant residues on the soil surface do not impair the establishment of sugar beet seedlings but successfully prevent soil erosion. However, this system controls weeds less effectively than conventional tillage. Many volunteer barley plants occur as weeds in sugar beet and in the following crop of wheat. This calls for additional herbicide applications before and after the sugar beet crop is planted. The increased costs involved and the difficulties in crop husbandry have made farmers reluctant to adopt this soil conservation system. Hence, a crop management system that offers sufficient protection from soil erosion but minimizes risks and costs of weed control had to be developed.

First, however, it had to be investigated why infestations of barley plants (up to 60 plants m^{-2}) occurred in sugar beet crops with reduced tillage (Rauber, 1985). Only a minor part of the scattered barley seeds emerged before winter (5–35 %, Figure 71). Until the sugar beet was planted, 7–55 % of the initial amount remained as viable seeds in the soil, and only 3–16 % grew into plants after sugar beet planting, producing 40–600 viable barley seeds m^{-2}. Hence the dormancy of the barley seeds caused the delay of emergence of the barley seeds. This delay was the main reason why volunteer barley infested sugar beet and the following wheat crop.

The survival of barley seed in the soil seed bank was strongly determined by the

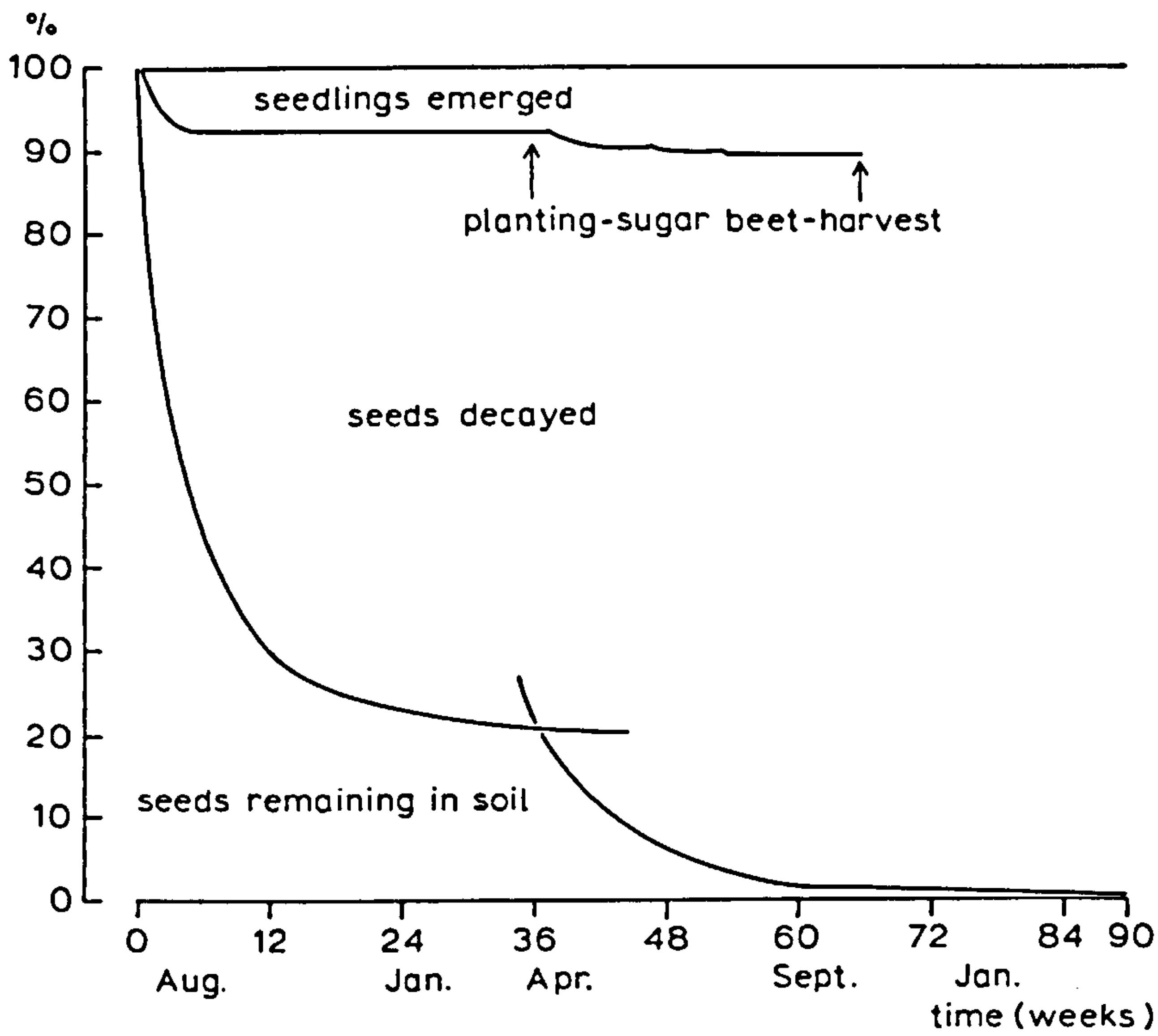

Figure 71. Percentage of volunteer barley seeds remaining in the soil during the growth of sugar beet and a subsequent crop of winter wheat (Rauber, 1985) (100 %: 256–1452 seeds m^{-2}).

degree of primary and secondary dormancy of the seed. In turn dormancy was produced by interactions between genotype and weather conditions during the phase of grain production and after ripening. Seed survival did not depend on soil cultivation methods (here, shallow cultivation or deep ploughing). However, the tillage system affected the vertical distribution of the barley seeds (Figure 70). Prior to planting sugar beet, only 2–7 % of the seeds were present in the top 12 cm of the autumn-ploughed plots, whereas almost all barley seeds were found in the top 12 cm of the soil tilled with reduced intensity.

Since only those barley seeds located in the upper 10 cm of the soil give rise to a growing barley population, the number of these seeds has to be reduced. This can be achieved by choosing a barley cultivar with low expression of dormancy and by burying the newly shed seeds by deep ploughing immediately after the barley harvest. This measure has been observed to reduce density of seed-producing barley plants in the sugar beet crop to 0.2 plant m^{-2} and to 17 viable new seeds m^{-2} (Isselstein, 1987; Table 17). Again using only a shallow soil cultivation to prepare the seed bed for sugar beet, autumn-germinated barley plants that survive the seed bed preparation can become strong competitors with a high seed production rate. To avoid this, a presowing application of a suitable herbicide is usually recommended. However, this application appears to be unnecessary if the

Table 17. Effects of barley cultivar and soil cultivation on the relative number of barley plants in sugar beet (Isselstein, 1987), as % of viable seeds shed onto the ground at harvest time (100 %: 245–972 seeds m^{-2}).

Cultivar	Longer dormancy		Shorter dormancy	
plants emerged before winter	5		35	
Soil cultivation	tine cultivation	ploughed early	tine cultivation	ploughed early
viable seeds remaining in the soil (0–10 cm) in spring	36	4	9	1
plants emerged after sowing of sugar beet	6.5	0.2	1.5	0.06

Competition surviving 'transplants' reduced in weight to 20 % of control (without green manure) competition from the green manure crop established in autumn is strong enough. *Phacelia* and *Raphanus* have been observed to reduce the density of volunteer barley to 1–16 plants m^{-2} as compared with 4–51 plants m^{-2} without a cover crop. The dry matter production of the remaining barley plants has been reduced to 20% of those grown without green manure competition. Hence, almost all surviving barley plants were killed by the effect of the subsequent shallow seed bed preparation. Regrowth of these autumn-germinated plants occurred only to the extent of < 0.3 plants m^{-2} (Isselstein, 1987). This infestation is below a density that calls for control measures.

11.3 Modelling the effect of tillage on weed population dynamics

To avoid intolerably high weed infestations, suitable farming systems that contain a certain amount of 'self-regulation' with regard to the weed population have to be employed. The planning of such systems can be supported by the use of mathematical models that quantitatively describe the effects of control measures on the density and composition of the weed flora.

The central parameter of a weed population is the quantity of reproductive organs per unit area present at a certain time. Changes in this seed bank are quantified by differences between initial and final quantities of reproductive organs. These changes are generated by empirical rates of development and by external influences.

If tillage effects are to be simulated, several sub-populations of buds or seeds will have to be defined with regard to their position in the soil. Tillage results in a certain vertical distribution and redistribution of these sub-populations (Figure 70). Reproductive organs situated in deeper soil layers are subject to different rates of decay and cannot develop into growing and reproducing plants. Many plant species employ mechanisms of dormancy in order to prolong the longevity of reproductive organs or to time germination, and this results in a seasonal pattern of seedling emergence. Since the degree of dormancy is age-dependent, sub-populations of seeds or buds have to be defined according to their time of origin. Finally, the population of growing plants can be divided into classes of development stages between emergence and decease.

All these aggregates in classes of time, space, and development increase or decrease by the rates listed below:

- rate of shoot or seedling emergence from buds or seeds
- rate of decay of reproductive organs in the soil
- rate of change in dormancy of reproductive organs
- mortality rate of emerged plants
- rate of seed or bud formation of surviving plants
- rate of seed losses by harvest or other cultural practices and losses caused by pathogens and predators.

The above rates, again, vary with time of emergence and with external influences, such as temperature and moisture. Since information about certain quantities and rates is still lacking, most existing simulation models use a less differentiated approach. More elaborate models have been devised for *Galium aparine* (Aarts, 1986), *Alopecurus myosuroides* (Cussans & Moss, 1982) and *Avena fatua* (Rauber & Koch, 1975), less elaborate models for *Agropyron repens* (Hacker & Hess, 1986) and several weed species (Zwerger & Hurle, 1988). All these models allow reasonable predictions of the effect of rotation and other weed control measures on the development of seed or bud density (Table 17).

Yet, these models only implicitly take into account the effect of competition. Therefore, a different approach is based on the competition model of de Wit (1960). In a series of replacement experiments Rauber (1984b) quantified the ability of cereal crops to compete with couch grass (Figure 72).

The relative crowding coefficient increased in the order: spring wheat < oats < winter rye < winter wheat < winter barley < spring barley. With the exception of winter rye and winter wheat, the relative reproduction rate α of new rhizome buds decreased in the same order. In field experiments the relative crowding coefficient of winter wheat with regard to couch grass ranged from 2.6 to 4.9 (Rauber & Boettger, 1985).

Rauber used the relative crowding coefficient to calculate the amount of new rhizome buds Iq_t formed per unit area during the growth period of the cereal crop by

$$Iq_t = \frac{q_t}{k_t\,(1\text{-}q_t) + q_t f_t} \cdot Eq_t \qquad \text{Equation 41}$$

where Eq_t is the amount of newly formed rhizome buds per unit area in pure couch grass stands during one growth period, and q_t the relative density of couch grass shoots.

The relative density of couch grass shoots q_t is derived from

$$q_t = \frac{Q_t\,a_t}{Q_t\,a_t + G_t f_t} \qquad \text{Equation 42}$$

where Q_t is the initial number of rhizome buds per unit area, a_t the fraction of shoot emergence from Q_t, G_t the number of cereal grains sown per unit area, and f_t the fraction of shoot emergence from G_t.

Until the beginning of a new growth period $(t+1)$ of the following cereal crop, the amount of rhizome buds increases or decreases by the relative rate of bud propagation v_t yr^{-1}

$$Q_{t+1} = Iq_t\, v_t \qquad \text{Equation 43}$$

By taking into account the relative rate of survival of dormant old buds v'_t which are still viable at $(t+1)$, Equation 43 becomes

$$Q_{t+1} = Iq_t\, v_t + Q_t\,(1 - a_t)\, v'_t \qquad \text{Equation 44}$$

During the sequence of growth periods with competition between cereal crops

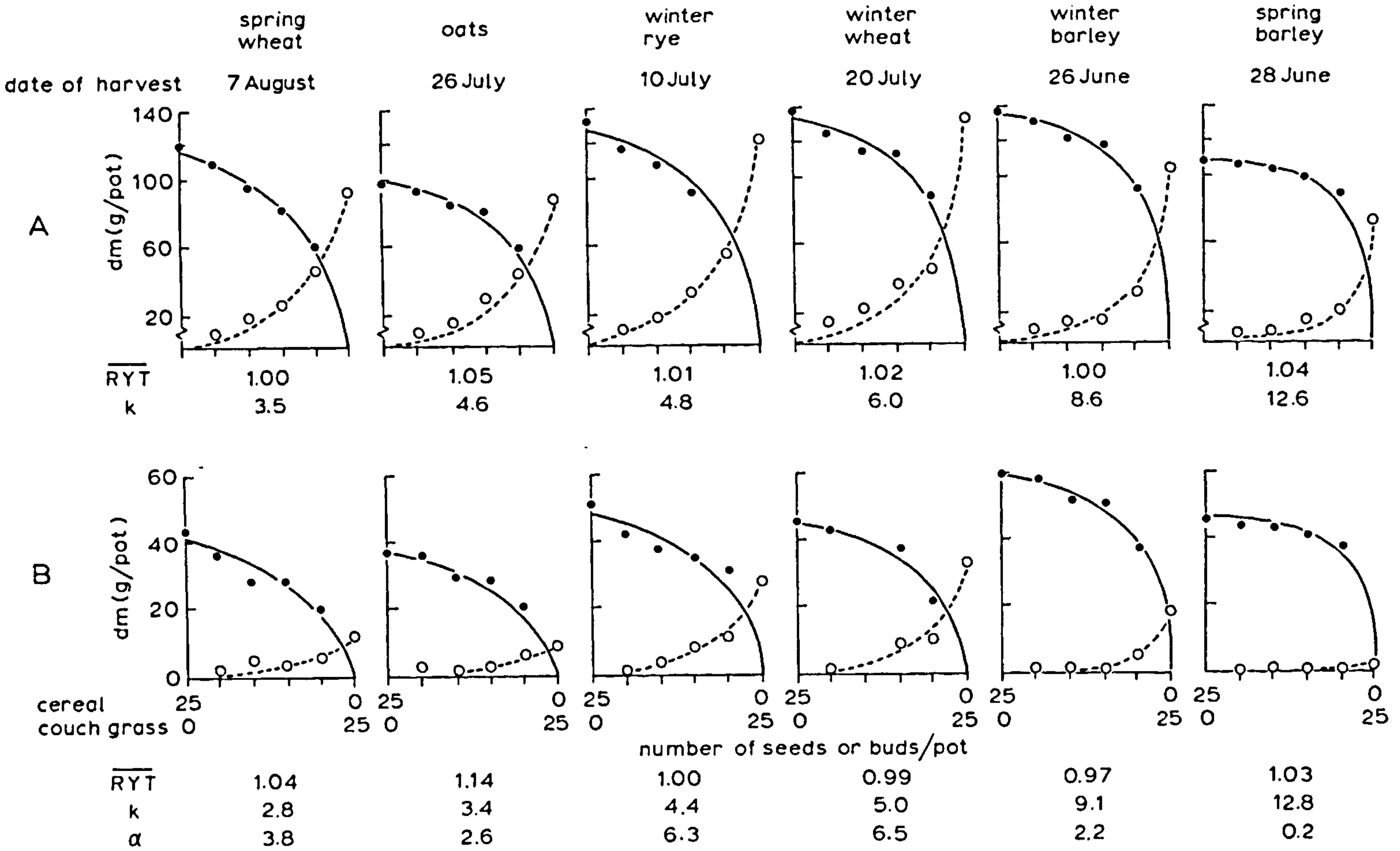

Figure 72. Effects of competition between cereal species and couch grass (Rauber, 1984b). A: cereals: shoot d.m.; couch grass: shoot d.m. + newly formed rhizome d.m. B: cereals: grain yield; couch grass: newly formed rhizome d.m. *RYT*: relative yield total; *k*: crowding coefficient; α: relative reproduction rate. Data from Baeumer et al., 1983.

and couch grass the density of the bud population changes, whereas the amount of cereal grains sown is kept constant by the farmer. This restriction has been observed by simulating the growth of couch grass populations with Equation 44. Figure 73 shows some results.

By assuming a relative rate of bud propagation $v_t = 2\,\mathrm{yr}^{-1}$, as experienced in a zero-tillage situation without the application of measures to reduce rhizome growth during the fallow period, the relative density of couch grass with regard to a cereal stand could be constantly kept below a threshold density of 1 shoot m^{-2} (i.e. the value of initial density) by growing spring barley continuously (Figure 73A). If rhizome growth is controlled during the fallow period by a measure that halves the bud population ($v_t = 0.5$) wheat can be grown continuously (Figure 73B).

A minimum relative crowding coefficient is necessary to maintain a given rhizome bud population

$$k_t = k_{\mathrm{min}}, \text{ if } Q_{t+1} = Q_t$$

k_{min} increases with relative rate of bud propagation v_t and with increasing amount of newly formed rhizous buds in pure couch grass stands. Hence, this simulation

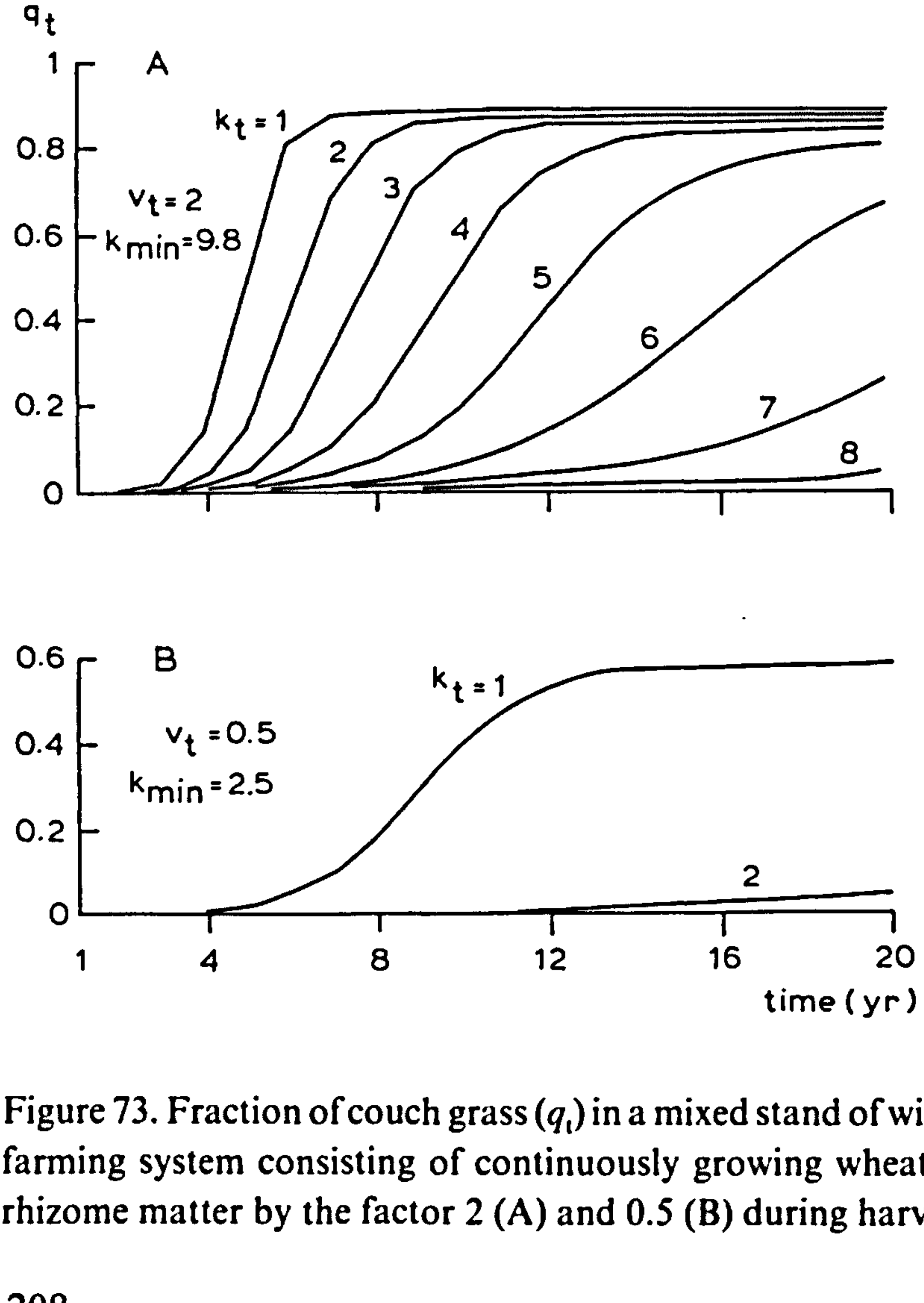

Figure 73. Fraction of couch grass (q_t) in a mixed stand of winter wheat and couch grass in a farming system consisting of continuously growing wheat (Rauber, 1984a). Increase of rhizome matter by the factor 2 (A) and 0.5 (B) during harvest and resowing of wheat.

model takes differences in growth conditions for rhizome bud formation as well as competition and control effects into account.

The drawback of employing the relative crowding coefficient in this simulation model is that only those results where mixtures are in the same range of densities used for calculating this parameter can be predicted. This limitation can only be overcome by employing a dynamic simulation model that describes the competition effects over time (Spitters & van den Bergh, 1982).

11.4 The economic threshold concept

The introduction of herbicides freed farmers from the physical burden of weeding. Encouraged by the economic conditions during the 1960s and 1970s they made liberal use of herbicides and developed simplified farming systems, such as monocultures of cereals or of maize. Today, shrinking profits are driving farmers to reduce production costs without impairing the high level of crop yield. This can partly be achieved by a more judicial use of herbicides.

Therefore, decisions about the necessity for weed control actions should be based on the economic threshold concept. The threshold density is defined by the weed density at which the cost of control just balances the financial benefits likely to result from treating the crop. The application of control measures is economically justified only if the observed weed density exceeds the threshold density. Hence, identifying the weed species present and monitoring their abundance are prerequisites for successfully employing the threshold concept.

The limits set for single weed species or for combinations of several species have been quantified by the regression of yield losses on weed abundance before the time of spraying. Because of the empirical character of this relationship the threshold density cannot be predicted precisely for a given situation. Therefore, it represents only the upper limit of a range of tolerable densities. The following effects will cause variations of the true threshold density:

- soil and climate (region), year (weather)
- crop, cultivar and rotation
- efficacy of the control measure (herbicide applied, date of application)
- costs of harvesting, drying and cleaning the seed as influenced by possible weed infestations
- yield of the crop per unit area
- market price per unit yield.

Hence, ineffective herbicide treatments and low crop yields will raise the threshold density.

So far, threshold densities have been quantified for some weeds in winter cereals grown in a cereal-dominated crop rotation with sugar beet as a 'break' crop every third or fourth year (Table 18). The threshold concept is used only for cereal crops; in sugar beet complete weed control is used. Average crop yields, costs and returns have been assumed for deriving the threshold densities.

If these limits are applied, the decision will be taken only with respect to the actual weed infestation. But this decision will affect decisions to be taken in the following years. Omitting a control measure may result in an unwanted build-up of the seed bank, which can cause increasing weed infestations of future crops and, in consequence, higher costs of weed control.

Therefore, the consequences of a long-term application of the threshold concept have to be assessed. This has been done in only two cases for cereal-dominated crop rotations with sugar beet as a 'break' crop (Kees, 1986; Kaiser, 1989). Compared with treatments aiming at complete control, no rapid increase in the weed infestation of sugar beet or in the seed bank population was observed, when the threshold concept was applied during 10 and 6 years. Differences between treatments existed, but became effective only after several years. So far, the chosen limits do not imply great risks. This may be caused by the fact that 'conservative' threshold densities, i.e. the lower limits of the threshold range, were used. Probably, the single-year economic threshold had been reduced by an arbitrary amount in order to prevent an unwanted increase of the weed population.

A more analytical approach was taken by Cousens (1986). He devised a simulation model that incorporated the available information on the population dynamics of two grass weeds, the effects of weed density on cereal yields and also the costs of herbicide application and prices of marketed grains. By systematically varying the threshold density in every set of successive simulation runs over years, he finally arrived at a threshold density that gave the greatest economic benefit for the time considered. Though far from being applicable in everyday practice, this approach takes into account the effects of competition and the population dynamics of weeds, if only superficially.

11.5 Discussion and conclusions

The research work reported above depicts not only the development of some aspects of crop production during the past three decades but also the change in the

Table 18. Threshold densities for some weeds in winter wheat and winter barley, early in spring (Bartels et al., 1983).

	Plants m^{-2}
Apera spica venti	20
Alopecurus myosuroides	30
Galium aparine	0.1
Fallopia convolvulus	2
Vicia sp.	2
Sum of other dicots	40

concepts and aims of weed control. The intensive use of agrochemicals and farm mechanization – though very successful in increasing crop yield – intensified the negative impact of industrial plant production on the environment. Soil compaction and erosion, contamination of soil and water by nitrate and pesticides, and the loss of habitats for wild plants and animals are side-effects causing public concern.

In order to reduce or even to avoid this negative impact on the environment, the concept of integrated plant production has been developed. This concept includes the notion of reducing the use of all directly acting chemical agents in crop husbandry, such as pesticides, and, wherever possible, substituting the more 'self-regulating' effects of other agronomic measures, such as carefully choosing crop and cultivar, crop rotation, and tillage method and intensity.

As has been shown for the case of firm-soil mulch-husbandry there are limits to employing this concept. Infestations of perennial weeds can only be controlled by repeated application of a non-selective foliar-acting systemic herbicide. Hence, for each situation a balance has to be struck between the necessity to control soil erosion by mulch-husbandry and the intention to restrict the use of herbicide. The decision depends partly on the persistence and mobility of the herbicide in the soil, partly on the economic necessity to grow crops that enhance infestation by perennial weeds.

'Break' crops are an efficient tool to control many weeds, especially those weeds that are troublesome in particular field crops (e.g. some annual weeds in winter cereals). The different planting time of 'break' crops implies some destruction of existing weeds and allows effective herbicides to be applied during the growth of the 'break' crop. These means have been used in the case of volunteer barley, which is particularly troublesome in sugar beet crops grown in a mulch-husbandry system. Since volunteer barley may be regarded as a representative of most annual weeds that can germinate in autumn as well as in spring, the system developed to control these weeds may be considered exemplary. Competition by a fast-growing green manure crop is sufficient to suppress most autumn-germinated weed plants to such an extent that it is unnecessary to apply a non-selective herbicide onto the frost-killed green manure crop. Spring-germinated weed plants are destroyed either by intense seed bed preparation and/or by post-emergence herbicide application.

The concept of integrated plant production has led to a re-appraisal of the role of weeds in integrated pest control. For instance, sugar beet stand density has been improved in no-plough situations by the presence of weeds, because of less damage to sugar beet seedlings by collembolans and other pests (El Titi, 1986). Many members of the epigeous soil fauna that act as predators of plant pests will colonize fields more readily if a weed population of great species diversity is present.

Integrated crop production includes the use of economic threshold density. Chemical control is carried out if the weed abundance exceeds the threshold density, i.e. at the weed density that cost of control equals the benefits. This supervised concept requires the farmer to restrain from prophylactic control measures, i.e. the pre-emergence application of soil acting herbicides. To postpone a control measure until the weed abundance reaches a certain level implies that the risk of having to control weeds is increased, but this is justified by the high frequency of cases in which herbicides have been applied without financial benefits. In sugar beet, for instance, the improved effectiveness of herbicide combinations applied in repeated small doses encourages post-emergence weed control. It has been shown that up to 50 days after planting sugar beet, weeds do not impair crop growth (de Groot & Groeneveld, 1986).

So far, the use of threshold densities as a basis for deciding on weed control measures has been accepted by only a small minority of farmers in West Germany. Acceptance is impaired by the farmer's inability or unwillingness to quantify the weed population present, a risk-avoiding attitude that rates weed populations just below the economic threshold as likely to cause future weed infestations. Also, most farmers are unprepared to accept the sight of weeds in fields.

Nevertheless, the application of 'integrated' weed control methods is enforced by the government in some cases. Dinozeb-acetate, the only herbicide available for post-emergence weed control in grain legumes, has recently been banned in West Germany. Therefore, chemical weeding has had to be replaced by mechanical weeding.

Faba beans planted with wide row distances allow almost complete weed control between rows by repeated hoeing. To control weeds at least partly within rows the old method of ridging has been used, i.e. burying the weeds within the rows by a soil cover up to 5 cm high. This measure not only reduces weed density but also increases Faba bean yield significantly, because of the improved resistance of bean plants to lodging (Baeumer, 1988).

Various conclusions can be drawn from the problems discussed and the research results presented in this chapter. Because of their increasing effectiveness herbicides initially became the predominant and in some cases the only means to prevent negative effects of weeds and volunteer crops on field crop production. This opened the way to changing farming systems towards more specialized cropping and to applying new techniques like no-plough cultivation, which only appear to be feasible when herbicide use is increased. However, altered economic conditions and the impact of extensive use of herbicides on the environment necessitate a re-appraisal of the goal and methods of weed control. In many situations containment of the weed population rather than complete eradication will suffice. There is a need for an integrated system-approach to weed control. It includes both direct and indirect effects of crop management on the growth and propagation of weeds. The elements of such a system are crop competition, cultivation and crop rotation, especially the use of green manure crops. The increased emphasis on processes that regulate weed growth without additional inputs can reduce the costs and the environmental impact of herbicide application.

Decisions about the necessity for weed control actions should be based on the economic threshold concept. The long-term effects of such a weed management system can be quantified by modelling weed population dynamics, taking into account changes in seed bank size. For this, more information is needed about seed production, dormancy and germination patterns, mortality of seeds and weed plants. These models should explicitly include a simulation of the growth of interfering weeds and crops, so that the possible effect of competition on crop yield can be predicted. Dynamic simulation models that take into account the interaction between weeds and crops and also the varying environmental conditions, such as those proposed by Kropff (1988) may play a role in the development of integrated control systems.

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12 On descriptive and mechanistic models for inter-plant competition, with particular reference to crop–weed interaction

C.J.T. Spitters

12.1 Introduction

Species growing together in mixed stands compete with each other for growth-limiting resources such as light, water and nutrients. The study of competitive phenomena in agricultural situations started around 1900 with experiments where different species – or cultivars of the same species – were grown alone in monocultures and together in mixtures. It was found that the yield of a species in mixture, when surrounded by other species, could deviate substantially from its yield when grown in monoculture surrounded by plants of its own species. Sometimes, the higher-yielding types in monoculture were the lower-yielding types in mixture, and vice versa (Montgomery, 1912). For a long period of time, the experimental results were only presented in tables or histograms (e.g. Sakai, 1955), and the general relationships were not recognized. Measures of competitive ability – if any – were restricted to specific designs (e.g. Stadler, 1921, p. 32). General methods of analysis and experimental set-up were lacking.

This situation changed in 1960 with the publication of *On Competition*. In that paper, de Wit introduced a general experimental design (the replacement experiment) to study the effects of competition between different plant species, together with a model to analyse the results of this type of experiment. The publication was a breakthrough and in the years that followed, the replacement approach was applied in many papers.

In the 1960s and 1970s a wide variety of competition models was introduced in agronomic literature. Nearly all of them were additive in that they partitioned the yield of a species in mixture into a linear, additive combination of parameters. These parameters characterized monoculture performance and several types of competitive ability (reviews by Trenbath, 1978; Spitters 1979, pp. 27-36). Neither of these models found wide application because each of them was restricted to a specific experimental design (e.g. a competitional diallel) and required relatively many parameters. With the de Wit model, in contrast, estimates from a particular experiment could easily be transposed to a different situation with another combination of the species studied. The universality of this model is based on the underlying empirical, non-linear relationship. The additive models, in contrast, rely upon an unconscious, linear expansion of the effects in purely statistical terms.

The de Wit (1960) approach is based on the replacement design. In a replacement series, a range of mixtures is generated by starting with a monoculture of one species and progressively replacing plants of that species by plants of the other species until a monoculture of the latter is produced. All monocultures and mixtures are grown at equal plant density (Figure 74), and basically de Wit assumed a constant total density.

In weed research, however, replacing one species by another species is of less practical interest than adding plants of the weed species to a given plant density of the crop (Figure 74). Several functions have been suggested to relate crop yield to weed density in these addition experiments (review by Cousens, 1985a, b). For these models too, the tight confounding with the particular experimental design prohibited wider application.

In the early 1980s, Suehiro & Ogawa (1980), Wright (1981), Spitters (1983a, b) and Watkinson (1981, 1984), introduced models that described the competition effects over a range of populations, varying in mixing ratio and total density. These models could handle both addition and replacement experiments. Like the de Wit model, they were based on a hyperbolic equation for the relationship between the yield of a species in monoculture and its plant density.

The above models are static; they describe the results at only one time. By taking into account the time course of the model parameters, de Wit c.s. developed a dynamic competition model (de Wit & Baeumer, 1967; Baeumer & de Wit, 1968; de Wit, 1970; de Wit & Goudriaan, 1978). By comparison with the static approach, the dynamic approach has the advantage of giving a better insight into the competitive phenomena and of being more flexible. For instance, with this model Spitters & van den Bergh (1982) evaluated the effects of time and efficiency of weed control, and the importance of relative time of emergence and plant height of crop and weeds.

The aforementioned models are all empirical, as they describe the outcome of the competition process by some empirical, regression equation. They do not elucidate the underlying eco-physiological principles of the competition process itself. Recently, it has been demonstrated that the growth of plants in competition can be described by expanding existing models of crop growth to include the

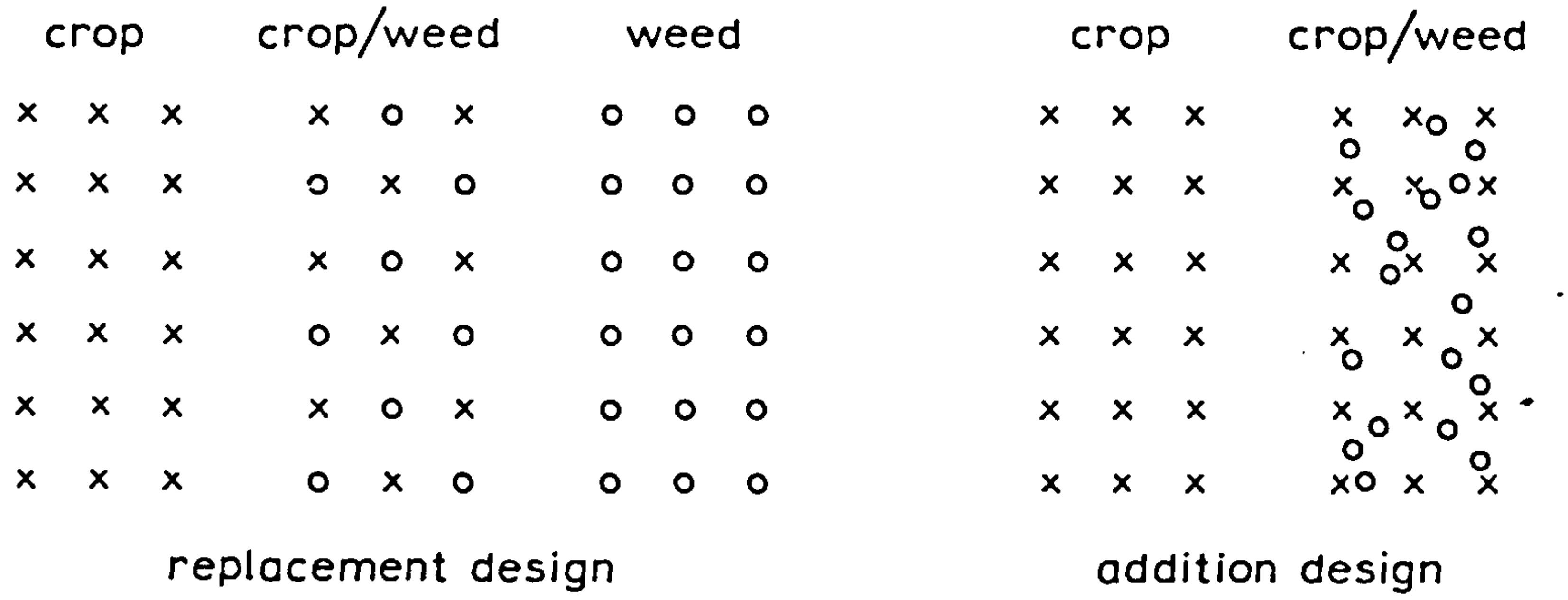


Figure 74. Replacement and addition design with crop plants (×) and weed plants (o).

simultaneous absorption of light, water and nutrients by the different species in a mixed vegetation (Spitters & Aerts, 1983; Spitters, 1984; 1989). The mechanistic approach unlocks competition research for an influx of crop physiological knowledge. In this chapter, both a regression approach and an eco-physiological approach to analyse inter-plant competition are discussed. Crop-weed interaction is highlighted.

12.2 The descriptive, regression approach

Over a wide range of densities, yield of total biomass and often also yield of a certain plant organ are asymptotically related to plant density (Holliday, 1960; Donald, 1963); the relationship being characterized by a rectangular hyperbola (Shinozaki & Kira, 1956; de Wit, 1960, 1961). This equation for intra-specific competition was expanded by Suehiro & Ogawa (1980), Wright (1981) and Spitters (1983a) to allow also for effects of inter-specific competition. Below, I will discuss this regression model, using the parameterization given in an earlier paper (Spitters, 1983a). The relationships are illustrated with results of an experiment in which maize and a natural population of barnyard grass (*Echinochloa crus-galli* (L.)P.B.) were grown in monocultures and mixtures in the field in Wageningen in 1983 (Spitters et al., 1989). The model will be applied to describe crop yield losses caused by weeds, and long-term dynamics of soil populations of weed seeds.

12.2.1 Model description

Crop yield is related to plant density, according to

$$Y = N/(b_0 + b_1N) \quad \text{or} \quad 1/W = N/Y = b_0 + b_1N \qquad \text{Equation 45}$$

in which Y is the biomass yield (g m^{-2}), N the plant density (plants m^{-2}), W the average weight per plant (g plant^{-1}), and b_0 and b_1 are regression coefficients. The parameter $1/b_0$ is the apparent weight of an isolated plant, and $1/b_1$ represents the apparent maximum yield per unit area (Figure 75).

According to Equation 45 and Figure 75B, $1/W$ is linearly affected by adding plants of the same species. That suggests that adding plants of another species also affects $1/W$ linearly, and Figure 76B gives credence to this assumption. Hence, for a crop in the presence of weeds, the reciprocal of the per-plant weight can be written as

$$1/W_{cw} = b_{c0}+b_{cc}N_c+b_{cw}N_w \quad \text{or} \quad Y_{cw} = N_c/(b_{c0}+b_{cc}N_c+b_{cw}N_w) \qquad \text{Equation 46a}$$

and for the associated weeds as

$$1/W_{wc} = b_{w0}+b_{ww}N_w+b_{wc}N_c \quad \text{or} \quad Y_{wc} = N_w/(b_{w0}+b_{ww}N_w+b_{wc}N_c) \qquad \text{Equation 46b}$$

where the first subscript indicates the species whose yield is being considered, and the second subscript its associate. The subscript *c* refers to the crop and *w* to the weed. In Equation 46a, b_{cc} measures the effect of intra-specific competition, while

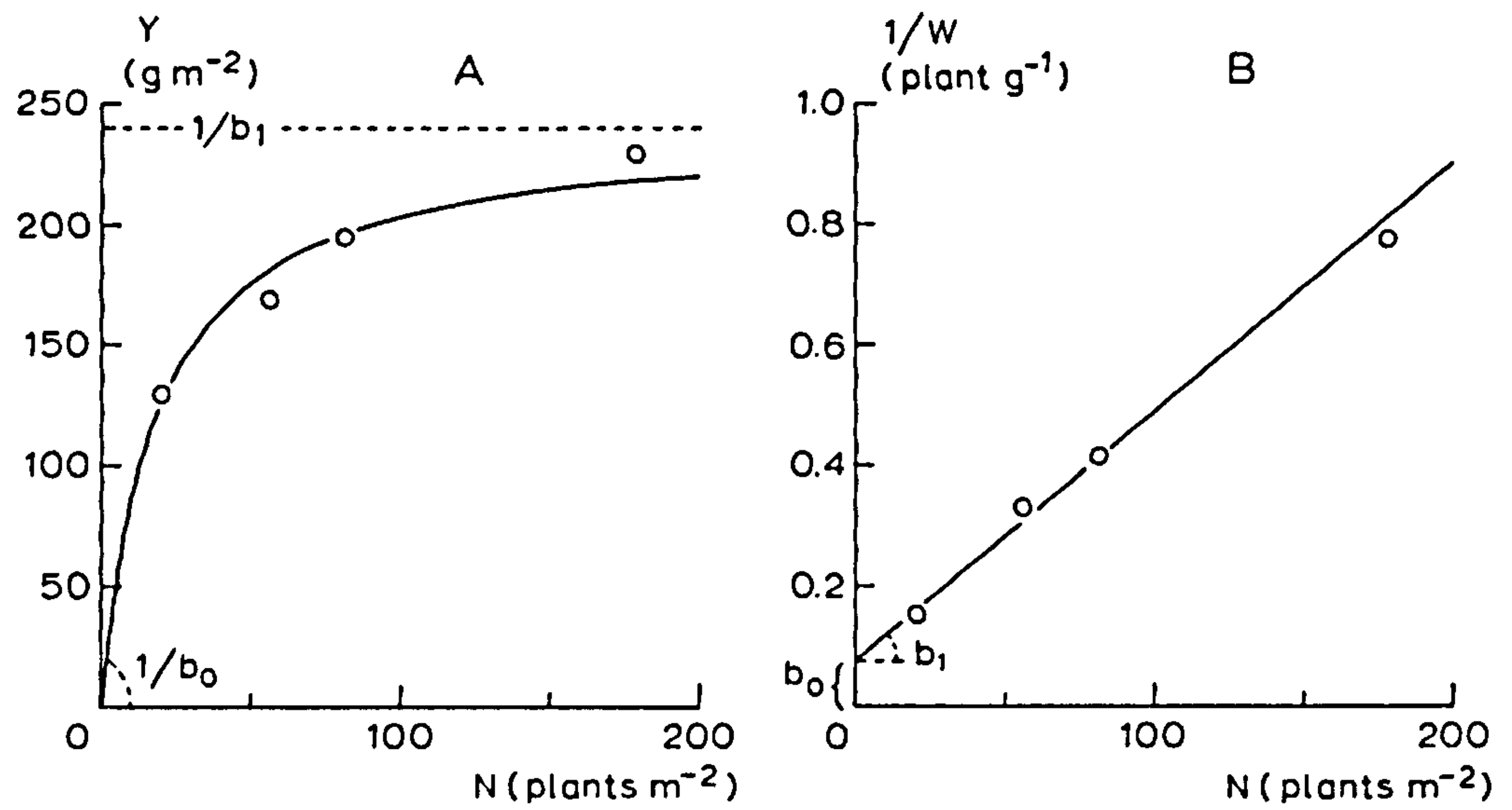


Figure 75. Density response of barnyard grass in monoculture, illustrating the meaning of the regression coefficients (b_0, b_1). Plots of (A) biomass per unit area, and (B) the reciprocal of per-plant weight against plant density. Fitted equation: $1/W=0.075+0.0042N$.

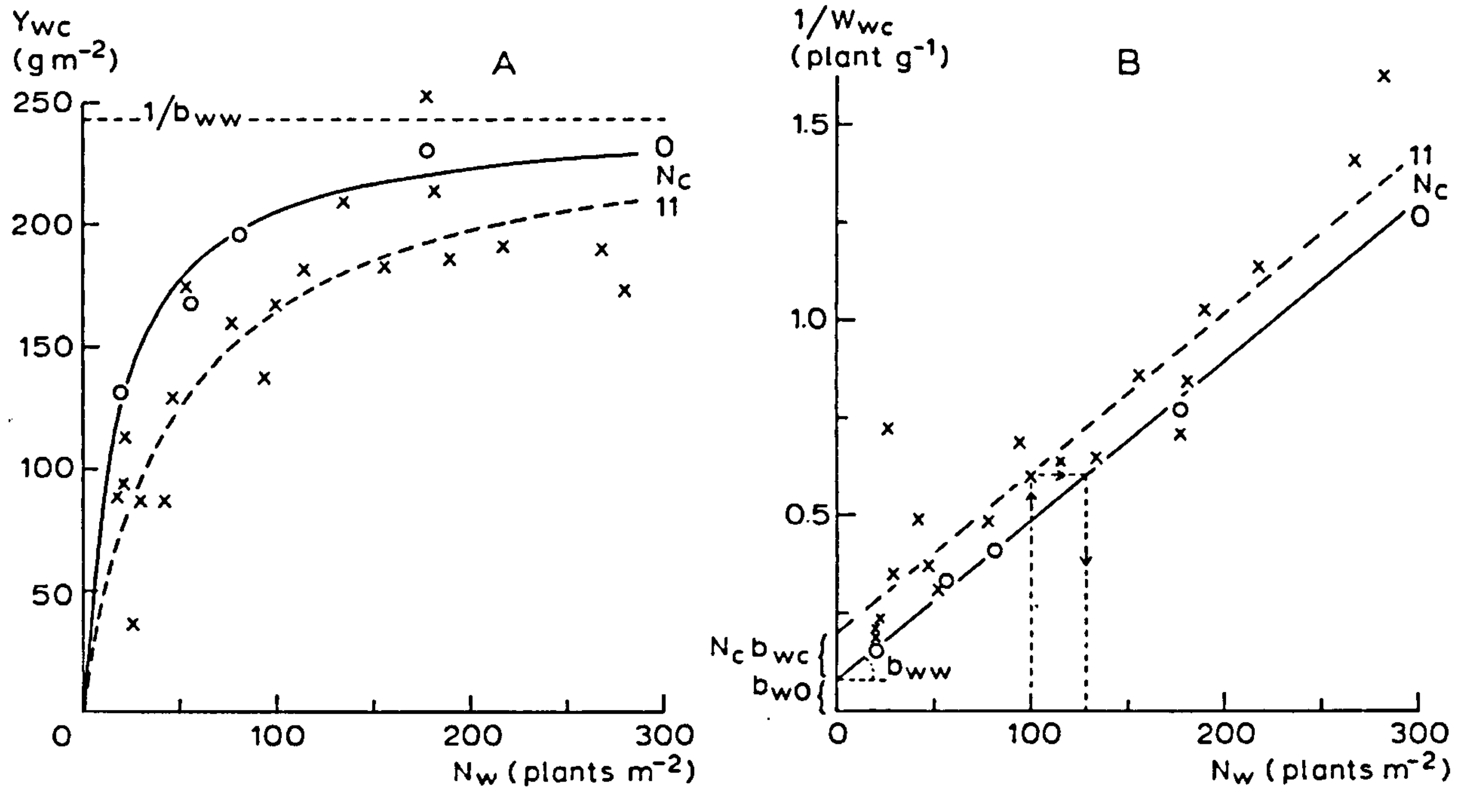


Figure 76. Density response of barnyard grass in monoculture (o, solid curves, $N_c=0$), and in mixture with 11 maize plants m^{-2} (×, dashed curves, $N_c=11$), illustrating the meaning of the regression coefficients (b_{w0}, b_{ww}, b_{wc}). The dotted lines indicate that addition of 11 maize plants had the same effect on the per-plant weight of barnyard grass as addition of 29 barnyard grass plants. Fitted equation: $1/W=0.077+0.0041N_w+0.0107N_c$.

b_{cw} measures the effect of inter-specific competition. The ratio b_{cc}/b_{cw} characterizes the relative competitive ability of crop and weed, with respect to the effect on crop yield. Figure 76B shows that the addition of 11 maize plants to a pure stand of barnyard grass had the same effect on $1/W$ of barnyard grass as the addition of 29 barnyard grass plants. Thus for a barnyard grass plant, the presence of one maize plant was similar to the presence of 2.6 other barnyard grass plants.

To meet the assumption of homogeneity of variances, the regression coefficients are estimated from Equation 46 by non-linear regression of Y on the plant densities. When a wide yield range is covered, the yields tend to be distributed log-normally, and the regression coefficients are therefore estimated by using non-linear regression to fit the logarithm of yield to the logarithm of the right-hand side of Equation 46 (Spitters et al., 1989).

The extension of de Wit's model to unify competition and spacing experiments was based on certain, restrictive prepositions (de Wit, 1960, p. 61; Baeumer & de Wit, 1968; Spitters, 1979, p. 83). Since these assumptions are in general not valid, analysis of competition experiments remained restricted to designs with constant total density, i.e. the replacement designs, until the introduction in the early 1980s of the generalized hyperbolic models, mentioned above. However, when in de Wit's 4-parameter model for a binary mixture, his β_1 in his Equation 8.5 is split up into β_{11} for Species 1 and β_{21} for Species 2, and similarly β_2 into β_{12} for Species 1 and β_{22} for Species 2, the result is a 6-parameter model that is equivalent to Equation 46.

12.2.2 *The special case of crop–weed competition*

A crop is usually grown at a constant plant density (Figure 74), which simplifies Equation 46 to

$$1/W_{cw}=a_0+b_{cw}N_w \quad \text{and} \quad 1/W_{cc}=b_{c0}+b_{cc}N_c=a_0 \qquad \text{Equation 47}$$

where $1/a_0$ is the average weight per plant in the weed-free crop. The yield of the weedy crop (Y_{cw}) relative to the weed-free yield (Y_{cc}) is then

$$Y_{cw}/Y_{cc}=a_0/(a_0+b_{cw}N_w)=1/(1+d_wN_w) \qquad \text{Equation 48}$$

where the 'damage coefficient' $d_w=b_{cw}/a_0$ characterizes the apparent fractional yield loss caused by the first weed plant added to the crop (Figure 77).

The aggregate yield reduction due to a multi-species infestation is found by expanding Equation 48 additively according to $d_wN_w=d_1N_1+\ldots+d_nN_n$ for the weed species 1 to n. The damage coefficients of the individual weed species can be estimated from separate trials with the respective weeds. Non-linear regression of crop yield on weed density, allows d_w and Y_{cc} to be estimated.

Since the damage relation is characterized by a single parameter (d), the model also facilitates the comparison of results from different experiments.

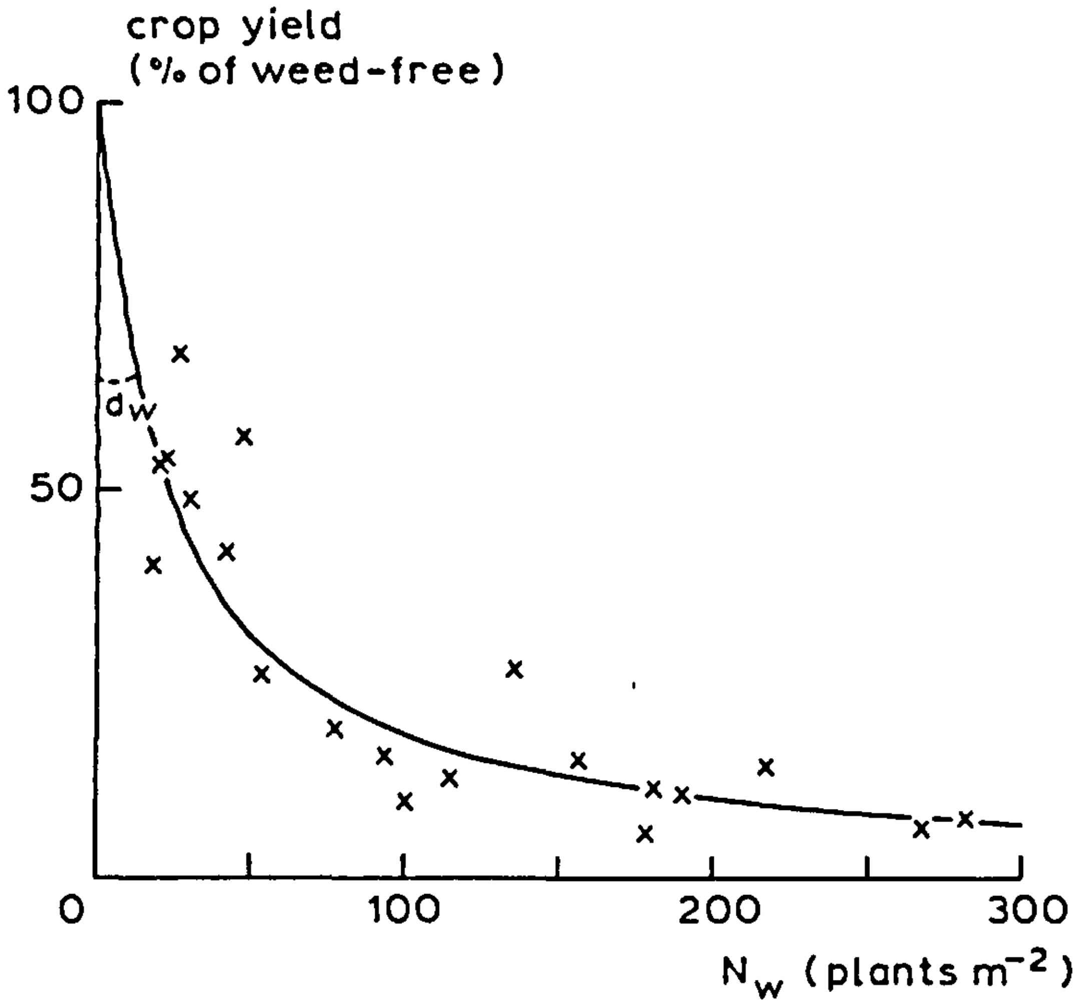


Figure 77. Yield of maize, expressed as % of weed-free yield, in relation to the number of barnyard grass plants (N_w). The damage coefficient (d_w) characterizes the apparent yield loss caused by the first weed plant added to the crop. Fitted equation: $Y_{cw}/Y_{cc} = 1/(1+0.044N_w)$.

12.2.3 Use in decision-support systems for weed control

Equation 48 can be used to predict the expected crop yield loss from the observed number of weed plants, and this prediction may be used in deciding whether a control measure is required. Counting the number of weed plants, however, takes time. Moreover, the relationship between crop yield loss and plant number of the given weed species varies between sites. This variation is thought to be primarily caused by the difference in time of emergence of crop and weed, which varies with the condition of the seed bed. Furthermore, within the same field, a species shows considerable variation in plant size; the big plants are more effective in competition than the small ones.

A better measure for the size of the weed infestation is derived as follows. The competitive ability of a species in mixture is strongly determined by its leaf area at the moment inter-plant competition starts (Subsection 12.3.3). Spitters & Aerts (1983) concluded, therefore, that the leaf area index of a weed species (L_w) early in the season, relative to that of the crop (L_c), will be a better action criterion for weed control than plant number. It can be derived that in Equation 48, N_w has to be replaced by L_w/L_c and the damage coefficient has to be expressed on a leaf area basis. This new damage coefficient $d'_w = d_w N_c{}'L_c/{}'L_w$, where $'L_c$ and $'L_w$ are the initial per-plant leaf areas of crop and weed, respectively. During early growth, the ratio L_w/L_c usually changes relatively little because differences in early leaf area are mainly caused by differences in starting position rather than by differences in relative growth rate (Equation 57). Use of the total leaf area index for each species accounts for the large variation in plant size within the species and for the difference in time of emergence between the species.

In the aforementioned experiment, 50% plant emergence of maize was two days later than that of barnyard grass. Three weeks after emergence of maize, the ratio between the per-plant leaf areas of maize and barnyard grass was 5.4. Thus, at the density of 11 maize plants per m^2, the value of 0.044 m^2 $plant^{-1}$ for the damage coefficent (Figure 77) can be replaced by a value of $11 \times 5.4 \times 0.044 = 2.6$ on a leaf area basis.

A practical measure of the effective leaf area of a species is its percentage of ground coverage. This can be estimated visually; or more precisely from photographs taken vertically above the vegetation or by viewing the vegetation through a frame divided into a large number of gridsquares and counting the gridsquares that are more than half-filled by the species (Burstall & Harris, 1983; Steven et al. 1986). Ground coverage of the weed species, relative to the crop, can be monitored in the field and can be the basis for a decision-support system for weed control (Feyerabend et al., 1976; Marx, 1980).

12.2.4 *Dynamics of soil seed population*

Weeds are not only controlled to minimize their negative effects in the current crop, but also to anticipate for these effects in the future crops. This type of strategic control is directed towards minimization of the soil population of weed seeds.

A simple model to keep track of the seed bank of an annual weed is depicted in Figure 78. The seed population is depleted annually by a fraction of P_g. A fraction P_e of the removed seeds succeed in establishing, and the established plants produce S_n seeds per plant, a fraction P_b of which is incorporated in the soil seed population. Thus, the net annual increment of the seed population is

$$\Delta n_t = (-P_g + P_g \cdot P_e \cdot S_n) \cdot n_t \qquad \text{Equation 49}$$

The early models of seed population dynamics of arable weeds assumed a constant seed production per plant, i.e. a constant value of S_n, irrespective of weed density (Cussans & Moss, 1982; Murdoch & Roberts, 1982; Wilson et al., 1984). Use of Euation 46, however, introduces the effect of weed density on the seed production per plant and, moreover, it gives an estimate of the concomitant yield reduction of the crop (Spitters & Aerts, 1983; Firbank et al., 1984).

To obtain a measure more or less independent of the fertility level of the site, weed seed production is expressed relative to the apparent maximum number of seeds produced per m^2, when grown in competition with the crop

$$Y_{wc}/Y_{wc}(N_w = \infty) = c \cdot N_w/(1 + c \cdot N_w) \qquad \text{Equation 50}$$

where $c = b_{ww}/(b_{w0} + b_{wc}N_c)$ and $Y_{wc}(N_w = \infty) = 1/b_{ww}$. The influence of a second weed species (x) is introduced by expanding the denominator of the expression for c by the term $b_{wx}N_x$. In Equation 50, Y is expressed in number of seeds produced

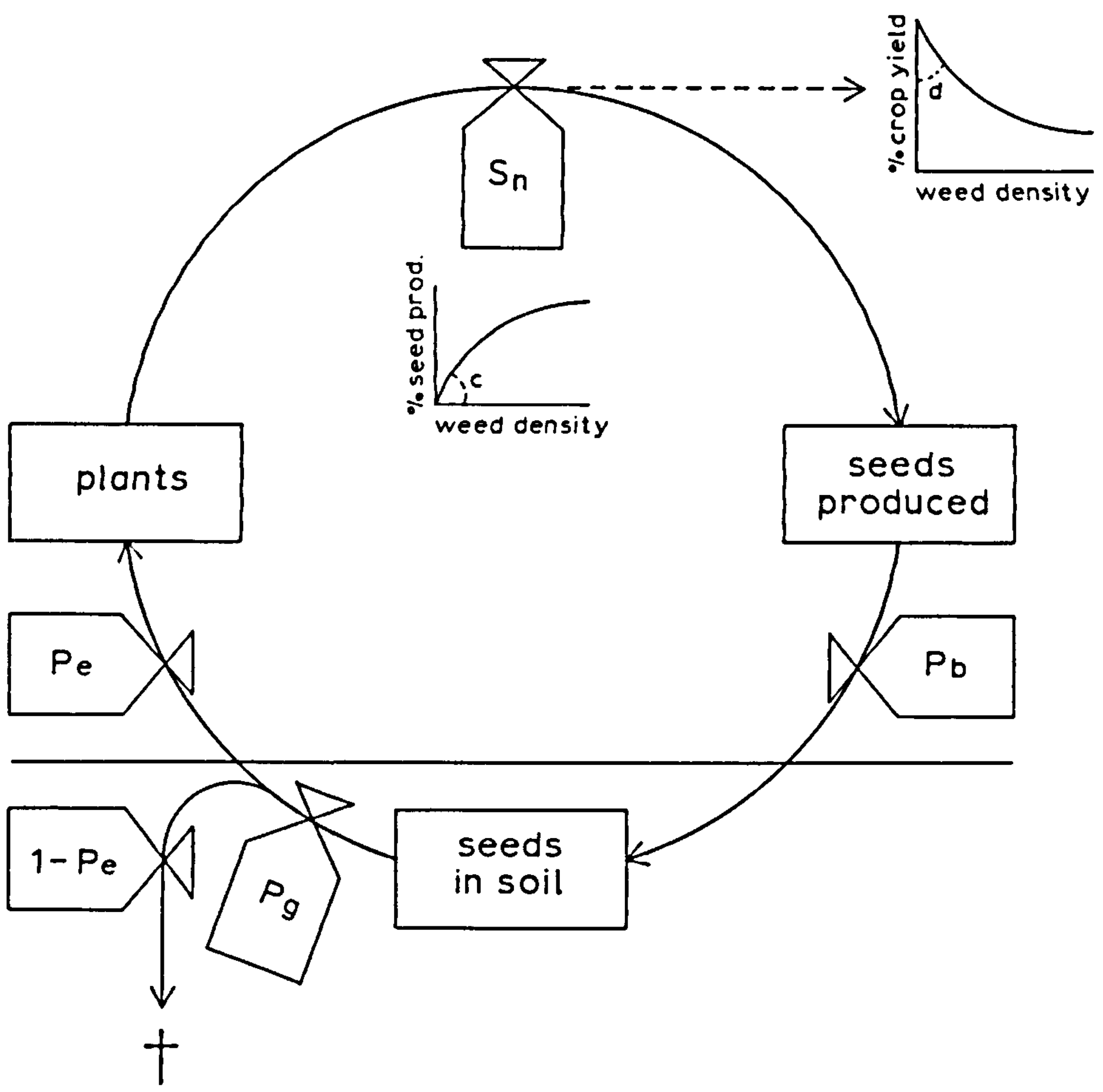


Figure 78. A flow diagram for the population cycle of an annual weed. The boxes represent state variables (numbers m^{-2}); P_g, P_e and P_b are fractions of depletion, seedling emergence, and seed burial, respectively (yr^{-1}); S_n is the number of seeds produced per plant.

per m^2, rather than in biomass, by taking into account the seed/biomass ratio of the weed and the average seed weight. The parameter c characterizes the initial slope of the density response and c/b_{ww} the seed production per plant at low weed density in the crop. Actual weed seed production is estimated by multiplying Equation 50 by the apparent maximum seed production ($1/b_{ww}$), which is set proportional to the predicted or observed weed-free crop yield.

Parameter values typical for wild oat (*Avena fatua* L.) in barley are $P_g = 0.68$, $P_e = 0.15$, $P_b = 0.60$, $c = 0.00124$, $d = 0.00116$, $1/b_{ww} = 30120$ seeds m^{-2} at a weed-free yield level of 5000 kg ha^{-1} (85% d.m.) (references in Spitters, 1989). In Figure 79, the effect of a post-emergence herbicide, killing 95% of the emerged weed plants, is illustrated in relation to the application frequency. In this situation, controlling wild oat once every second year restricted yield losses to 5% or less. Such a control strategy would then be sufficient because with yield benefits of less than 5%, the benefits of the application usually do not outweigh the cost. The long-term population dynamics are, however, sensitive to the percentage of weed plants surviving the control measure. This also stresses the importance of reliability of control, particularly to avoid control failures, as was shown by Vleeshouwers & Streibig (1988).

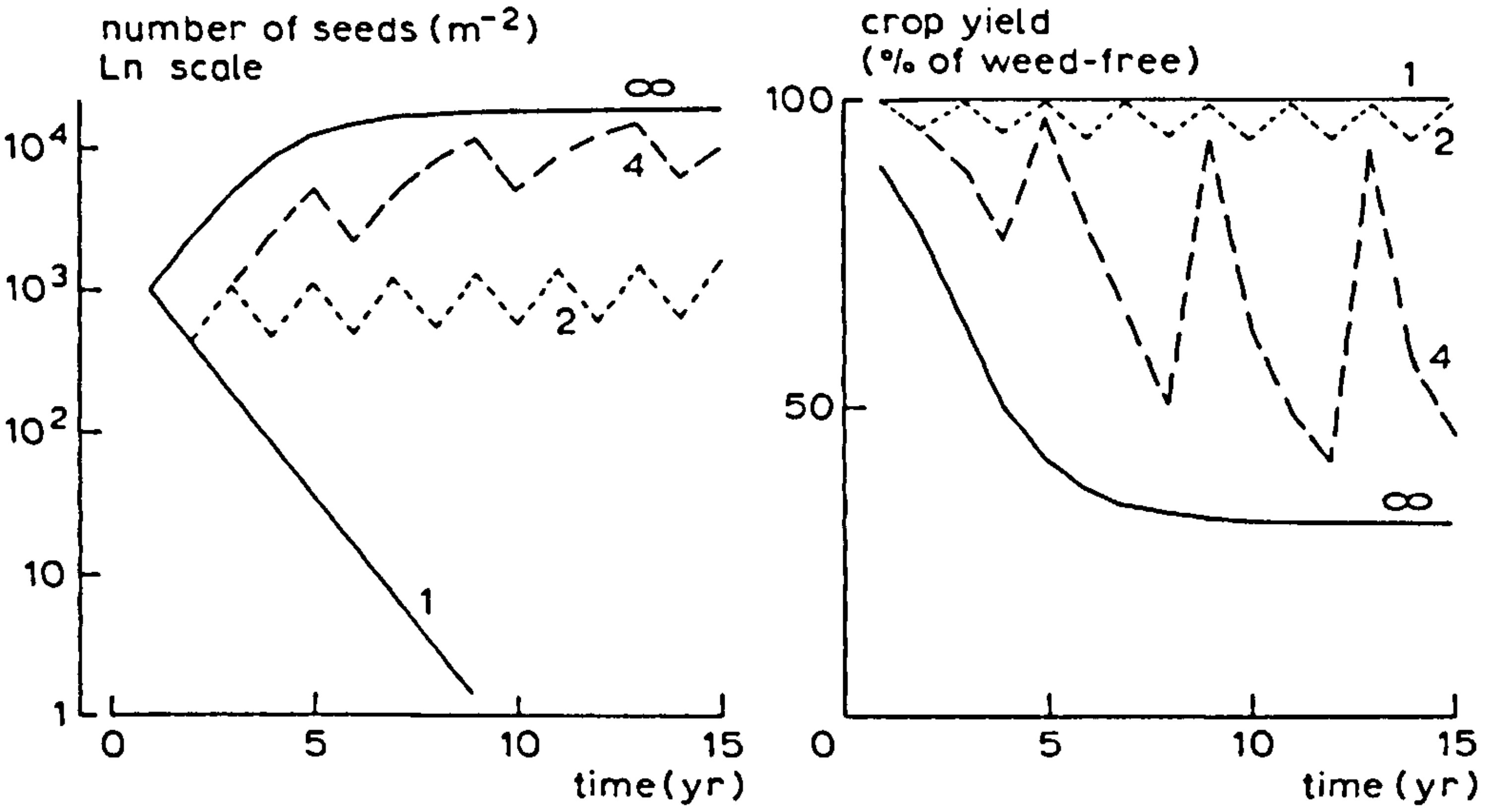


Figure 79. Simulated time course of soil seed population of wild oat, and the concomitant yield loss of spring barley. Herbicides were applied either annually, once every 2 or 4 years, or not at all. Herbicide application killed 95% of the weed plants.

12.3 The eco-physiological approach

Inter-plant competition can be defined as that interaction between the plants in which they restrict each other's growth by capturing growth-limiting resources from one another. Weeds reduce crop yield mainly because they absorb light, water and nutrients that would otherwise be used for crop growth. The competition process can therefore be described in terms of the distribution of the growth-limiting factors over the species in mixture and the way each species uses the amounts acquired in dry matter production. I will illustrate this eco-physiological approach with a very simple model of competition for light (Figure 80; Spitters, 1984). More detailed simulation models have been published elsewhere (Spitters & Aerts, 1983; Spitters, 1989).

12.3.1 A very simple model of competition for light

The growth rate of a canopy is more or less linearly related to its light interception (review by Gosse et al., 1986). Since light interception is exponentially related to total leaf area, the growth rate of the canopy is

$$\Delta Y = (1 - \exp(-k \cdot L)) \cdot PAR_0 \cdot E \qquad \text{Equation 51}$$

in which ΔY is the daily growth rate (g m^{-2}d^{-1}), L the leaf area index (m^2 leaf m^{-2} ground), k the extinction coefficient, E the average light utilization efficiency (g d.m. MJ^{-1}), and PAR_0 the incoming photosynthetically active radiation (MJ m^{-2}d^{-1}). Incoming PAR (wave bands 400-700 nm, 'light') amounts to 50% of total incoming solar radiation (300-3000 nm).

In a mixture of identical species, each species intercepts an amount of light that

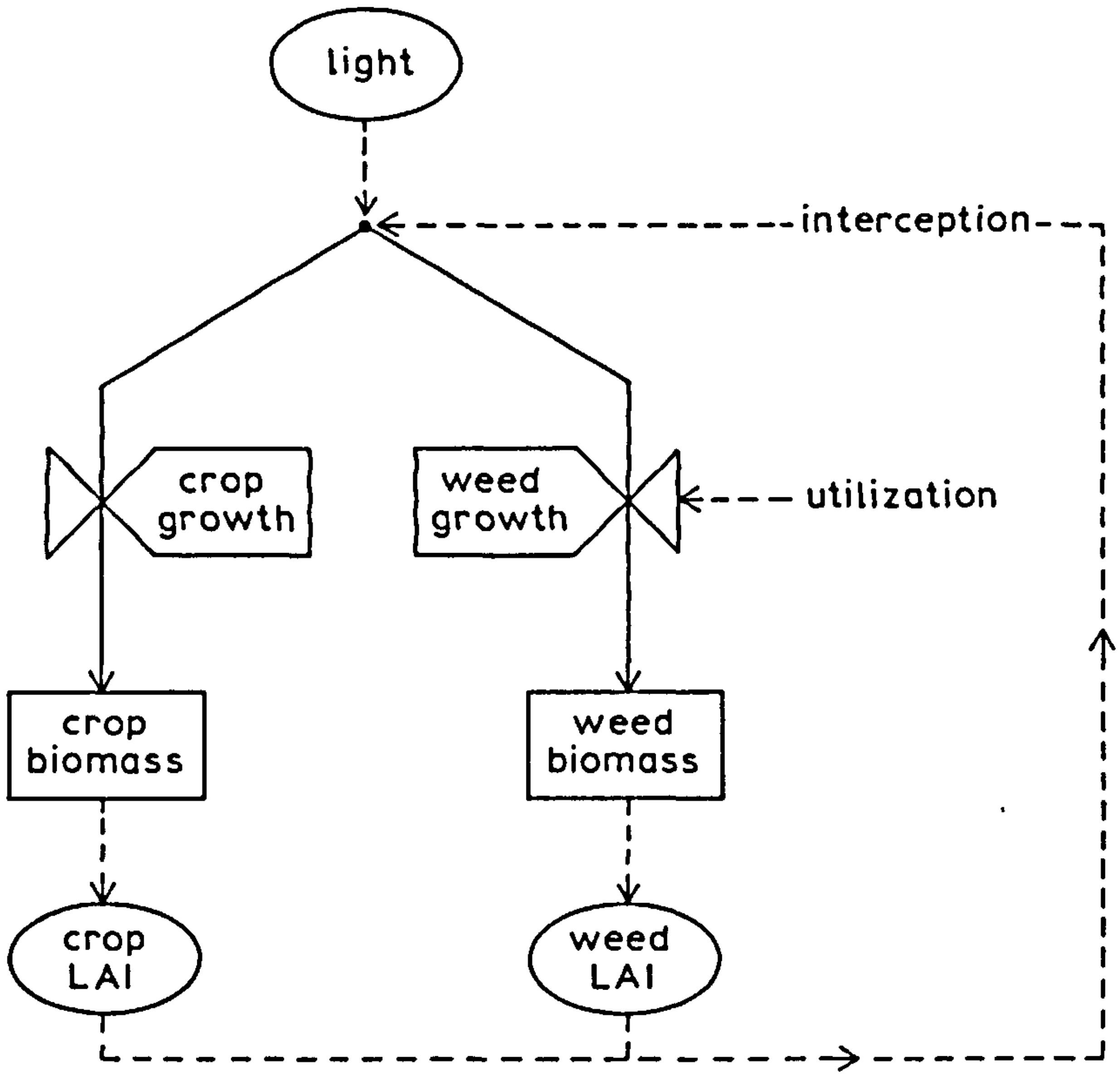


Figure 80. Simplified scheme for the simulation of competition between crop and weed for light.

is proportional to its share in the total leaf area. Following the proportionality between growth and light interception, Equation 51 gives for the growth rate of Species 1 in mixture with Species 2

$$\Delta Y_1 = \frac{L_1}{L_1+L_2}(1 - \exp(-k\cdot L_1 - k\cdot \mathrm{L}_2))\cdot PAR_0\cdot E_1 \qquad \text{Equation 52}$$

where the subscripts refer to Species 1 and 2, respectively.

The share of a species in total growth increases, however, when it intercepts more light per unit of leaf area. This is achieved with a greater extinction coefficient, e.g. because of a more horizontal leaf angle distribution, and with a greater plant height. In the distribution term of Equation 52, the leaf areas are then weighted according to their respective light absorption. In a mixture of short and tall species, the light interception is set proportional to the light intensities at half of the plant heights. For Species 1

$$\Delta Y_1 = \frac{l_1\cdot k_1\cdot L_1}{l_1\cdot k_1\cdot L_1 + l_2\cdot k_2\cdot L_2}(1 - \exp(-k_1\cdot L_1 - k_2\cdot L_2))\cdot PAR_0\cdot E_1 \qquad \text{Equation 53a}$$

Assuming the leaf area of a species evenly distributed over its plant height (Figure 81A) gives the following for the relative light intensity of Species 1 at half of its height (H_1)

$$l_1 = \exp(-\tfrac{1}{2}k_1\cdot L_1 - \frac{H_2 - \frac{1}{2}H_1}{H_2}k_2\cdot L_2) \qquad H_2 > \tfrac{1}{2}H_1 \qquad \text{Equation 53b}$$

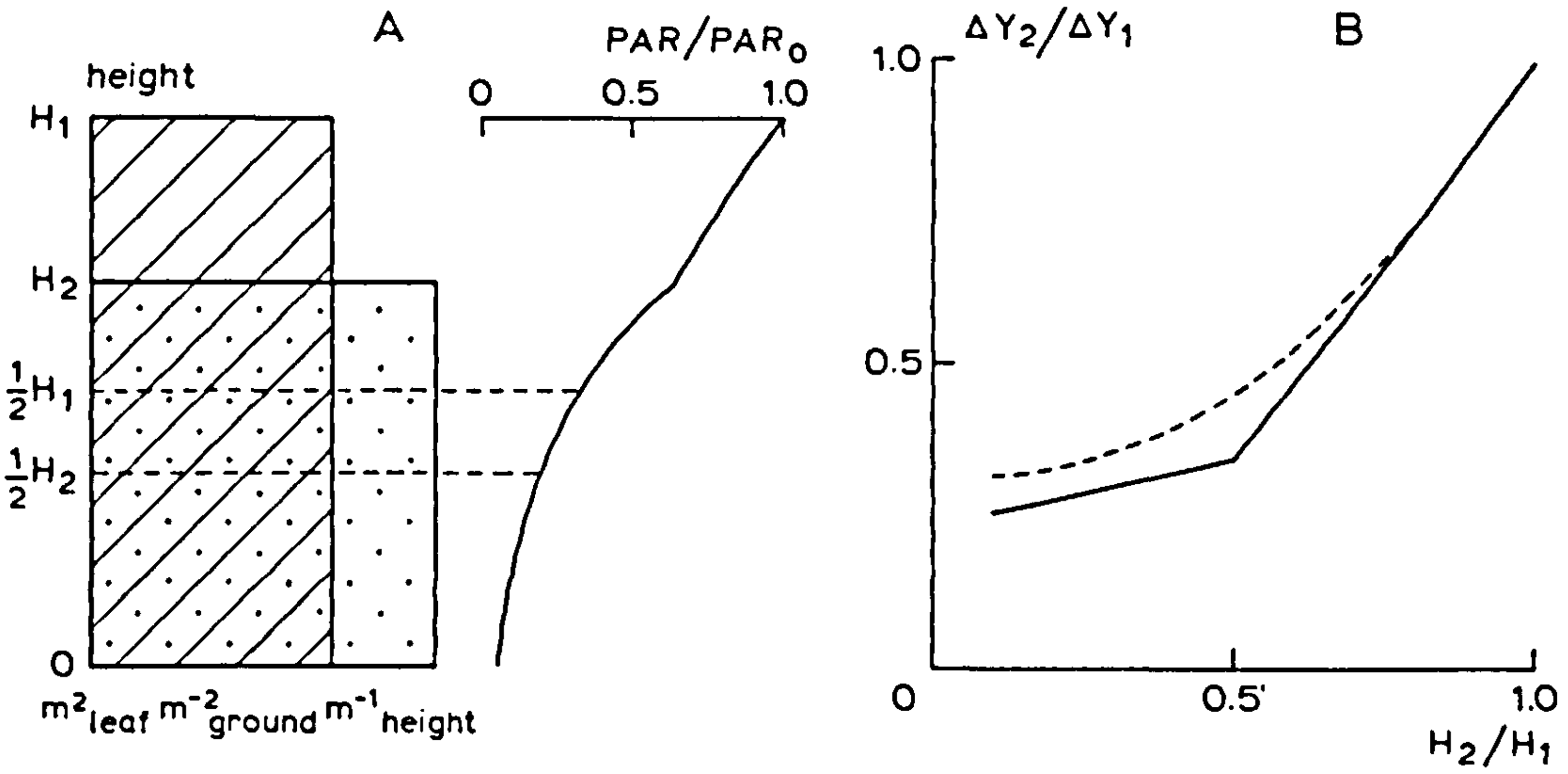


Figure 81. Schematic representation of the summary model of competition for light. A: In the summary model, the share of each species in total light interception is assumed to be proportional to its leaf area, weighted by the light intensity at half of its plant height. This intensity is calculated from the exponential light profile (PAR/PAR_0), assuming a uniform distribution of leaf area over plant height (H) for each species. B: The ratio between the growth rates of the two species in mixture ($\Delta Y_2/\Delta Y_1$) simulated by the summary model (solid curve) and by a detailed model (dashed curve). Each of the two species had a leaf area index of 2.

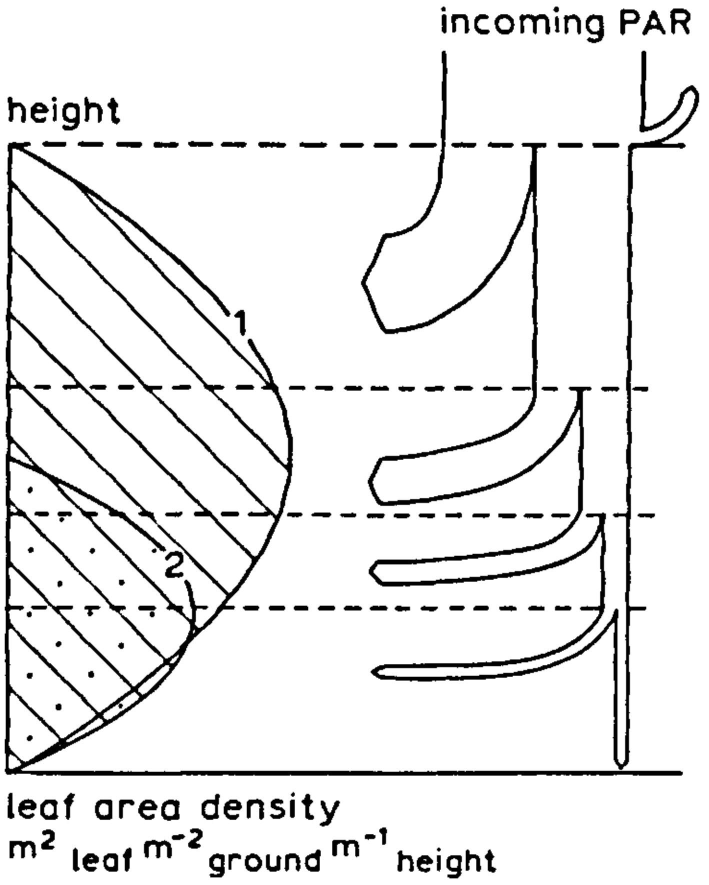
Compared with a detailed model of competition for light, Equation 53 gave a good approximation (Figure 81B).

In the detailed approach to competition for light, the light profile within the canopy is simulated and light utilization is calculated for each canopy layer separately (Figure 82; Spitters & Aerts, 1983; Spitters 1989). For that, the canopy is stratified into various, horizontal height layers. The illumination intensity at the various heights is derived from the exponential light profile. This is done for sunlit and shaded leaf area separately, taking into account the profiles of both the diffuse and direct light flux. From the photosynthesis–light response of individual leaves, the rate of CO_2 assimilation per unit leaf area is calculated for each species and for each layer separately. Multiplication by the leaf area of the species in the layer gives its assimilation rate in that layer. Summation over the various canopy layers and over the hours within the day gives the daily assimilation rate of each species in the mixture. After subtraction of respiration losses, the daily growth rates are obtained.

In the simple model, leaf area is calculated by multiplying the accumulated biomass at time t (Y_t) by the leaf area ratio (LAR_t, $m^2\ g^{-1}$) at that time

$$L_t = LAR_t \cdot Y_t \qquad \text{Equation 54a}$$

This assumes that leaf area growth is limited by dry matter growth. Before canopy closure, however, leaf area growth is usually restricted by the potential rates of cell division and expansion, which depend on temperature rather than on the



	absorbed PAR $MJ\ m^{-2} d^{-1}$		CO_2 assimilation $kg\ ha^{-1} d^{-1}$	
sp	1	2	1	2
	3.42	0	271	0
	1.53	0.12	146	12
	0.50	0.31	53	33
	0.20	0.20	22	23
	5.65	0.63	492	68

Figure 82. Schematized calculation of light absorption and CO_2 assimilation of a tall and a short species in mixture. In the simulation, calculations were performed for each of 20 horizontal canopy layers at selected moments of the day, and these results were accumulated to daily values for each of the four layers shown. The tall (1) and short (2) species had leaf area indices of 3 and 1, respectively. Incoming *PAR* was 7.07 MJ $m^{-2}d^{-1}$.

supply of photosynthates. In this early phase, leaf area growth is more or less exponential. As will be discussed later, the competitive ability of a species is strongly determined by its early growth. Therefore, a more accurate procedure is followed in which leaf area is assumed to increase exponentially until the beginning of mutual shading at a total *LAI* of 0.75

$$L_t = N \cdot {}'L_0 \cdot \exp(R \cdot t) \qquad L_1 + L_2 < 0.75 \qquad \text{Equation 54b}$$

where N is the plant density (plants m^{-2}), $'L_0$ the apparent leaf area per plant at emergence (m^2 plant $^{-1}$) found by logarithmic extrapolation of leaf area data, R the relative growth rate of leaf area ($m^2\,m^{-2}\,d^{-1}$) and t the time in days after plant emergence.

The relative growth rate (R) is strongly affected by temperature and the early growth is therefore described with time expressed in accumulated degree-days rather than in days. Both leaf area ratio (*LAR*) and plant height (*H*) are a function of phenological development, which is mainly driven by temperature. Both are therefore given as a function of degree-days after emergence. Under adequate moisture supply, germination and plant emergence are also approximately linearly related to temperature. Germination of weeds is triggered by soil cultivation, and thus weed emergence is calculated by a certain temperature sum after last cultivation, i.e. seedbed preparation. Crop emergence is caluclated from sowing date, using a fixed temperature sum.

In the detailed model, the total daily growth rate is partitioned to leaves, stems, roots and storage organs, according to keys that are a function of the development stage of the species. Leaf area growth is calculated from the dry weight increment of the leaves and the specific leaf area of the new leaves, and the decrease in leaf area as a result of senescence is also taken into account. Simulation of specific leaf area and senescence rate in response to shading need special attention, because leaf area is of paramount importance for competitive ability, including during full ground coverage (Equation 52). Simulation of early leaf growth is further improved by calculating leaf area per plant from leaf appearance rate and the final size of the successive leaves (e.g. Sinclair, 1984).

In the simple model, crop yield is obtained by multiplying the simulated final biomass of the crop by a fixed harvest index, which is the ratio between the yield of the desired plant organs and the total biomass.

In the foregoing, competition for light was discussed. Stress conditions are accounted for by using a multiplication factor for the light utilization efficiency (E). The multiplication factor takes a value between 0 and 1, depending on the degree of stress. Many models have been published to describe the effect of drought and nutrient shortage on crop growth. Most of the simple approaches can easily be attached to the competition model to describe the growth reduction of the mixed stand as a whole. However, when soil moisture or nutrients are in short supply, uptake of these elements by an individual species in the mixture will be related to that species' share in total root length. When the competing species differ markedly in their leaf area to root length ratio it is especially important to account for these differences, elsewhere (Spitters, 1989) a simple model was presented for this.

If the nature of the stress is unknown, the light utilization efficiency may be calibrated against the observed or expected yield level of the crop.

The various versions of the model have been validated against results from field experiments with mixed stands of maize and barnyard grass (Spitters & Aerts, 1983; Spitters, 1984), and sugar beet and fat hen (Kropff, 1988).

12.3.2 Sensitivity analysis

The model described above can be used to illustrate the effect of various morpho-physiological attributes on the competitive ability of a species. For this, two isogenic species were assumed to grow in an $\frac{1}{2}:\frac{1}{2}$ mixture and in monoculture. Total stand density was 200 plants m^{-2}, and both species started with a leaf area of 1 cm^2 per plant at emergence. The relative growth rate of leaf area during the juvenile phase was 0.15 d^{-1}, while the leaf area ratio decreased linearly from a value of 150 cm^2 leaf area per g plant weight at emergence to zero at full ripeness, 100 days after emergence. The light extinction coefficient was 0.7 and the light utilization efficiency was 3 g of dry matter formed per MJ of intercepted light. Plant height increased from 1 cm at emergence to 1 m, 80 days later. Incoming PAR averaged 8 MJ $m^{-2}d^{-1}$.

In subsequent simulation runs one attribute value for the first species was increased by 20%, so that in any run the species differed in only a single characteristic. Only *LAR* and *R* were simultaneously changed. To study the effects of fertility level, the simulations were also performed for an environment with a 20% higher light utilization efficiency.

The results of the sensitivity analysis are depicted in Figure 83. All attributes affected the yield of the species much more when it was grown in mixture than when it was grown in monoculture. In mixture, the advantage of a 20% greater leaf area at plant emergence was maintained over the whole growing period, whereas in monoculture it had a much smaller effect. In mixture, the biomass production of a species increased disproportionately after increasing its light absorption per unit leaf area – either by having taller plants or a greater extinction coefficient – or after increasing its utilization of the absorbed light, or its leaf area formed per unit plant weight.

The 20% increase in fertility level of the site resulted in a 27% higher yield for the reference crop. In contrast to this large effect on total production, the competitive relations were hardly influenced (Figure 83). Only the effect of plant height became more pronounced as a result of increased shading, invoked by a greater total leaf area index.

In the next section the effects will be explained using the classical growth analysis.

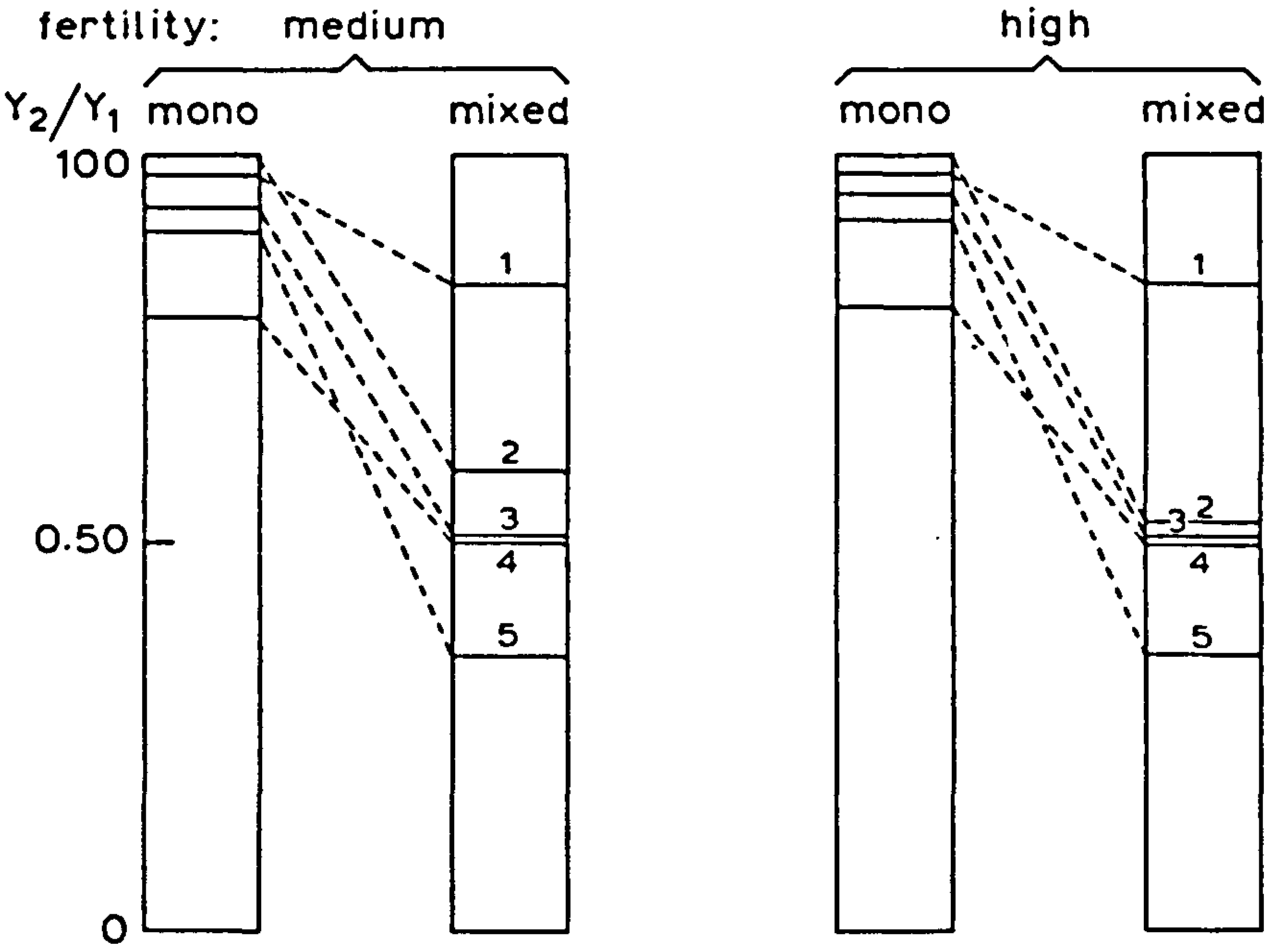


Figure 83. Simulated effect of single attributes on the ratio in biomass production of two isogenic species (Y_2/Y_1), grown at two fertility levels in monocultures and in mixture. For Species 1, the attribute in question was enhanced to a value of 120% of that of Species 2. Attributes: 1) initial leaf area per plant, 2) plant height, 3) extinction coefficient, 4) light utilization efficiency, 5) leaf area ratio. The simulated biomass yields of the reference type in monoculture were 15.6 and 19.8 t ha^{-1} under medium and high fertility, respectively.

12.3.3 *Classical growth analysis*

In experiments to study the growth pattern, the stand is normally harvested at intervals and at each harvest, leaf area is measured and the dry weights of the various plant organs are determined. Apart from using a simulation model to analyse the experimental results, we can partition the observed growth rates into various components. In the classical growth analysis the relative growth rate is considered; it is defined as the dry matter increment ($\mathrm{d}Y/\mathrm{d}t$) per unit of biomass present (Y). This relative growth rate (RGR, in $\mathrm{g\,g^{-1}\,d^{-1}}$) is split up into the growth rate per unit leaf area (net assimilation rate, NAR in $\mathrm{g\,m^{-2}d^{-1}}$) and the leaf area to plant weight ratio (leaf area ratio, LAR in $\mathrm{m^2g^{-1}}$)

$$RGR = NAR \cdot LAR \qquad \text{Equation 55}$$

The leaf area ratio is partitioned into the fraction of total dry matter allocated to the leaves (leaf weight ratio, LWR in $\mathrm{g\,g^{-1}}$) and the leaf area per unit leaf weight (specific leaf area, SLA in $\mathrm{m^2g^{-1}}$)

$$LAR = LWR \cdot SLA \qquad \text{Equation 56}$$

This approach is only sensible when growth rate is proportional to leaf area; NAR being the proportionality factor. This is approached during the juvenile phase when plants are still standing free and light interception is proportional to leaf area. It does not hold when the foliage fully covers the ground. Incoming light is then fully intercepted and additional leaf area does not contribute to additional light interception. Then, growth rate per unit ground area, rather than growth rate per unit leaf area, tends to be constant. When studying crop growth, therefore an analysis in terms of light interception per unit ground area and growth per unit intercepted light (Equation 51) should be used, rather than the classical growth analysis. In mixture, however, the growth rate of a species tends to be proportional to its leaf area over the entire period of growth (Equation 52) and so the classical growth analysis is appropriate.

In Figure 84, the simulation results obtained with the simple model described above are presented. In the first situation (solid curves), the species were only differentiated in their starting position. On a logscale, the distance between the curves remained the same over the whole growth period (Figure 84A), i.e. the biomass ratio of the species (Y_1/Y_2) was constant. Consequently, the absolute difference ($Y_1 - Y_2$) increased rapidly in time (Figure 84B).

The leaf area at an early time t is defined by the exponential equation

$$L_t = N \cdot {'L_0} \cdot \exp\left(R \cdot (t - t_e)\right) \qquad \text{Equation 57}$$

Thus, a species acquires a favourable starting position by having a large plant number (N), a great apparent leaf area per plant at emergence (${'L_0}$), a high relative growth rate of leaf area during the juvenile phase (R), and an early emergence (t_e). For instance, in an isogenic mixture, an advantage in emergence of only a single day will give, at $R = 0.15\ \mathrm{d^{-1}}$, a 16% better starting position and so a 16% greater

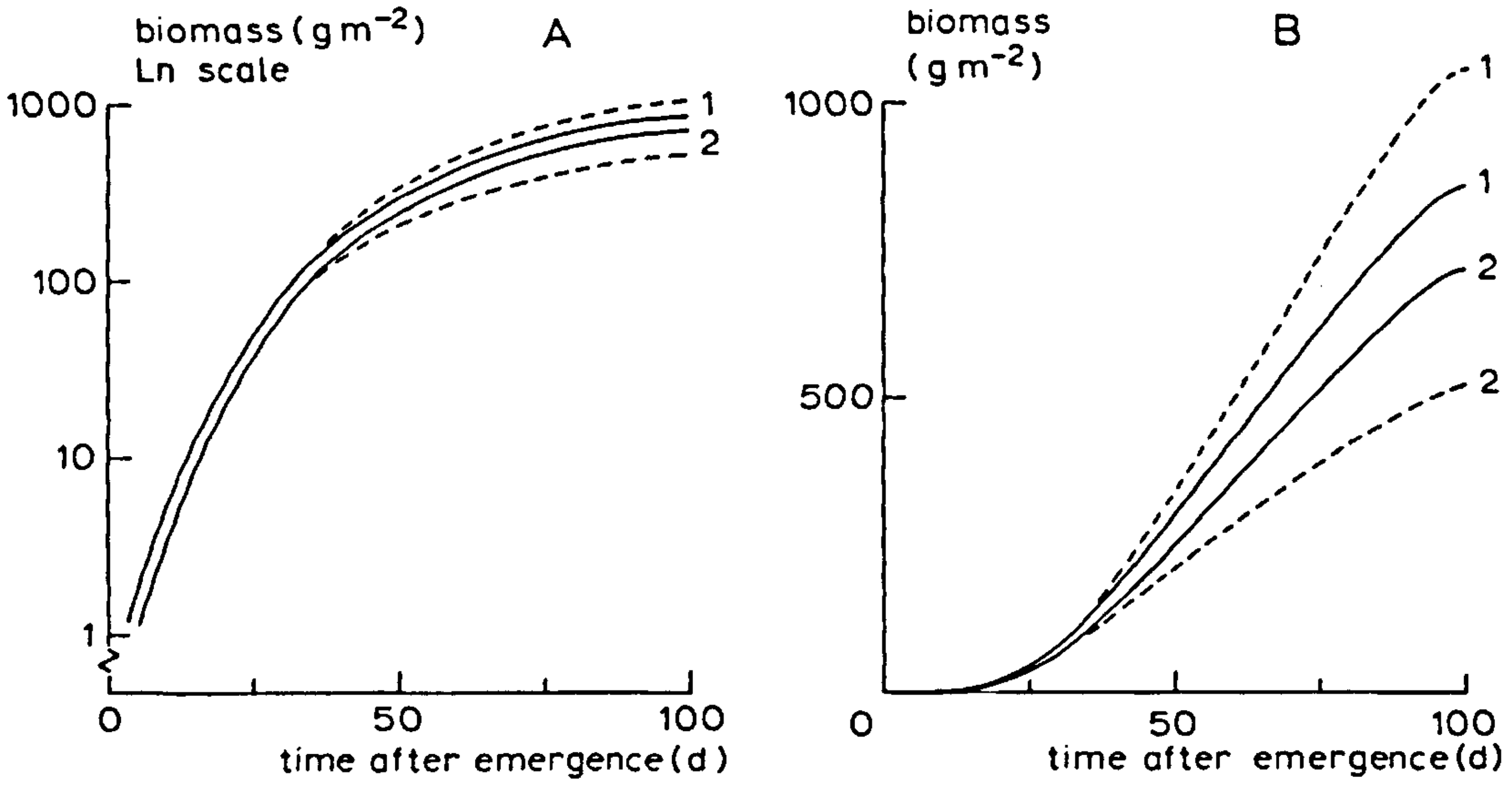


Figure 84. Seasonal course of simulated biomass of two species growing in mixture. Species 1 started with a 20% greater leaf area than Species 2, and was either of the same height (solid curves) or 20% taller (dashed curves) than Species 2.

final yield. This emphasizes the paramount importance of the starting position for the competitive ability of a weed and the importance of accurate initialization in competition models.

In the second situation (dashed curves in Figure 84), the species were also differentiated in plant height. On logscale, the distance between the curves changed with time, indicating a shift in the biomass ratio (Y_1/Y_2) and thus differences between the species in relative growth rate (RGR). From the exponential growth equation it can be derived that the change in Y_1/Y_2 over the time interval Δ equals

$$\frac{Y_{1_{t+\Delta}}/Y_{2_{t+\Delta}}}{Y_{1_t}/Y_{2_t}} = \exp\left((RGR_1 - RGR_2)\cdot\Delta\right) \qquad \text{Equation 58}$$

This enables analysis of changes in relative abundance in mixture in terms of the growth analysis components *RGR*, *NAR* and *LAR* (Equation 55).

The net assimilation rate can be partitioned into the light absorption per unit leaf area (MJ $m^{-2}d^{-1}$) and the efficiency with which the absorbed light is used for dry matter production (g MJ^{-1}). In mixture, a greater light absorption per unit leaf area is achieved with a greater plant height, because light intensities are greater at the top of the canopy, and with a foliage architecture such that a greater extinction coefficient is obtained. More efficient use of the absorbed light can be the result of a greater photosynthetic capacity of the leaves and a smaller whole-plant respiration rate per unit leaf area. A greater *LAR* is obtained with a relatively greater allocation of assimilates to leaves (*LWR*) and with thinner leaves (*SLA*).

In conclusion, if the species do not differ in relative growth rate, their relative differences in mixture will be maintained over time. Differences in *RGR*, invoked by variation in morpho-physiological characteristics, change the relative abundances of the species in mixture. The fertility level of the site primarily affects the total production of the vegetation, but in agricultural situations it has a much smaller effect on the inter-species distribution of the dry matter produced.

12.4 What kind of model should be used?

Two types of competition models have already been discussed: the regression models in which the competition effects are described by some empirical equation; and the mechanistic, simulation models in which the competition process is explained from the underlying eco-physiological principles.

Skoog's statement (1955, cited by Loomis et al., 1979) that 'we can claim to understand the plant when we can express it all in a mathematical model' is an incentive to develop very comprehensive models. Constructing such physiologically detailed competition models is primarily a way of doing research. For people other than the modeller himself and perhaps an inner circle of colleagues, the detailed model tends, however, to be a black box, whose simulation results cannot be verified and, therefore, do not convince. To achieve a wider application, we would probably do better to follow Simberloff & Boecklen (1981, p. 1224), who stated that a more complicated theory is a *panchreston,* a concept that, by attempting to explain everything, explains nothing. In terms of Ockham's razor: 'multiplicity ought not to be posited without necessity' (William of Ockham, 14th century). Indeed, the simple model for light competition already clarified the main principles of competitive interaction between plants. The simple physiological approach may also offer a frame to analyse the results of competition experiments; the model version that is to be used must be adjusted according to the aims of the researcher. The regression approach can also be useful in this respect, as it summarizes the observed experimental results with a minimum number of parameters.

A weak point of the physiological models is usually their lack of precision. They contain many functions and parameters, each having its own uncertainty. These errors accumulate in the simulated final crop yield. Practical weed management, however, requires reliable predictions, deviating from the actual yields by not more than a few per cent. The regression models seem to be better suited for this purpose, in particular when their variables have a causal basis, and their parameters are estimated from many experiments carried out in the conditions under which the model has to perform.

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AGRICULTURAL PRODUCTION SYSTEMS

13 Agricultural production systems

C.R.W. Spedding

13.1 Agriculture

Although it can be, and often is, argued that farmers must always have thought about their farms as systems and managed them as whole units, this really betrays the kind of loose thinking that a systems approach is designed to improve. It is rather like the reaction of those who, encountering systems thinking for the first time and demanding a very simple explanation, respond by concluding that it is only common sense.

Quite apart from the implied devaluation of what usually turns out to be a scarce commodity, this reaction fails to confront the problems of how this common sense is arrived at and fails to see that retrospective recognition of 'common sense' (like that of 'success') may tell you nothing about how to achieve it.

Indeed, it is interesting to compare the large number of people who can now see that systems thinking is valuable (even essential) with the quite small number who, 30 (or even 20) years ago, could see that it would be so. What seems common sense now, looked rather different at that time and most of those closely involved became very familiar with, first, opposition from those who did not understand the approach and then, later, support from those who did not understand the approach either. It was a matter of speculation as to which people were the more dangerous.

Whilst it is clear that most farmers understood that important interactions occurred within their farming systems and that management had to take account of this, for most of agriculture's history it was not possible to express this complexity and thus not possible to communicate it to others, discuss it with others or even think clearly about it. Learning by experience was accepted as the only way to arrive at an adequate understanding of a farm and, of course, it is most important not to imagine that any theoretical approach will ever be a substitute for experience. Systems thinking and methodology must be thought of as additional tools: but this does not diminish the importance of tools – they are frequently the keys to progress.

Neither could farmers think quantitatively about their problems – certainly not in the detail required – nor make the kind of calculations that are needed to think about complex, dynamic systems that are greatly affected by the contexts in which they have to operate over long time periods.

When the context was dominated by climate, in the sense of long-term weather, change only occurred slowly and farming could evolve with it. Now that farming is dominated by an economic climate that can change rapidly and drastically, it is not possible for farming to keep pace in the same way.

Thus, whilst not ignoring the practical values of experience, intuition and local knowledge, the current dominance of economic factors in agriculture requires a degree of management and a knowledge of how the system to be managed functions, beyond anything that these qualities (of experience, etc.) can supply unaided.

This need exerted a pressure on agricultural economists to produce models of farms that could be manipulated to explore the consequences of change. Linear programming was a typical attempt to do this and agricultural economists and management specialists thought of themselves as the people who looked at farms 'as a whole'. But, typically, the view of the whole was an economic one that used technical information: it did not incorporate biological processes or biological understanding. This was understandable, in the sense that agriculture, even subsistence farming, is essentially an economic activity. This implies a concern with the productive use of resources: it does not imply necessarily that inputs and outputs are expressed in monetary terms. However, agriculture is also essentially applied biology and, in a parallel development, ecologists were applying themselves and their thinking to production systems, including those of agriculture (Conway, 1987).

13.2 Production systems

Although ecologists and economists are both concerned with relationships between inputs and outputs, their outlook and terminology have generally created a gulf between them and, whereas economists used money as their unifying expression, production ecologists chose energy.

In both cases, I suspect that the idea of a common means of expressing everything stemmed from a fundamental misconception that one single picture of a system is both desirable and adequate. It is, of course, neither.

One has only to contemplate the notion of a single picture of anything to see the futility of such an idea. Consider a picture of a horse: it will nearly always be a picture of one side of the outside of a horse. To imagine that this one of innumerable possible pictures (each valuable or even essential for different purposes) can serve as *the* picture is to oversimplify the very complexity with which we know we have to grapple (Spedding, 1988).

It is the essence of a systems approach that it deals with the real complexity of systems without over-simplification. It only simplifies (in models) in relation to a specified predetermined purpose. And it is the existence of purpose that characterizes agricultural production systems. Agriculture is always a purposive activity, although the purposes are usually multiple and there is often no easy way of reconciling or integrating them (van Keulen, Chapter 15).

In ecology, the emphasis has generally been on relationships that are only purposive in the senses that a purpose is imposed by the point of view of the observer, that constituent organisms can be imagined to have purposes, or that an ecosystem has to be maintained in some steady or near-steady state (homeostasis).

In the second case, the purpose has to be deduced from the behaviour of the organism and it may be going too far to imply that this derived purpose is actually the driving force behind the behaviour. In addition, the behaviour of the system cannot necessarily be deduced from the behaviour of the constituent organisms.

In the first case, of course, one is entitled to say of any system 'I choose to view it in this way' and to defend the usefulness of doing so. Ecosystems can indeed be managed to fulfil a predetermined purpose but they cannot be said to be constructed to that end. But in agriculture, systems are essentially designed to be purposive.

The first contribution of ecology to agriculture was to stress the importance of unrecognized and unforeseen interactions. This played a major part in the recognition that a narrow view of production systems, which focused only on the desired outputs (= products) and objectives, ignored some very important consequences. Pollution is probably the best example. Systems that used inputs very efficiently to produce the desired products cannot be viewed as wholly successful if they also give rise to undesirable outputs.

In order to foresee whether this is likely to happen or not, it is necessary to have a model that is not restricted to the production process of major interest. Thus, the fact that agricultural purposes provide a means of simplifying models of agricultural production systems carries with it the risk of missing other consequences of changes made. Ultimately, this leads to an important general proposition: those who advocate change have an obligation to explore the full consequences of making such a change. This means that it is not sufficient to be reasonably sure that such a change will actually achieve the objectives sought: it is also necessary to ensure that it will not lead to other, undesirable consequences unrelated to the objectives. (Or, in economic terms, if it does so, that these consequences are recognized and costed.)

In agriculture, these two strands of thinking, economic and ecological, came together in the late 1950s and early 1960s. The need for a synthesis emerged gradually and was expressed in the demand for bio-economic models (Charlton & Street, 1975). This was rapidly reflected in developments in different parts of the world, in farm management (Dent & Anderson, 1971; Dillon, 1973; Eisgruber & Lee, 1971), in pest control (Conway, 1973), in ecology (Jeffers, 1975; van Dyne & Abramsky, 1975), in hill farming research (Eadie & Maxwell, 1975), in grazing management (Kemp, 1960; Jones & Baker, 1966; Morley & Spedding, 1968; Jones & Brockington, 1971; Arnold et al., 1974), in biological research (Innis, 1975), and in agricultural policy and marketing (Allen, 1975). Many of these developments were reported at a symposium on the study of agricultural systems, the proceedings of which were published in 1975 (Dalton, 1975).

In the U.K., however, in the mid-1960s the need for synthesis was emerging within the biological sciences underpinning agricultural research and it was for this reason that the first organizational steps taken at the Grassland Research

Institute (as it then was) at Hurley (U.K.) were to establish a Systems Synthesis Department.

13.3 Systems synthesis

Grassland research was a natural launching pad for this venture, because of the need to put together, in a useable form, the results of research in the separate disciplines of soil, plant and animal science. The even greater multidisciplinarity of grassland farming, to include management, economics, veterinary science, entomology, etc., gradually became clear. It was also recognized that what happened in one phase of an animal's (or plant's) life could affect what happened later, so it became necessary to synthesize research results obtained in different phases.

The main aim, however, was to construct new production systems from the building-blocks provided by research, to achieve production targets, all of which could be expressed as a blueprint for practice. It was slightly worrying at the time to be told by some farmers that they did not want to be told how to farm: what they wanted was information that they could use to construct their own systems, which might be unique to their farms. The answer, that this trial and error approach was inefficient if research could say nothing about the consequences of inserting the new information into existing systems, was not as obvious then as perhaps it should have been. The development of systems thinking and the use of systems techniques in agriculture cannot be described as a neat chronological sequence, since it did not happen that way. In different parts of the world and in many different disciplines, the need for a 'different' approach became clear to particular individuals, generally because they began to appreciate the grave weaknesses in the way they currently went about their research, extension or educational tasks. There has thus always been an element of necessity about a systems approach and a recognition that this way of thinking about agriculture, its problems and its improvement had to be adopted. Questions about whether the value of the approach could be demonstrated seemed, in a sense, irrelevant: they should, of course, have been directed at particular techniques and methods used within the approach.

In developing countries the dissatisfaction with conventional research often stemmed from the repeated failure of imported plants, animals and practices to achieve the expected and hoped-for results in the ecological and economic frameworks within which they had to operate.

The need to understand existing systems before embarking on change, the main remit given to the International Livestock Centre for Africa (ILCA) when it was established in 1976, might have emerged more clearly much earlier, had there been a better dialogue between researchers and farmers. This was not due to a lack of willingness to meet and discuss matters of common interest – this happened a good deal – but to the lack of a clear framework for thinking about the problems. This is a good illustration of the need for and value of theory. As a well-known

Russian statesman is reported to have said 'In the long run, there is nothing more practical than a good theory'.

The first activities of the Systems Synthesis Department at Hurley did not involve any kind of dynamic modelling and the first steps towards modelling were taken in about 1966 after consultation with Kees de Wit, who had recently perceived the potential of DYNAMO as a biological simulation language. In 1969, a symposium (Jones, 1969) on the use of models in agricultural and biological research was held at Hurley and both the meeting and the work of the GRI benefited greatly from the presence and enthusiasm of Kees de Wit who contributed a typically stimulating paper on *Dynamic Concepts in Biology*.

From that time on, more and more people came to recognize the need for modelling techniques to be applied in agricultural R&D (see Dalton, 1975), but it was recognized that the original concept of synthesis was too narrow and that systems analysis (in the rather narrow sense) and synthesis needed to be combined. Modelling was increasingly used within agricultural research disciplines and subject areas but the application to whole production systems raised additional problems.

13.4 The study of production systems

Production systems in agriculture nearly always contain, as important constituents, soil, plants, animals, people, money, mineral and organic inputs, water and some parts of the atmosphere. If an observer does not see any or all of these, he probably has not looked hard enough. There are very few cropping systems, for example, that do not contain innumerable animals, but these animals are often quite small. Nor are many of these constituents normally of minor significance to the functioning of the system.

Thus a model of a production system requires inputs from all these disciplines and is required by them, if they wish to ensure that their results are relevant to practical application, directly or indirectly. And it can certainly be argued that all agricultural research should be relevant, directly or indirectly. Why else is it undertaken?

The idea that scientists carrying out research into crop plants or agricultural animals may simply be trying to 'understand' them, ignores the fact that understanding has always to be sought for a purpose. There is no kind of general understanding (or model expressing it) that will serve all purposes, and the achievement (by research) of the required understanding has to be guided by a definition of the purpose for which it is sought.

Ensuring relevance is a major objective and purpose of a systems approach to agriculture. The study of production systems thus implies multidisciplinarity and an overall guidance of research derived from a model of the whole system being studied. It thus raises organizational problems of how multidisciplinary teams are formed and operated. If they are put together on a permanent basis, they get accustomed to working together but may lose the disciplinary roots and special knowledge that gave them their value. If they are put together only when required, they may have no idea how to operate in this mode. In any event, the team leader has to be a 'systems' person, who understands his dependence upon the members of the team, but who can interact with them productively.

Early suspicions that scientists were going to be told what to do by those who knew less about their specialisms than they did themselves were serious impediments to progress, but collaboration seems to pose less difficulty now. Part of the difficulty was that systems-educated leaders were not being produced. They were, however, emerging from a wide variety of subject areas, entirely dependent upon an individual recognizing a need and doing something about it. It became clear that, although many argued that a 'systems' person should always have had experience in depth of one discipline, the precise point of origin was immaterial. It mattered less where someone had been, than where they were going. The essential tool for leadership became a picture or model of the content and function of the whole system, to which specialists could relate. The provision of this tool is the central feature of a systems approach.

13.5 A systems approach to agriculture

The need for such an approach rests on the proposition that the operational units of agriculture are systems and thus have the properties of systems. The relevant education, therefore, must ensure that the systems concepts and properties are understood. The initial applications of systems thinking to agriculture followed considerable experience of it in engineering and it was perhaps natural that a rather mechanistic approach characterized the first efforts. This was unimportant where a farmer operated a highly controlled system (e.g. battery egg production), but mattered considerably when dealing with an African subsistence system where the farmer and his family were integral parts of the system and where non-agricultural activities (e.g. water and fuel collection) were difficult to separate from farming.

These sorts of problems led to the distinction between 'hard' (i.e. rather mechanistic) systems and 'soft' systems (e.g. those containing people), and the recognition that the kinds of research and thus the kinds of models that could be used for 'soft' systems were often very limited (Checkland, 1981). One important implication of the difference is that realistic assessment of the potential for improvement is drastically different in the two cases. It is possible, at the 'hard' end of the range, to devise quite new systems or to make changes that can be expected to make an existing system better. At the 'soft' end, it is more realistic to accept that slight shifts in the right direction may be as much as can be hoped for or predicted (Breman, Chapter 16).

In any event, I believe that the two questions by which I usually characterize the first steps in a systems approach to agricultural improvement (Spedding, 1988), still hold. They are:

- What is the system to be improved? (implying a model)

- What constitutes an improvement?

The mathematical modelling effort is essentially descriptive, but on a selective and more precise basis than any verbal model. As with the development of any new subject, 'agricultural systems' began with a rather less selective descriptive phase (for example, Duckham & Masefield, 1970; Grigg, 1974; Spedding, 1975; Ruthenberg, 1976). The use of mathematical models to describe sub-systems and component biological processes developed steadily with major efforts having to be made to convince those with an antipathy to mathematics that computer modelling was a technique that they could nevertheless use (de Wit & Goudriaan, 1978; Brockington, 1979; Penning de Vries & van Laar, 1982; France & Thornley, 1984). By the early 1970s mathematical models were being developed in many parts of the world, but rather more of processes than of whole agricultural systems.

Since that time, the published literature has grown enormously, much of it associated with the establishment of the journal *Agricultural Systems* in 1976. The number of papers published in the journal has risen each year and a glance at the titles gives an indication of the range of systems studied, the number of countries from which papers have come and the range of levels of detail at which studies have been carried out. The name of de Wit appeared on the cover from the outset, as a member of the editorial board.

13.6 Impact of a systems approach

This volume of work and literature is one way of measuring the development of the subject and one way of illustrating the usefulness of the approach. But it only relates to research, where it may now be regarded as well established. Inevitably, this leads to the use of modelling as a way of identifying gaps that need to be filled by more research and thus to an indication of R&D needs.

This is not quite the same as assessing R&D priorities, which involves comparative assessment across a wide range of research fields, and this is probably a field – much neglected currently – where the approach has a further contribution to make. Not, it has to be emphasized repeatedly, as a substitute for judgement but as an aid to it.

Since R&D interfaces with extension, there has also been a significant impact in this area, but there has been surprisingly little recognition of the importance of 'copying' in agricultural improvement. Yet copying what is perceived (on another farm or on a research station) as a 'better' system must be one of the most common ways of attempting to improve an agricultural system.

Since not everything can be copied (actual plants, animals and people cannot be exactly duplicated and, in some cases, it may be difficult to find even similar units) and not everything needs to be (e.g. trivial elements), it is important to be clear about what must be copied and with what exactness. This raises questions as to who can say this and with what confidence. The greatest confidence can surely be placed on an operator who has developed a model that defines the essentials and can demonstrate that it behaves sufficiently like the real system.

In education, the impact of a systems approach has been substantial in a diffuse kind of way but limited in specific examples of concrete change or systematic thought about it (e.g. Hawaii, 1985).

The Hawkesbury experience in Australia (Bawden et al., 1984) is the best documented; in the U.K., Reading University has made some progress and the Open University has applied a systems approach to its courses in food production. Agricultural education in Wageningen has also reflected systems thinking and in Thailand, Chiang Mai has launched an M.Sc. in Agricultural Systems. In education, generally, progress has been disappointingly slow, partly due to the difficulties of changing established courses lasting several years and having an annual intake of students.

Progress has also been slow in applying systems thinking to agricultural policy – although some eminent systems thinkers have certainly applied themselves in this area (de Wit et al., 1987; de Wit et al., 1988). Policy-makers are generally sceptical of systematic methods, suspect any suggestion of planning and are rather alarmed at the idea of it being known where they are trying to get to – except in the most general terms – in case they never arrive.

It is, of course, true that the world changes rapidly around the policy-maker and political imperatives have a strength quite out of proportion to their permanence. However, at the very least, policy-makers should accept the need to explore the consequences to the system as a whole of any changes they do propose or institute. Modelling techniques are also increasingly used to define and consider major options and thus to improve the decision-making process. Even so, there is a need for much more and better use of a systems approach in this as in all aspects of agriculture.

In recent years, especially within the EEC, there has been an increasing need to consider agriculture as only one of the options for land use and, even where it is the major user, to regard it as a form of land management – for conservation, for management of the countryside, for recreation and the preservation of landscape – and not merely a productive system.

Policy-makers are having to grapple with such problems and a systems approach has proved relevant to this, even greater, level of complexity (de Wit et al., 1987).

The systems approach, to me, has always been a combination of philosophical concepts and (largely modelling) methodology. Expertise has developed markedly in the latter, much of it around central figures like de Wit. Somewhat less obvious progress has been made in improving the level of thinking about agricultural problems, apart from actual modelling exercises, where systems thinking has much to offer.

So, in addition to the specific additions to the scientific literature relating to agricultural production systems that carry his name, one of the major contributions of Kees de Wit has been the clarity and courage of his thinking.

We should never underestimate our dependence upon men and women of stature; and remember the words of Isaac Newton: 'If I have seen further than others, it is because I have stood on the shoulders of giants'.

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14 The crop model record: promise or poor show?

N.G. Seligman

'...model building is an enjoyable if arduous task whereas model testing can be heartbreaking. Perhaps this is why so many crop models are published without being tested...' (Whisler et al., 1986)

'A recurring observation as one reviews the literature of computer-based medical decision making is that essentially none of the systems has been effectively utilized outside of a research environment, even when its performance has been shown to be excellent.' (Shortliffe et al., 1979)

14.1 Introduction

At a symposium held on the occasion of the 50th anniversary of agricultural research in Israel, Professor C.T. de Wit gave a survey of achievements in worldwide agricultural research. He maintained that 500 years was a more appropriate period to review, because the last major contribution was Liebig's *Chemistry in its Application to Agriculture and Physiology* published in 1840. Many would contest this thesis, but whatever other minor achievements there may have been in the interim, can Theoretical Production Ecology be relegated to the same bleak category? Or should we regard de Wit's contribution as the remodelling and development of an age-old discipline traceable to Joseph's long-term yield predictions that were based on esoteric theory and flimsy data but were successfully applied to guide strategic food-security planning? More recently in 1735, Réaumur had the idea of relating day-degrees to phenological development and so conceived one of the more robust 'summary models' (or 'conservative relations' *sensu* Monteith, Chapter 1) that lives on to this day (Alm et al., 1988; Hesketh et al., 1988). Within this ancient discipline, the year 1958 could mark the beginning of the modern era (if not the revival) of theoretical production ecology when de Wit, in *Transpiration and Crop Yields* first defined the now well-known 'conservative relationship' underlying the mass of empirical data accumulated by Briggs & Shantz (1913) and others. This was soon followed by *Photosynthesis of Leaf Canopies* in 1965 which ushered in the computer as the instrument for simulating crop growth.

In the following years, crop models proliferated in a worldwide endeavour to describe the growth processes and explain the behaviour and yield potential of crops. At first, the motivation was probably scientific curiosity and a desire to exploit the possibilities offered by the modern computer. This was soon followed by the expectation (or rationalization?) that comprehensive explanatory analysis of growth processes would contribute to better research, plant breeding, crop management and agricultural education. But already in 1973, John Passioura ridiculed the excessive enthusiasm then prevalent for complex crop models. Eight years later Monteith (1981) echoed the same sentiments. This evaluation is still very widespread even if not published explicitly. The function of crop models in research is indeed barely perceptible in the flood of professional literature that fills the agricultural libraries, and their impact on the farm planning and farm management scene is probably even less. Yet crop models are still proliferating and their merits are still being extolled, especially by the practitioners themselves (Whisler et al., 1986; de Wit & Penning de Vries, 1985; van Keulen, 1983; Loomis et al., 1979). The popular texts on simulation modelling published by de Wit & Goudriaan (1978) have been followed by others more specifically directed at crop modelling (van Keulen & Wolf, 1986; Penning de Vries & van Laar, 1982). This is an appropriate moment to look back and try to see whether crop models have lived up to expectations and to guess what promise there is for the future of this branch of theoretical production ecology. The answers are necessary not only to counter the critics, but especially to clarify some of the issues that face agricultural research at a critical crossroads when the traditionally generous government support is, in many countries, becoming a thing of the past (Brown, 1987; de Wit et al., 1987).

14.2 The crop model rationale

Mathematical models are the foundation of modern physical science. Biology submits reluctantly to the rigours of mathematics, but it must rely on it for describing and structuring many quantitative aspects of biological function (France & Thornley, 1984; Thornley, 1976). The integration of functions describing growth processes into a dynamic mathematical system has become a practical and exciting adjunct to experiments in crop photosynthesis, respiration and transpiration, and has made it possible to test assumptions about canopy growth processes in a consistent and comprehensive conceptual framework (de Wit et al., 1978; de Wit, 1970). Crop models have gone one step further in simulating a full cropping cycle from germination through to harvest maturity and analysing its response to a variable soil and aerial environment.

Crop modellers are keenly aware of the complexity of a crop and have recognized the simplistic nature of even a comprehensive model (Whisler et al., 1986; de Wit, 1970). The approach to defining the simplified system has varied widely not only with the varying objectives of different practitioners, but also with their preferences and capabilities. As a result, crop models range from very detailed process models like the cotton model GOSSYM (Whisler et al., 1986) and the soya bean model SOYMOD (Meyer et al., 1979) to the relatively simple 'summary' models like the cotton crop models developed by Wallach et al. (1980). At least 14 crops have been modelled by different groups in various countries (Whisler et al., 1986) and there are numerous published models of different crops. Among them, more than 12 wheat models have appeared (including van Keulen

& Seligman, 1987; Angus & Moncur, 1985; O'Leary et al., 1985; Stapper, 1984; Weir et al., 1984; Hochman, 1982).

Extension of simulation models to the crop level has been undertaken for a variety of reasons that typically include: hypothesis generation and hypothesis testing, sensitivity analysis, finding 'gaps in knowledge about the system' as a guide for further research, interdisciplinary integration, improved crop management strategies, regional planning, identification and evaluation of plant characteristics that can help to define plant breeding aims. Other spin-off objectives include better communication between research workers in different fields and better understanding of complex crop responses. We can discuss these objectives under the headings: research, yield prediction and agricultural planning, farm management, and education. Some of the representative models can serve as indicators of the state of the art.

14.3 Research

The canopy photosynthesis model of de Wit (1965) and the subsequent comprehensive models of assimilation, respiration and transpiration (de Wit et al., 1978) set out to explain some quantitative aspects of crop growth in terms of the underlying processes. These models and others that were developed at the time (e.g. Loomis et al., 1967) dealt mainly with the question of potential growth and established what today appear to be the biological limits for agricultural production (Loomis & Williams, 1963). They set benchmarks for measuring agricultural achievement and defined production goals that were soon shown to be approachable technologically. They were used as vehicles for speculative thinking about crop behaviour and put previously qualitative questions like leaf angle effects on canopy photosynthesis into a quantitative context (Loomis et al., 1967; de Wit, 1965).

Later studies on respiration widened the scope of the photosynthesis models (Penning de Vries, 1974; 1975). Detailed crop micrometeorology models (Goudriaan, 1977) coupled with photosynthesis and transpiration models (de Wit et al., 1978) gave rise to process-based summary models (Goudriaan, 1986; Goudriaan & van Laar, 1978) and more elegant plant environment models (Chen, 1984). All these contributed to the refinement of specific crop models, that included both comprehensive models (Ng & Loomis, 1984; Fick et al., 1973) as well as summary models of plant growth and soil water processes. One of the first of these was ARID CROP, a model of annual grassland production (van Keulen et al., 1981; van Keulen, 1975).

Some of the achievements of the modelling activity of this period were quite impressive. An example is the study of growth in semi-arid conditions where in many years, potential production was shown to be limited by nutrient deficiency rather than by lack of water (van Keulen, 1975). These findings set the stage for comprehensive research projects on primary production in Israel and in the Sahel (Penning de Vries & Djitèye, 1982; van Keulen et al., 1982). The Sahel project was subsequently awarded a special prize of merit by the Dutch Ministry of the Environment.

Whereas the first wave of plant growth simulation models produced demonstrably valuable insights into the quantitative aspects of plant growth, in the second stage the achievements tended to be more diffuse. In many cases, the added complexity of plant development, ontogeny and assimilate allocation to different plant organs, on the one hand, and the convergence on finer and more specific performance criteria, on the other, made it increasingly difficult to clearly demonstrate new findings or insights. So, for example, a well-validated model was used to examine possible reasons for the decline in cotton yields in the U.S.A. since 1965 after a threefold increase between 1935 and 1965 (Reddy et al., 1987). The model showed that impairment of root function, possibly as a result of herbicide effects, could have accounted for yield decline. This may have helped to draw attention to the problem even though herbicide damage to roots and consequent yield reduction had been demonstrated experimentally 20 years previously.

One of the applications of crop models is to examine the sensitivity of crop response to changes in plant characteristics so as to define breeding aims. However, there are very few examples of a breeding programme that was inspired by a crop model. Whisler et al. (1986) discuss a simulation analysis to determine the effect on cotton crop performance of different water use strategies where leaves were either 'water-savers' or 'water-spenders'. This characteristic was identified experimentally as a possible means of manipulating water use efficiency under certain conditions (Roark & Quisenberry, 1977). It was later found that a water-saving strategy indeed led to higher yields under dry conditions (Quisenberry et al., 1985). The simulation model GOSSYM 'confirmed' the result. But '...the use of physical/physiological process orientated crop simulation models in crop system design, including breeding, is still in its infancy...' (Whisler et al., 1986). Consequently, the 'acceptability' of simulation models among plant breeders is very uncommon. In fact, most crop simulation models have had very limited transferability to any other discipline, and at best have served the immediate purposes of the scientist or team that assembled them.

The successful research model could well be a model that fails – but for the right reasons – even though models that succeed, even if for the wrong reasons, are generally more popular (Klemes, 1986). In a study of water stress in wheat, growth could not be simulated adequately for certain stress conditions (Hochman, 1982). On closer analysis, it appeared that the assumption that stomatal response would be unimpaired after stress had been removed, was an oversimplification for such conditions. While the simulation identified a problem, it also proved (again) that under stress conditions, the responses of the plant can bring elusive processes into play. As such conditions are common for most crops, the crop model often treads dangerous ground.

In many cases, the insights gained from crop model analysis tend to be trivial or highly equivocal. As in so many areas of research, it is much easier to find good answers than to formulate good questions. But the search goes on and the use of simulation models as 'research models' has continued and still raises expectations (Whisler et al., 1986). Some of the insights have been anything but trivial. The analysis of effects of CO_2 control of stomatal opening on assimilation and transpiration is probably one of the better examples (de Wit et al., 1978).

14.4 Yield prediction and farm planning

Comprehensive crop models have not excelled as yield predictors, mainly because of the large data base they require and the heterogeneity of large areas for which yield predictions are necessary. As a rule, yield prediction has depended on statistical regression models, sometimes improved by accounting for the soil moisture balance (Baier & Robertson, 1968) or by calculating crop transpiration with simplified procedures (Zaban, 1981). In order to overcome some of the unforeseen vagaries of weather and crop, models have been developed which use field data for repeated updating. A tulip bulb model uses intermediate harvests to update the yield prediction (Benschop, 1985) but the model has not been applied in practice.

A study of the use of remote sensing to update crop models for yield prediction indicated that updating the initialization of a simple crop model with the accumulated interim remote sensing data gives more stable estimates of final grain yield than updating based on the most recent measurement of crop status (Maas, 1988). There are cases where leaf area estimates with remote sensing appear to be more accurate than those derived from leaf area models, but routine application is hampered by problems of consistency in interpretation of data, mainly because of the effect of canopy architecture and variable optical characteristics of the crop on the reflected radiation, as well as by problems of cloud cover, long repeat cycles, cost and availability of satellite data (Kanemasu et al., 1985). Yield predictors for alfalfa based on a simple model have been proposed by Fick (1984), and numerous attempts have been made to use crop models for yield prediction in greenhouse crops. These have ranged from simple regression models (Liebig, 1981) to comprehensive crop models (Shina, 1988). Routine use of such models has not yet been implemented on a commercial scale.

Crop models have been used for estimating expected yields in areas where the crop has not been grown before (Fukai & Hammer, 1987). Passioura (1973) felt that an expert in the crop of interest would make a more reliable estimate. That is usually an untested hypothesis – perhaps fortunately – for the modeller or for the expert. Crop models based on relatively simple biological relationships are being used in routines for planning optimum farm management strategies in collaboration with extension services (Kingwell & Pannell, 1987). These are still being actively developed.

14.5 Management

'Will computer software replace the coffeeshop?' (Wink, 1988a). The considerable effort being invested in the development of crop models for farm management applications has been documented by Doyle & Edwards, 1986; Whisler et al., 1986; Fishman et al., 1985; Nordblom et al., 1985; Rotz, 1985; Savoie et al., 1985; Smith et al., 1985; Thanel et al., 1985; Wallach et al., 1980, and others. Some crop models have been incorporated into systems for optimum management of the greenhouse environment (Shina, 1988; Liebig, 1981; Challa & van de Vooren, 1980; Challa et al., 1980; Seginer, 1980). Some are part of pest management programmes (Barlow, 1985; Rabbinge & Rijsdijk, 1983; Hearn et al., 1981; Wallach et al., 1980). The 'crop component' in these management models can be anything from a full-blown comprehensive model (Whisler et al., 1986) to relatively simple summary models (Barlow 1985; Rabbinge & Rijsdijk, 1983; Wallach et al., 1980), some of which are embedded in advanced optimization routines (e.g. Chen, 1986). Those that have very simple constant biological relationships (e.g. Hepp, 1988) seem to be accepted more readily than more complex models. A revised version of the model ARID CROP (Ungar & van Keulen, 1982; van Keulen et al., 1981) has been used to evaluate the long-term overall stability of different grazing and feeding stategies in the semi-arid region (Ungar, 1985). The identification of large areas of high stability even under fluctuating growing conditions is of interest in itself even if the model is not being used directly for management.

For management and planning purposes, model formulation is more like an engineering project where problem specifications determine the level of resolution and efficiency required. Pragmatic rather than scientific criteria for success would be a more appropriate guide for evaluation in such situations. The successful projects that use crop models are on the whole aimed at improving disease and pest control decisions (Rabbinge & Rijsdijk, 1983; Hearn et al., 1981) and have become accepted relatively widely, although initial enthusiasm for some successful applications has not always been maintained over time (Daamen & van der Vliet, 1988). Others have been relatively simple models aimed at specific operations like timing of boll opening in cotton so as to improve scheduling of harvesting operations (Wallach et al., 1980). Some crop models developed for aiding pest control decisions have been difficult to maintain because of changes in the resistance and parameters of population dynamics of the pest, as well as unusual crop responses that were neither forseen nor understood (E. Kletter, personal communication). It has been even more difficult to raise-end-user enthusiasm for the use of comprehensive crop models. 'Perhaps the most extensive crop simulation evaluation effort to date is that of Marani & Baker (1981). They made several improvements in GOSSYM...were able to obtain good simulation of seasonal time courses...' (Whisler et al., 1986). Whereas the model itself did not gain farmer acceptance in Israel, a summary model for irrigation scheduling was applied to a limited extent. In the U.S.A., a project has been launched to use GOSSYM as part of an expert system in cotton extension (Whisler et al., 1986). In Australia, a cotton pest control model has attained relatively wide support and acceptance (Hearn et al., 1981).

The difficulties encountered in attaining acceptability of crop models of any level of complexity are apparently very common. In Michigan, U.S.A., a powerful, well-run, computerized farm accounting system is used mainly for income-tax accounting, even though individual enterprise analysis is available on request (Harsh et al., 1988). Budget-orientated software specially tailored for farmers' needs, based upon simple bio-economic crop models, have been developed for many farm decision situations. They have been used on farms only to a limited extent, and then mainly by extension and consulting agencies. Similar problems of acceptability occur in the field of medical decision aids (Shortliffe et al., 1979), and are possibly related to different ways of thinking appropriate to different types of activity. Practitioners often find abstract, hypothetical thought processes inappropriate or even inadequate for the multidimensional multiple-objective reality in which they must perforce operate. Whatever the reason, and despite the considerable effort invested in crop management models, their impact on farm practice has been very small. The new farm generation that has grown up with computers may find wider use for them, but that remains to be seen.

14.6 Education

Building a crop model or a version of a crop model can be a valuable heuristic experience. Not only is it necessary to become acquainted with a large body of literature, but the act of testing the adequacy of one's perception of the target system is generally very sobering. Most crop models that apply to new situations require 'adjustment' that can range from valid setting of boundary conditions, to model development that takes into account phenomena previously ignored (Penning de Vries et al., 1987; Steiner et al., 1987; Reddy et al., 1985). Unwarranted 'fiddling' with parameter values can make the simulation study '...the most cumbersome method of curve-fitting yet devised' (de Wit, 1970). Yet sometimes, 'fiddling' as part of a careful sensitivity analysis can be a useful educational tool (Penning de Vries et al., 1987).

Crop models have been the subject of a number of doctoral and masters theses (e.g. Shina, 1988; Stapper, 1984; Dayan, 1978; Morgan, 1976; van Keulen, 1975) and have been part of simulation courses that have been given 'to spread the gospel' (van Keulen & Wolf, 1986; Penning de Vries & van Laar, 1982). An interesting project on the simulation of rice cultivation problems in Southeast Asia involved an international group of crop, soil and plant protection scientists who, after the course, went home again and prepared case studies on disease and pest problems, nitrogen nutrition, sowing dates, planting density, iron toxicity effects, genotype variation, etc. (Penning de Vries et al., 1988). The results of these studies were presented at a concluding symposium about 8 months later (Penning de Vries et al., 1987). The course raised much enthusiasm among the participants and the majority felt that they had gained a valuable research ability.

The results of the case studies indicate that 'transfer of the technology' is feasible, especially with the increasing availability of powerful PCs. On the other hand, the results of the case studies highlight some of the chronic problems encountered when using crop models in practice. Even though the course participants could draw upon the expertise of the course supervisors and worked on a model that had been prepared by experienced scientists, the results of the case studies tended to reveal the inadequacies of the model for the specific problem chosen, even after adjustment. Most conclude with a statement that '...more research is necessary...'. (Unequivocal results were obtained only in a long-term problem where there was no opportunity to validate the model!) These case studies were admittedly prepared by novices in the field and so should not be judged too harshly. The point is that even after much preparatory work, the application of crop models in specific situations still requires much experience and effort. Even so, the excercise certainly encouraged interdisciplinary activity, gave the participants a clearer picture of the sensitivity of the systems they study, and indicated areas where they thought more research would be useful.

14.7 The balance of achievement

The principles guiding valid crop modelling were discussed by de Wit (1970) and the requirements for the acceptability of models in practice have been defined repeatedly (Harsh et al., 1988; Shortliffe & Clancey, 1984; Charlton & Street, 1975). Nevertheless, crop modelling has not matured over 25 years to a stage where its function and utility is no longer open to question. The objectives that were set for different crop models covered a wide range from research through to applications in management and agricultural development planning. The record is uneven, but probably stands up best to scrutiny in a research environment where, when used judiciously in conjunction with experimentation, it has inspired structured research programmes that have increased understanding of crop behaviour and, in particular, of potential production limits (Whisler et al., 1986; de Wit et al., 1978). Certainly, crop models provide an effective means for 'falsifying' hypotheses about crop growth (as any crop modeller soon learns!) and as long as they continue to do so, their role in the future of agricultural research could well be assured. They can also highlight the equivocal nature of many experimental 'facts' (van Keulen & Seligman, 1987).

The greater understanding gained from crop modelling, or, for that matter from other branches of agro-biological research, does not necessarily lead to significant application in the short run (Spedding, 1979). Crop plants and the production systems in which they operate exhibit a 'conservatism' that is the basis of the robust and generally predictable functioning on which the farmer depends. This conservatism sets limits that are more severe than those that face engineering technology. As a result, the eventual impact on farm practice of crop models developed in a research context is diffuse by the nature of things. It can be expressed indirectly by various pathways, including better interdisciplinary communication and collaboration in research. Research models have had no noticeable effect on plant breeding aims and practice, possibly because breeding is concerned more with relatively unequivocal objectives like pest and disease resistance, increased tolerance to environmental constraints like heat, cold, drought and salinity, improvement of quality, appearance, product uniformity, shelf-life, etc. The importance of these objectives is self-evident and crop models seem to have little more to offer. Crop models that can estimate the importance of identifiable plant characteristics for determining long-term yield increase and yield stability should have been able to contribute to defining plant breeding aims, but this has not been evident.

Possibly the greater disappointment in crop model performance is in the field of farm management. There are surprisingly few examples of successful applications, even when the models have been specially tailored for use by farmers or extension personnel. Shortliffe & Clancey (1984) summarized a similar problem in the development of computer-aided medical diagnosis systems. They suggest that in addition to accuracy of decisions it should be shown that there is a demonstrated need for the system, that it performs at least as well as an expert and, among other characteristics, is cost-effective. They conclude that '...remarkably few [systems] have met...the criterion of need...'. This 'need' may also be difficult to demonstrate in the case of crop models for management purposes, partly because farm practice '...includes many non-scientific factors that make for some confusion as to just what science can contribute...' (Spedding, 1979). This may be the reason why the coffee shop (Wink, 1988a), or the pub, is still a preferred venue for exchange of management information.

Consultants and extension personnel may well find that crop models already meet some of their needs and improve the service they can provide for the farmer. The field is still wide open and progress will probably come with experience and with better understanding of the role that biological and bio-economic models can play in farm management, planning and development.

14.8 Conclusion

Although the crop modelling record has chalked up many disappointing performances and dead ends, it achievements, especially in research and education have been impressive and, judging by the continuing interest and activity, the future of crop modelling has just begun. If '...the next generation of agricultural plants and animals is but a gleam in the eyes of molecular biologists...' (Wink, 1988b), should crop modellers be any less optimistic? A central aim, if not the ultimate challenge of crop research, is to explain crop behaviour. Crop models are a powerful tool for testing our understanding of crop behaviour – as the frequent discrepancies between model and reality so eloquently testify! The valid use of models to falsify hypotheses in an integrated crop context and as part of a research programme, surely is reason enough not to '...declare a moratorium...'

on crop modelling (Monteith, 1981).

The crop simulation approach pioneered by de Wit and the Wageningen school of Theoretical Production Ecology has had a recognizable and increasing influence on agricultural science worldwide. It is a developing technique and the onus is on the ingenuity and perspicacity of agricultural scientists to find appropriate applications. Although the more ambitious expectations have yet to be fulfilled, this should not deter the new generation of crop modellers. It should be a source of encouragement to them that, even after de Wit, there are still major challenges ahead!

14.9 Acknowledgments

'Fools rush in where angels fear to tread' is the pervading feeling one has after attempting to evaluate the record of crop models, particularly after illuminating discussions on the subject with G. Stanhill, I. Noy-Meir, Z. Enoch, H. Talpaz, E.D. Ungar, I. Spharim, E. Kletter and H. van Keulen. If there is any substance to this review, then most of the credit goes to them.

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15 A multiple goal programming basis for analysing agricultural research and development

H. van Keulen

15.1 Introduction

Agriculture, one of man's first organized activities, can be practised with few and non-sophisticated resources: a piece of land, some seeds of a useful plant species, or some head of a desired animal species, some sunshine, a source of water and a limited amount of human effort. For centuries, man has depended on these for the supply of food, clothing, shelter and other basic necessities. However, in the last 50 years, population increase, particularly in the developing world, has led to a rapidly growing demand for food. The consequences for food production have been aggravated by the fact that this development has been associated with rural exodus and increasing urbanization, leaving the remaining rural population with the burden of producing more and more, over and above their own subsistence needs.

In the Western world, the parallel development of the industrial sector provided the possibilities for linkage and exchange with the developing agricultural sector, so that external means of production became available at relatively favourable terms of trade. This led to increased production per unit area, at a rate that exceeded the rate of population growth (de Wit & van Heemst, 1976). Eventually, wasteful application of inputs has resulted in overproduction, environmental pollution and a serious risk to the sustainability of current production systems. In addition, there is growing public concern about the quality of the rural environment, which now not only has to meet the demands for food production and a reasonable income for the farmers, but also demands for environmental diversity, landscape and recreation. Can all these demands be met simultaneously? To answer that question it is necessary to know the trade-offs between the various goals and the degree of possible substitution.

In large parts of the developing world where the conditions are much less favourable, agricultural production has not kept up with population growth, not even by bringing more and more marginal and fragile lands into cultivation. Development programmes aiming to increase food production mainly through measures geared towards higher yields per unit area, such as irrigation and fertilizer application were therefore initiated. Some were successful and more food was indeed produced, but in many cases they failed, partly because the external inputs required were not available or too expensive. In those situations the increasing demand for food is being met, usually inadequately, by overexploitation of the natural resource base, which leads to environmental degradation and threatens the sustainability of the production systems.

With the main emphasis on food production, other functions of the rural environment have not received sufficient attention. These omissions often hampered implementation of the suggested measures for improvement, or seriously impeded their efficiency and increased environmental degradation.

This situation gave rise to the concept of integrated rural development. which attempts to take the different functions of the rural environment into account, while considering the aspirations of the various interest groups. This approach soon encountered conflicting interests between the preservation of the rural environment, the regional development goals and the special goals and needs of the individual farmers and rural settlers. Major problems in analysing such situations include the lack of information on the relative importance of the various functions and aspirations, and the degree to which they are mutually exclusive. The problem of conflicting goals and how to resolve them is the subject of this chapter.

The aim is to explore technically feasible development pathways for the agricultural sector in a region, while giving full weight to the different socio-economic, biological and physical boundary conditions as well as to the different goals of the community. The analysis shows to what extent the various goals can be met, given the major constraints, and in particular estimates the trade-offs between costs and benefits incurred in order to attain the various goals. By considering both the technical constraints and the multiple socio-economic goals, the method proposed can foster communication between planners and decision-makers on the one hand, and between scientists and planners on the other. It makes the consequences of development strategies explicit and can also contribute valuable information for deciding on research priorities.

15.2 The method

The approach to the development pathway problem is through the interactive multiple goal linear programming method (Spronk & Veeneklaas, 1983; Nijkamp & Spronk, 1980), which requires an input–output model, a set of goal variables, and an interactive multiple criteria decision method.

15.2.1 The input–output model

When applied to rural development, the input–output model contains the technical coefficients that describe the range of techniques available for agricultural development and associated activities in a rural environment. Each activity is defined by its relevant output and input coefficients, which are derived from a well-defined way of producing a given product. Cropping activities require coefficients that define the yield of both marketable product and crop residues, the material inputs required to realize that yield, such as fertilizer, irrigation water and biocides, and the labour to do the season-specific fieldwork. The coefficients should include quantitative estimates of the environmental effects (including pollution, soil erosion and soil fertility coefficients), associated with each activity.

The production techniques should not only include those activities that are currently practised in a region, but also alternative activities that are practised in other comparable regions and are potentially applicable in the region under consideration, as well as activities that are still in the R & D pipeline. The range of appropriate activities in the highly developed countries will be different to those in the developing world. However, they can all be included in the activity set and the method will choose the appropriate technologies, according to the development scenarios.

Present production levels and the inputs required to realize these are well-known in the Western world (de Wit, 1968). However, quantitative data on the unintended and undesirable outputs of these production techniques and their contribution to environmental pollution are still scarce and subject to debate (de Wit et al., 1987). Agricultural research should therefore increase its efforts in this direction (Vereijken & van der Meer, 1988).

Quantitative information about alternative agricultural production techniques for both developed and developing countries can, in principle, be derived from dynamic simulation models, despite their well-recognized shortcomings (Seligman, Chapter 14). In the Western world emphasis is shifting from increasing production to decreasing the negative effects of the present highly intensive production techniques. The *leitmotiv* today is 'integrated agricultural production techniques', i.e. techniques that not only serve the goals of sustainable high production and an equitable income for the farmers, but also contribute to environmental goals. Environmental pollution in agriculture is on one hand associated with the excessive use of biocides, and on the other hand mainly a problem of nutrient imbalances. The effects of reduced use of biocides are being investigated experimentally, although the data base is as yet narrow. Simulation models that deal with nutrient balances are as yet insufficiently developed, because the underlying processes are imperfectly understood (cf. van Keulen & Seligman, 1987). That makes it difficult to predict the effects of changing practices on the fate of potentially hazardous emissions to the environment. Therefore, technical coefficients of alternative production techniques have to be derived either from theoretical considerations (Aarts et al., 1988), where lack of sound data make them controversial, or from the limited practical experience with such production techniques (Vereijken, 1989). The wider ecological implications of agricultural practice will therefore demand increasing attention in the future, especially in the framework of agrosystems research.

For developing countries, supplementary information on the present production techniques would have to be generated by methods like Farming Systems Research (FSR), an approach that gained widespread acceptance in the mid-1970s as an alternative to the commodity-oriented research geared to increased production per unit area. Unfortunately, this multidisciplinary research effort, although advocating the systems approach, has not produced much appropriate quantitative data on current and new techniques that could provide a basis for a more comprehensive analysis of development. In overreacting to the commodity-oriented research ethos, FSR has tended to emphasize socio-economic and environmental problems at the expense of research on the biological processes that govern agricultural production (Fresco, 1986). The consequence is that much of the agro-technical information necessary for the type of analysis pursued in this study has to be derived from statistical data which are not always reliable (Paulino,1987), or from studies not intended for the purpose, where the agronomic conditions are often poorly defined (cf. van Heemst et al., 1981). The recent emphasis on Farming Systems Analysis (Fresco, 1988) may help in solving some of these problems.

An additional problem in defining the technical coefficients of the present production activities in both developed and subsistence situations is the requirement of sustainability that is implicitly assumed in the analysis. This assumption requires that the technical coefficients describe production techniques that do not result in deterioration of the production capacity of the agro-ecosystem in the long run. In many instances, it is evident that in the developing world the outputs of production techniques currently practised can only be realized at the expense of exhaustion of the natural resources and the subsequent risk of loss of production capacity (van Keulen & Breman, 1990). A satisfactory solution for this problem must be found, because it is unrealistic to exclude production techniques widely practised at present from the fund of techniques available. Some short-term exhaustion of resources may be necessary at one stage of development, but this exhaustion should be phased out in a later stage when more conservative production techniques become feasible.

Dynamic simulation models that predict crop growth and yield at different production levels can be used to quantify alternative production techniques for primary production (van Keulen & Wolf, 1986). A hierarchical approach to agricultural production modelling has been developed (Penning de Vries, 1982), where at the highest level it is assumed that all the constraints to crop production, such as water shortage, nutrient deficiencies, weeds, pests and diseases that can be feasibly removed by appropriate management measures have indeed been eliminated. Crop growth and yield are then basically determined by genetic crop properties (length of the growth cycle, assimilation characteristics of the crop and the distribution of dry matter between marketable product and crop residues) and the environmental factors that are difficult to modify (radiation, temperature and daylength). These production levels require high input levels, and though they are not always appropriate, they provide a yardstick for the present level of achievement and indicate the scope for improvement. At successively lower production levels an increasing number of constraints, such as water shortage or nutrient deficiencies are taken into account. This system can provide a wide range of yield levels for a given situation, each with its specific input requirements. In many developing countries the basic data on weather, soils and crops are either not available, or of such doubtful quality that the results of the calculations are at best only rough indicators of the true coefficients. However, these results form a baseline, derived from explicitly and consistently formulated causal relationships between environmental factors and crop performance. As better data become available, the calculated production levels and the required inputs can easily be updated.

Dynamic simulation models for animal production in relation to available feed resources are far less developed, mainly because of the complex relationships at the interface between pasture and forage supply and quality on the one hand and feed consumption and animal response on the other. It is therefore much more difficult to derive the technical coefficients of alternative production techniques in this sector. To partially overcome this problem, animal production techniques are formulated as target-oriented, so that the mix of inputs is derived from the predetermined production levels. Quality is closely related to nutrient content, which in turn is governed by nutrient availability from the soil. As mentioned earlier, models describing that aspect are still speculative, hence the prediction of quality and quality distribution is still largely based on semi-empirical relations, making extrapolation and prediction difficult (Freer & Christian, 1983).

15.2.2 The goal variables

The possibilities of the interactive multiple goal linear programming technique are exploited best if initially a large number of goal variables is defined. The goals should cover all the major interests in the region, to ensure that the options for technically feasible development pathways are kept as open as possible. Goal definition is an important part of this approach, but must often be derived by indirect methods, because in actual practice it is often difficult to extract explicit development goals from policy-makers and other interest groups with a stake in the development process. The development goal should be defined in physical and not in monetary terms, but this is not always possible.

Sustainability, which is a major concern in any agricultural production system, should be treated as a major goal. However, as sustainability is an elusive term, it can be difficult to define in terms of the variables incorporated in the model. For the current production techniques in the Western world, sustainability involves the growing public concern about the emissions of noxious compounds to the environment and the accumulation of undesirable compounds like heavy metals and biocides in the soil. In this case, sustainability can be translated into physical terms, such as minimizing the loss of nitrate from the rooted soil profile, minimizing ammonia volatilization to the atmosphere and minimizing the use of mobile and persistent biocides. Sustainability must also consider soil conservation. Soil formation is such a slow process that even in the absence of direct water or wind erosion more soil is lost in agriculture than can be formed. Quantification of the consequences of this process deserves more attention in agricultural research.

In most developing countries sustainability is threatened predominantly by overexploitation, in which the export of essential plant nutrients exceeds the imports into the system. That leads to gradual exhaustion of the soil and to decreasing yields, which can have two major consequences: the yields may drop to such a low level that farming is no longer worthwhile because the efforts invested in cultivation are not compensated by the energy in the harvested products, or the lower dry matter production and the removal of all material from the field may lead to greater exposure of the soil surface and hence to physical degradation with its associated lower infiltration capacity. Formulating the goal of sustainability for these systems in physical terms relevant to the model presents greater problems. A possible solution could be to incorporate the 'rate of degradation', defined as the difference between inputs and outputs in the production techniques, as an additional output, and define minimization of that output as a goal variable.

The required level of production of food, both staples (energy) and animal protein is a goal in agricultural development. For the Western world, this goal at the national level is to set a limit to the production volume to prevent overproduction and its consequences for agricultural policy and to promote an equitable development in both the developed and the developing world. For the farmers in developed countries this is not a desirable goal because of its consequences for their income and for the economic viability of their production system. In rural development programmes for developing countries, where self-sufficiency in food is often a major policy consideration, maximizing food production would obviously be a goal at the national level. However, there is also a potential conflict between food production and the production of cash crops that could supply foreign exchange. It could well be that increasing the proportion of cash crops in the rotation, where the application of external inputs is economically attractive, could also safeguard self-sufficiency in food production (Breman, Chapter 16). Optimizing the foreign exchange balance by cultivating cash crops and food crops in a judiciously chosen combination could therefore equally well be a goal at the national level. The farmer's position may be different, especially where the economic environment does not provide incentives for the maximization of production. In that situation, minimizing risk may be a much more important goal at the farmers's level. Translating that goal into terms relevant to the model needs much more attention.

Regional income is important in rural development programmes in both the Western world and in developing countries, because an equitable income for the farming community is a primary objective. The level of income is directly related to the prices of inputs and outputs of the agricultural activities. Therefore, income is strongly governed by national and international policies on subsidies and guaranteed prices, which are difficult to predict. Moreover, government taxation policy is important, as in general the model only considers the difference in value between outputs and inputs as income. That, however, can be taken care of if the taxation policy is known. When carried out on a regional scale, a more important weakness in the analysis is that income distribution and its consequences are not taken into account. This can have very strong impacts on the possibilities for development in a region, as it affects purchasing power, the distribution between the expenses for consumption and savings, and hence the possibilities for investments, which in turn affect the possibilities for, for instance, land reclamation and land regeneration and thus the production level.

Another consideration is the number of people that has to derive its livelihood from the agricultural sector. Achieving a reasonable level of employment for the rural population is therefore also an objective in agricultural development. The relative importance of this goal greatly depends on the economic environment in which production takes place, particularly the possibilities for alternative employment outside the agricultural sector. In many developing countries the agricultural sector absorbs 'hidden' unemployment; that is, many more people are involved in agricultural activities than would be necessary from the point of view of optimizing labour productivity. Therefore, there is a trade-off between regional income and employment.

The rural environment not only serves purposes connected with agricultural production, as expressed in the goal variables described so far, but also has environmental and recreational uses. Experience with the interactive multiple goal linear programming method has shown that it is even more difficult to formulate these goals in terms relevant to model variables than the goals related to agricultural activities (de Wit et al., 1988).

The list of goal variables could and should be extended substantially, but the specific goals to be considered depend on the local situation. Interaction with the interest groups at an early stage of the analysis is therefore necessary.

15.2.3 The interactive analysis

In the interactive procedure a feasible, widely acceptable solution is attained by successively optimizing the various goal variables, preferably in close collaboration with representatives of the planning and sectoral interests. The 'solution' is a mix of technologies ('activities') arranged in such a way so as to define an optimum development pathway within a planning horizon. In the first cycle the lower bounds of all goals considered are set at their minimum values, to ascertain that a feasible solution is obtained that satisfies all these minimum requirements concurrently. (It may be that a feasible solution that satisfies the minimum requirements for all goals does not exist. That then raises the political question of who will be forced to accept benefits below what is regarded as a minimum.) Now, each of the goals is optimized separately with the lower bounds of the other goal variables as minimum goal restrictions. The combined results of this first iteration cycle define the scope of choice, i.e. they indicate for each of the goal variables the most favourable value that can be obtained and the worst value that has to be accepted.

However, as the various goal requirements are not identical, a conflict will arise when limited resources are to be distributed among different activities that contribute differently to each of the goals. Consequently, the ideal solution where all the goal variables reach their individual maximum value simultaneously, does not exist. Hence, an acceptable compromise has to be found. In subsequent iterations, more satisfactory solutions from the point of view of the sectoral interests are obtained by successively tightening the minimum goal restrictions on one or more of the goal variables, and repeating the optimization for the other goal variables. The choice of the goal restrictions and the degree to which they are tightened reflect the specific sectoral interests or those of the planner who represents all the sectoral interests to varying degrees.

The stepwise maximization of the various goals under increasingly tighter restrictions on the other goals reduces the solution space. In due course a solution is arrived at where none of the goals can be improved without sacrificing on one of the others. The result is that the costs of realizing one goal more completely can be explicitly expressed in terms of what must be sacrificed on the other goals. The planner can thus quantify the opportunities for exchange between the various goals within the feasible solution space.

15.2.4 An example of results

The method described above has been applied in a joint Dutch–Egyptian research project on land use planning in the northwestern coastal zone of Egypt (Ayyad & van Keulen, 1987), a semi-arid region with a Mediterranean climate. The agricultural activities in the region comprise animal husbandry (mainly sheep and goats), rainfed arable farming with barley as the main crop and the cultivation of fruit trees, particularly olives and figs. For each of these activities, various production techniques at different levels of intensity, characterized by different output levels, with their associated inputs such as capital and labour needed for water harvesting, the amounts of chemical fertilizer and concentrate feed were defined. The constraints to agricultural development in the region are the regional resources of land types, labour availability and availability of subsidized external inputs (e.g. fertilizers and concentrate feed).

Some results are shown in Figure 85, where for the purpose of illustration, only three goal variables have been considered: livelihood (or consumable income), employment (or labour requirements) and contribution to regional balance of payment (in this case export of meat that commands a substantially higher price than meat sold on the local market). In the first iteration cycle, the feasible region that characterizes the initial freedom of choice, is defined. The results show that for consumable income the values range between 5.6 and 79.8 million LE (Egyptian pounds), for export between 0 and 22.9 million kg and for employment between 27 600 and 5100 person–years. For the sake of illustration the aspirations of the local population were explored further. In the second iteration cycle, the minimum level of employment was set at 19 800 person–years, allowing an unemployment of 10 % of the present population, and development aid was reduced to zero. The results show that this requirement considerably reduces the set of feasible options. The maximum values of both consumable income and export decline substantially, the main reason being the elimination of develop-

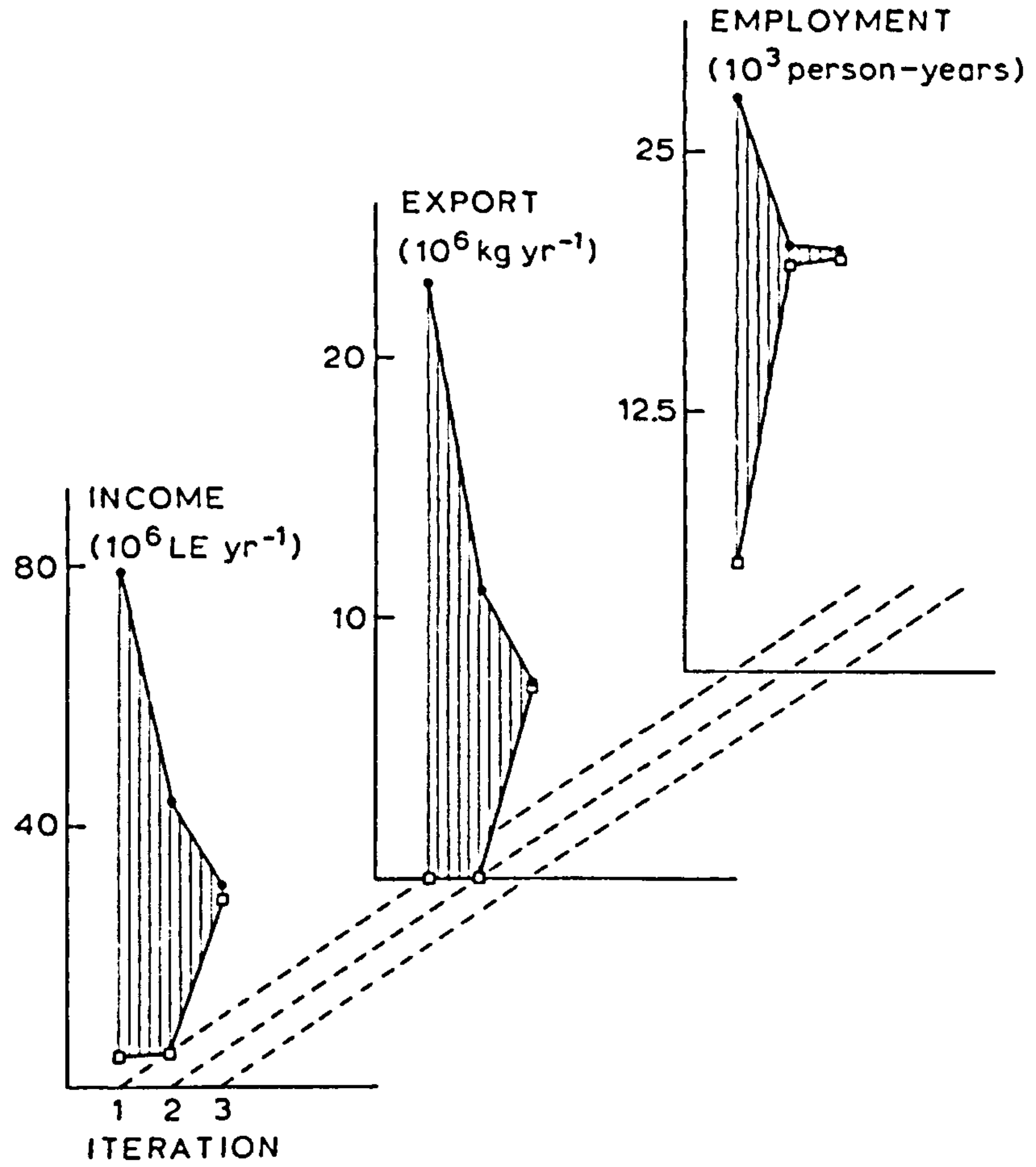

Figure 85. Graphical presentation of the iterative procedure for three goals. In the first iteration cycle the maximum attainable goal values for each goal are determined (●) and the minimum acceptable values (□). In the second iteration cycle a minimum goal constraint for employment was introduced, which reduces the possible range for the other goals. In the third iteration, a minimum goal constraint for export was also introduced.

ment aid. In the subsequent iteration cycle, the minimum goal restriction on meat production for export is set at 7.5 million kg.

Optimization of the other two goals shows that the freedom of choice has become very small now, i.e. improvement in one of the goals can only be achieved at the expense of one of the others. In other words, the decision-maker now has to consider the relative importance that he attaches to the different goals and has to make a choice, taking also into account the aims and aspirations of other interest groups and his bargaining position in possible negotiations.

15.3 Discussion

This method of analysing the possibilities for agricultural development on a regional basis can help in deciding on feasible development pathways under a wide range of technical and quantifiable socio-economic conditions. In the model, a large amount of general and local knowledge on actual and potential production techniques, regional resources and constraints and prices of inputs and outputs can be harnessed to a dynamic planning process that explicitly takes a large number of technical possibilities and sectoral interests into account. The model has a strong technical base, in which non-quantifiable and politically determined socio-economic considerations, such as ownership of the means of production, distribution of income, and uncertain economic behaviour are not taken into account. This ensures that unexpected, but technically feasible development pathways will be given full consideration. On the other hand, disregarding these aspects may result in overoptimistic expectations for development in a region. For instance, integration of animal husbandry and arable farming may be a desirable development, but if that requires common use of scarce resources, such as rangeland and water, achieving that goal may require policy measures to promote cooperation, and legislation may be required to regulate such cooperation. This then brings the political dimension into play and can help to define the benefits and costs that could motivate desirable change. The advantage of this approach is that it clearly defines the technically feasible development options that form the arena for negotiation and political intervention. In other words, it defines the 'margins for strategy' (de Wit et al., 1988). Therein lies the importance of separating as strictly as possible the technical coefficients of the present and possible alternative agricultural activities from the socio-economic environment in which these activities are to be implemented. The consequences of the proposed development pathways can be evaluated in terms of economic viability and social acceptability. If some of the non-quantitative and politically determined socio-economic constraints then appear insurmountable within the planning horizon, it may be necessary to adapt some of the goal restrictions and repeat the planning exercise until a workable plan is attained.

By quantifying the implications of implementing a certain viewpoint, the model can also serve as a basis for negotiations between various interest groups in a region, which may lead to a compromise and thus provide a broader base for the proposed regional development plan. In this way the results of the model can be used to improve communication between planners and policy-makers and between policy-makers and various interest groups in a region. This can help to smooth the way to a more balanced development in which the interests of all the parties that are involved are taken into account.

The validity of the results of the model depends on many factors. These include the accuracy of the technical coefficients in the input–output model, whether the goal variables have been properly defined and quantified and the degree to which the technical and socio-economic possibilities can be treated separately. Technical coefficients often cannot be determined with great accuracy, but generally, modest accuracy is sufficient for the level of resolution aimed at in a regional planning model. However, there is a danger of the technical coefficients of alternative production techniques being estimated too optimistically by their advocates, and critical evaluation is therefore necessary. Equally important are the goal variables, which are often difficult to identify, difficult to translate into terms relevant for the model and difficult to quantify. Goal formulation for regional development is therefore an area that warrants intensive study. The separation between quantifiable, mainly technical aspects and unquantifiable socio-economic aspects is an essential feature of the approach. It allows us to distinguish between the technically feasible options in a region and the elusive behavioural factors that often strongly influence actual development policies. As a result, the analysis can help to define political issues more meaningfully, and so '...render unto Caesar, what is Ceasar's...', while pointing to feasible pathways for development.

It should be realized that the results of the model are only an intermediate step in formulating development policies. The model results do indicate the requirements for desired development options, but do not determine what policy measures should be taken to actually bring them about. That means that a post-model analysis is necessary, to translate the requirements for external inputs, investments, education, research, etc. into practical actions. In this analysis, especially the social acceptability of the proposed developments should be carefully considered.

15.4 Conclusions

The application of the interactive multiple goal linear programming technique for analysis of rural development possibilities yields three results. Firstly, it enables internally consistent, technically feasible development pathways for a widely acceptable combination of goal values to be identified for a region. Secondly, it reveals the costs of achieving full realization of one goal in terms of the sacrifices on other goals under the prevailing regional constraints. Thirdly, it translates the selected combination of goal values into the required production techniques necessary for their achievement, from which requirements for land reclamation, imports of means of production, export of products, credit facilities, education, etc. can be derived. These results then provide a consistent starting point for further socio-economic and policy analysis.

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16 Integrating crops and livestock in southern Mali: rural development or environmental degradation?

H. Breman

16.1 Introduction

This chapter could have had a second subtitle: 'It ain't necessarily so', inspired by the song from the folk-opera *Porgy and Bess*: 'The things that you liable to read in the Bible, it ain't necessarily so'. For me, not a student of de Wit's, not even a modeller, this motto characterizes my attitude towards him and made research under his guidance inspiring. Moreover, I am convinced that such an attitude to models and simulation is a prerequisite for their fruitful use. In this chapter I will illustrate the usefulness of models and systems analysis for policy-supporting research on rural development and attempt to provide building blocks for a bridge between socio-economic and agro-ecological research for rural development.

I will present an example of more rapid problem identification. The present situation in rural southern Mali will be described, based on the results of simulation of rangeland (Penning de Vries & Djitèye, 1982) and crop production (SOW, 1985). If sociologists and economists working on rural development in the region would accept this description, confidence in the use of simulation models would increase. That is another prerequisite for fruitful application of models in rural development, especially in situations as difficult as those in the Sahel.

I will go on to suggest possibilities for rural development in southern Mali, paying special attention to the option originating from local farming systems research: integrating crops and livestock. Maybe disciples of de Wit will conclude that 'it ain't necessarily so'. This should provoke them to formulate improved suggestions, thereby decreasing the need for expensive and disappointing trial and error to arrive at sustainable agriculture for the Sahel.

16.2 Problem identification in rural southern Mali

16.2.1 The region

Southern Mali is selected because of data available, but the area is also characteristic of the landlocked, poorly opened Sudan savannah of West Africa. Southern Mali covers an area of almost 100 000 km^2 between 10° and 14° N and 4° and 8° W. Average rainfall over the last 30 years ranged between 700-1200 mm yr^{-1}, which under the prevailing conditions results in a growing season of 4-5 months.

The 2.8 million inhabitants live in almost 4000 villages whose distribution is very heterogeneous and is related to the suitability of land for agriculture, which is determined by rainfall and soil properties. In the centre and the north, where on average 50% of the land is suitable for arable farming, population density correlates positively with land suitability (Table 19). The correlation may be influenced by data availability: only population densities per municipality are available.

In the south, where 70% of the land can be cultivated, population density is, however, only about two-thirds of the regional average (20 against 30 persons km^{-2}; PIRT, 1983). This trend continues further south into Ivory Coast, population density decreasing with increasing annual rainfall (Bengaly et al., 1988). Here, land suitability no longer correlates positively with water availability, as leaching of nutrients becomes important. River blindness and sleeping sickness are other reasons for the lower population density.

The landscape is a tableland traversed by temporary and permanent small streams and rivers, with valleys of various widths. The soils on the plateau are shallow and stony. On the slopes they are deeper, but with lower infiltration capacity, causing runoff. As a consequence, in general only the valley bottoms can be cultivated without too much risk of crop failure and lack of sustainability.

Official statistics on land use are rather unreliable (Breman & Traoré, 1987), but on the basis of interpretation of satellite images (PIRT, 1986) and personal observation, it has been estimated that about 25% of the total land area in the region is cultivated, except in the very south, where only about 10% is cultivated. Fallow land also accounts for about 25% of the area. Villages and roads, mostly in the valleys, account for more than 10%. This implies that in the centre and the north of the region all suitable land (about 50%), including fragile soils, is already in use.

Table 19. Population density in relation to the suitability of the land for agriculture in the Sudan savannah in southeast Mali. Each density class is characterized by the relative importance (%) of six suitability classes. Suitability increases from top to bottom.

Persons km^{-2}	<5	5–10	10–20	20–50	>50
Area (%)	7	24	42	24	3
Rocks or water	15	10	5	4	1
Sandy	16	4	3	6	5
Plains; fine loam or clay*	39	24	26	26	19
Lateritic subsoil	27	59	52	35	32
Flood plains	2	2	5	9	25
Plains; loamy sands*	1	1	4	11	17

* Plains soils of heavy texture have a low suitability because of drainage problems and workability.

The major crop is sorghum, followed by millet, peanut, maize and others. About 10% of the cereal production is marketed, mostly on the domestic market, compared with about 50% of the peanuts and all the cotton, which is exported. This implies that about 80% of the cultivated arable land is in use for regional consumption.

Livestock is becoming increasingly important, with animal traction and manure as the major products (Breman & Traoré, 1987). An unknown number of livestock owners, often wrongly overlooked by development projects, migrated from the Sahel during the drought and are trying to use the waste lands of the region in competition with the sedentary herds of the arable farmers.

The CMDT (Compagnie Malienne pour le Développement des Textiles) constitutes a major factor in rural development in the region. This state organization was responsible for the development of cotton production in all its aspects: extension, supply of credit, fertilizers, pesticides and agricultural implements. purchase and processing of cotton and marketing of fibre, cotton seed and cotton cake. CMDT is at present responsible for total rural production, including animal husbandry. Rural development as such has become the final goal: crop diversification, public health, literacy, erosion control and the position of women are all receiving attention.

Cotton production has increased spectacularly since 1960 (from 2000 to almost 70 000 tons of fibre per annum), demonstrating that farmers adapt with surprising speed. The cereal yields of the region are amongst the highest of the country indeed, but their increase has been limited. For the country as a whole food production has not kept up with the expanding population. As a consequence, commercial imports and food aid are steadily increasing, testifying to the increasing dependence on food from abroad (OECD, 1988).

16.2.2 Socio-economic bottlenecks

Before discussing the bottlenecks to rural development in the region, the term ‘development’ has to be defined. For the time being ‘increasing well-being of the population’ will suffice. This is an elusive definition, but a more explicit description will be possible after the analysis presented in this section.

The socio-economic bottlenecks to development that have been suggested are so numerous and diverse that they can be treated here only superficially. As a consequence, in most cases the evidence presented here refers to the entire Sahel region, instead of to southern Mali only.

In certain bottlenecks social aspects dominate. The disruption of societies by over 60 years of colonial rule and its negative consequences is blamed for the loss of efficient production systems, the loss of traditional knowledge and land use regulations, the artificial frontiers, the introduction of cash crops and the disintegration of family structures (e.g. OECD, 1988; Bassett, 1988). Cash crops are probably the most frequently blamed. They occupy the best soils, pushing food production to marginal soils and, indirectly, animal husbandry into the dessert (e.g. Franke, 1987; Franke & Chasin, 1980). A quotation from 1915 is illustrative of the French colonial policy: 'If we try to develop cotton, it is to provide an export trade with a raw material, while facilitating import of European cloth. Hence, the native must be persuaded from the outset to deliver his cotton to commercial houses so that local weaving will gradually be suppressed' (Bassett, 1988). Social inequality is another major bottleneck. It embraces the position of women, the neglect of the rural population by authorities and the loss of control over the means of production by the original producers (e.g. Breman & Traoré, 1987). The growing inequality aggravates the situation and partly explains the failure of development programmes aiming at aiding the poor. The suggested lack of responsibility of farmers is a special case (e.g. Franke, 1987). Closer examination of this argument reveals that it may have various interpretations. Either, they will have to learn how to behave, or they have to pay for all services, or advantage should be taken of their skills. The relative rigidity of rural production systems and lifestyle is also considered to hamper development (OECD, 1988; Giri, 1983).

Various economic bottlenecks, have also been recognized (see Breman & Traoré, 1987). Government policy on taxes, subsidies, prices, imports and exports provides insufficient incentives to the farmers to produce (e.g. Delgado & Staatz, 1980); indeed, the government's entire financial policy is open to criticism. Furthermore, marketing structures and the distribution of revenues are far from optimal (e.g. Harriss, 1982), and the international situation (e.g. world market developments, policy of the European Community, restrictions imposed by the International Monetary Fund or donors) is not favourable either.

This list is by no means exhaustive and the problem is that it becomes increasingly difficult to see the wood for the trees. There is lack of hierarchy, a headache for modellers.

16.2.3 Agro-ecological bottlenecks in relation to socio-economic bottlenecks

It is interesting to consider the bottlenecks listed above in relation to the development priorities for southern Mali formulated by the Malian Department for Farming Systems Research (DRSPR). These are: integration of crops and livestock with strong emphasis on animal traction and manure production, strengthening rural extension, erosion control and improving the position of women. Do these priorities reflect an order in agro-ecological and socio-economic bottlenecks? Closer examination shows rather the reverse. Several of the bottlenecks listed above are recognized, but considered impossible to remove by on-farm research. Animal traction and manure are advocated because the farmers are ready to accept them: there is a shortage of land and fertilizers are expensive. Erosion control could be in line with the priorities of farmers, but the women's programme is certainly a 'top–down element'. However, DRSPR does not examine its priorities in relation to existing bottlenecks, nor does it consider the adequacy of traction and manure as production targets against ecological criteria in the long run. Hence, the development priorities for southern Mali have

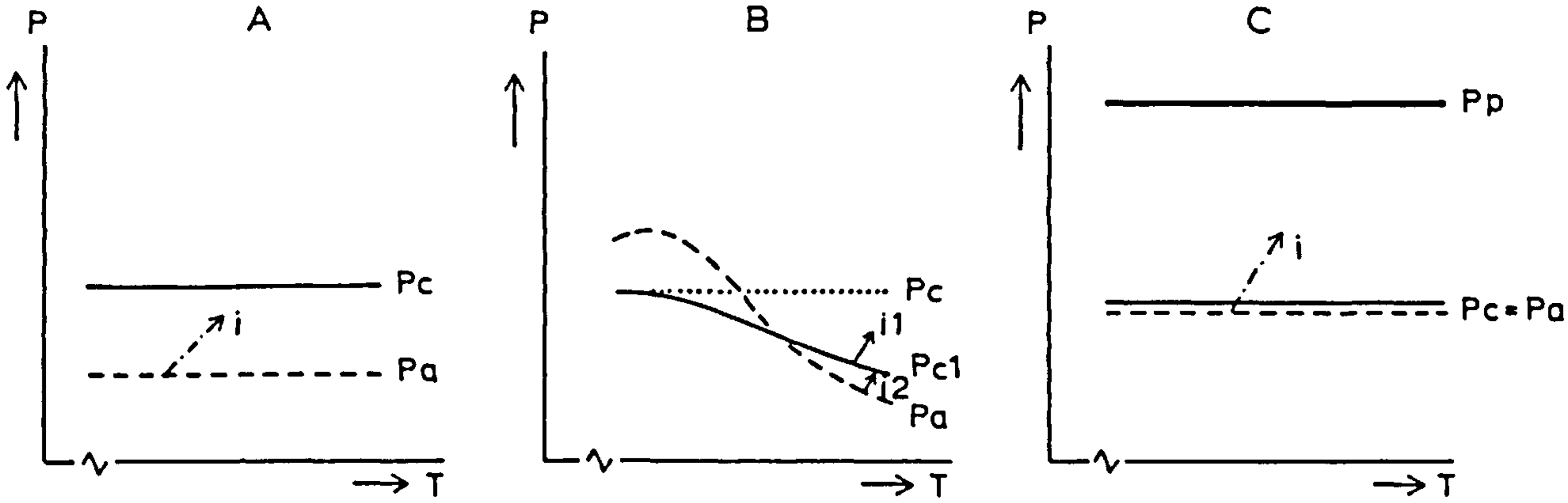

Figure 86. Schematized presentation for the identification of possible development interventions (*i*), on the basis of comparison and analysis of the level of agricultural production at the carrying capacity of the natural resources (*Pc*) and the actual level reached by local production systems (*Pa*). A: underexploitation. B: overexploitation. C: maximum exploitation (*P*: production of crops, pastures, forests, water, etc.; *T*: time; Pp: potential production as determined by climatic conditions and genetic potentials of species and varieties).

been set rather arbitrarily.

Systems analysis and modelling can help to work less intuitively, to identify and classify bottlenecks, as is illustrated in Figure 86. An agro-ecological analysis is needed to establish whether a region is underexploited (A), overexploited (B) or used optimally (C). The maximum level of sustainable production at the current level of inputs (*Pc*) has to be determined by systems analysis, which also must identify the major constraints. The actual level of production (*Pa*) must be derived from farming systems research, which should also identify the factors determining it: is underexploitation the result of ignorance or social inequality? Is overexploitation a consequence of irresponsible behaviour, of ignorance or of circumstances beyond control of the local population, considering overpopulation? What is the major constraint to increased carrying capacity of the natural environment: lack of skills, lack of the necessary means of production or lack of economic incentives to use them? Whatever the reason, if the production capacity cannot be increased, optimum resource utilization easily turns into overexploitation under increasing population pressure. Different interventions (*i*) are necessary in all these cases.

16.2.4 Analysis of the situation

Applying the approach outlined above, southern Mali appears to be a region where overexploitation is rapidly increasing as a result of overpopulation, especially in the centre and the north (Breman & Traoré, 1987; Berckmoes et al., 1988). This is illustrated by comparing the 'average' production system with an intensified system as practised by 20% of the farmers in the region (Table 20). The data for the intensified system refer to a group of 9 farmers, studied over a 6-year

Table 20. Comparison of the average production system in southern Mali with an intensified production system (characteristic for 20% of the farmers).

	Average	Intensified system	
		1983	1987
ha person^{-1}	0.4	0.8	0.8
Crops			
cereals (%)	58	50	54
cotton (%)	14	45	43
legumes (%)	11	3	3
sundries (%)	17	2	–
Inputs			
ha plough^{-1}	7	6	5
N fertilizer (kg ha^{-1})	5	27	20
livestock (TLU** person^{-1})	0.3	1	1
rangeland (ha TLU^{-1})*	7	4†	3†
Yields			
cereals (kg person^{-1})	225	285	370
cotton seed (kg person^{-1})	70	515	520
leguminous fodder (kg TLU^{-1})	230	85	65

* without nomadic herds; ** Tropical Livestock Unit; † if system should not use more rangeland per farmer than the 80% less intensified systems.

period (Berckmoes et al., 1988). To show that the farmers behave rationally in the present situation of overpopulation, recent developments in the intensified system are also illustrated.

The average production system concentrates on cereals. At the current production level at most 10% can be marketed, assuming a subsistence need of 200 kg person^{-1}yr^{-1}. Production of cotton is limited and the use of fertilizers negligible. As the ratio cultivated land/fallow is 1:1 (Subsection 16.2.1), there is a danger that arable land will be rapidly exhausted and degraded. For the rangeland the situation seems more favourable: 7 ha are available per tropical livestock unit (TLU, a standard ruminant of 250 kg liveweight), at a carrying capacity of 5 ha TLU^{-1}, if all crop byproducts are used on the farm and no other herds graze the waste lands (Breman & Traoré, 1987). Currently, however, herds originating in the north exploit the region and most of the cotton seed and part of the peanut byproducts are used elsewhere. The availability of ploughs and draught animals is another threat for the rangeland.

In practice, large deviations from this average situation occur. The Department for Farming Systems Research distinguishes three classes of farmers in their on-farm research, based on ownership of agricultural implements and cattle. Type C production units do not own ploughs or draught oxen, Type A units are well equipped and own a herd of at least 20 head of cattle. Type B is intermediate. The poorly equipped production units often borrow implements in exchange for labour, which endangers the timeliness of their operations. Therefore, the A unit yields are higher than those of C units, but within this last group exceptions do exist: for example old respected farmers assisted by Type A farmers (de Steenhuijsen Piters, 1988).

The data in Table 20 for the intensified (Type A farmers) indicate possible real intensification: compared to the average system there is higher production per person, more fertilizer use and a higher degree of mechanization. In addition, the production of the cash crop cotton is higher, both in area and in yield per unit area; manure availability is only slightly higher, animal density per person is three times higher, but the cultivated area per person is double. The carrying capacity of the rangeland, however, is clearly exceeded and it is unlikely that the amount of fertilizer used is enough to maintain soil fertility.

The trend from 1983 to 1987, i.e. less cotton and more cereals, less fertilizers and increased mechanization and herd size, is the result of two extremely dry years, which affected food production much more than cotton production, and higher prices of pesticides and fertilizers on the local market and a fall in cotton price on the world market.

The sustainability of the production systems in southern Mali has already been questioned. That doubt increases when the nitrogen balance of the arable cropping component of these systems is examined. Neither the average system, nor the intensified system is in equilibrium (Table 21). The terms of the nitrogen balance presented here were quantified on the basis of the results obtained in the project 'Primary Production in the Sahel' (Penning de Vries & Djitèye, 1982).

It was assumed that all cereals produced above the level of self-sufficiency are sold, in addition to half of the peanut seed and 70% of the cotton seed. Moreover, all byproducts (leguminous fodder, cereal straw, 30% of the cotton seed, bran, etc.) were assumed to be consumed by the own herd. Cotton stalks and leaves, however, are completely burnt. Without burning, losses occur by volatilization and are about half. Runoff lossed were assumed to be proportional to water losses, i.e. 20% of the N input by rainfall and algae; losses by leaching were calculated as a fraction of the available mineral N, proportional to the fraction of infiltrated water percolating below 2 m. Erosion losses were estimated to be 5 kg $ha^{-1} yr^{-1}$, i.e. 13 000 kg of topsoil containing 0.4% N (Kessler & Ohler, 1983) for the intensified system, and for the average system with a lower degree of mechanization 3 kg $ha^{-1} yr^{-1}$. Losses of N from manure and fertilizer were neglected.

In the intensified system losses are even higher than in the average system, because of the export of cotton seed and increased losses by runoff, leaching and

Table 21. Nitrogen balance (kg ha^{-1} yr^{-1}) of cultivated land of the average production system in southern Mali in comparison with an intensified system.

	Average	Intensified system	
		1983	1987
Inputs			
rainfall, algae	9	9	9
leguminous crops	4	3	2
manure	3	7	7
fertilizers	5	27	20
Total	21	46	38
Outputs			
sales:			
• cotton seed	3	16	16
• peanuts	1	1	–
• cereals	1	2	3
consumption losses:			
• people	4	2	2
• livestock	13	12	13
runoff, leaching, erosion	8	15	14
fire	4	19	19
Total	34	67	67
Balance	–13	–21	–29

erosion, and by the burning of straw. The situation has deteriorated since 1983 as a result of the restricted use of fertilizers.

The data in Table 21 corroborate the conclusion drawn from Table 20: sustainability of land use in the region is threatened by overexploitation, which presents a great danger to the region and the country. Self-sufficiency in food production is becoming more unlikely, and the production of the most important cash crop is in danger, with serious implications. To cope with population growth, intensification of crop production is required through the use of imported inputs, which are more profitable for cotton than for food crops because of the low and decreasing purchasing power on the national market. In other words, cash crops are necessary for rural development aiming at self-sufficiency in food production. However, limited use of fertilizer for economic reasons, and export of cotton seed and peanut cake out of the region (Table 21) hamper that development.

The analysis enabled the various agro-ecological bottlenecks and different socio-economic constraints to be identified and arranged in order of priority. To convince those not acquainted with modelling and systems analysis, the relation between the conclusions and the assumptions underlying the model must be explicitly formulated. Simplification is both the strength and the weakness of modelling and systems analysis (Seligman, Chapter 14). For outsiders, even if they understand a model, it is practically impossible to judge the limits of its applicability and hence the validity of its results. To illustrate this, two examples will be given. First, when discussing Table 20 it was concluded that a grazing pressure higher than 5 ha TLU^{-1} signifies overgrazing. That conclusion is based on production capacity in dry years, at the current ratio of cattle and small ruminants, with maintenance of the herd as production goal; in other words, environmental criteria were not considered (Breman & Traoré, 1987). Secondly, when estimating the losses of N (Table 21) an average value of 50% was used for consumption losses for food and for fodder, for men and animals. However, losses from urine varying between 20 and 90% have been reported (Penning de Vries & Djitèye, 1982)!

However, if specialists cannot falsify the conclusions on the basis of better local parameters, and if generalists cannot falsify them by indicating the possibilities for higher outputs without resource degradation, the current analysis is the best available. In that case, four considerations are important for the precise indentification of socio-economic bottlenecks:

- economic criteria increasingly influence behaviour
- prices of agricultural products and means of production, both at the farm gate and at the national border are of prime importance
- the question who controls the use of the natural resources needs more attention
- family planning and alternative employment have to be considered.

This short list raises the question of whether attempts to promote rural development should be directed at the farm level or at the policy level. The analysis also casts doubts on the appropriateness of the approach of the Department for Farming Systems Research at the farm level, with its emphasis on animal traction and manure. Because of the shortage of rangeland and high quality crop byproducts this approach results in increasing inequality, rather than being a solution for the poor by providing cheap alternatives to tractors and fertilizers. 'There are signs of an emerging class of rich farmers, each owning several pairs of animals and several animal-drawn implements, using more productive techniques than 'traditional' farmers and employing wage-earners' (OECD, 1988).

It is not clear whether this growing inequality is a constraint or a necessary condition for development. Hence, clarifying that point should be a priority for socio-economic research, in addition to research aiming at removing the bottlenecks indicated. Both the fact that in the intensified systems more cereals are produced for the national market than in the average systems, and the necessity to produce in a competitive way for the world market should be taken into account. The key question to be addressed by such research has to be to what extent the exploitation of people prevents the optimum exploitation of the natural resources.

16.3 Development policy and research requirements

16.3.1 Definition

Identifying the bottlenecks is not sufficient to formulate the policy needed for development, without a more explicit definition of 'increased well-being of the population'. The latter was clearly put into words by a Sahelian nomad: 'We were never as miserable as this year. No more cattle, no animal husbandry, no milk. No community life according to our tradition, no friendship, no charity. Everybody is only concerned with his own stomach' (Maliki, 1984).

Consequently, increased agricultural production and increased sustainability have to be pursued; not only for the region but also for the much less endowed rest of the country.

16.3.2 Integrating crops and livestock

Integration of arable farming and animal husbandry in itself is not a solution. Using systems analysis, the area of rangeland needed per hectare of cultivated land for different animal production targets was calculated (Table 22; Breman & Traoré, 1987). It is already difficult to feed draught oxen adequately in parts of the northern savannah, because of the intensity of arable farming (25% in the north, 10% in the extreme south). Breeding draught animals presents more difficulties, and maintaining soil fertility is impossible everywhere if carrying capacity is respected and import of livestock from outside the region is impossible.

Table 22. Rangeland requirements (ha) per ha of cultivated land for different production targets in the savannah region of Mali.

Zone	Production Target		
	feeding draught oxen	breeding and feeding draught oxen	breeding and feeding draught oxen + maintaining soil fertility
north savannah	0.5–4	10	15
south savannah	0 –2	8	15

Availability of agricultural byproducts was only considered in detail in the case of proper feeding of draught oxen: the lower number in Table 22 refers to their complete use by the oxen, the higher number to the situation were only cereal straw is available as the legume straw is sold or fed to sheep, cotton seed is exported and cereal chaff is fed to chickens.

If integration of extensive arable farming and animal husbandry does not lead to increased production using sustainable production techniques, intensification is unavoidable. The current prices of agricultural products and means of production imply that intensification is economically more attractive in arable farming than in animal husbandry. That should ultimately lead to a situation where instead of crop production profiting strongly from animal husbandry, the reverse will be true because the increasing availability of high quality agricultural byproducts will enable a significant production of animal protein on the low quality rangelands of southern Mali (Penning de Vries & Djitèye, 1982), where today practically only production of manure and animal traction is feasible. The first production systems to be considered in that context would be systems with a short cycle, like poultry, that can take advantage of surplus production, of which the frequency will increase through intensification, to avoid crashes of cereal prices.

More direct intensification of animal husbandry could be remunerative through the production of draught animals for the regional market or for export, and for dairy farming in the vicinity of cities.

16.3.3 Intensification of agriculture

With respect to intensification, two general questions are to be answered: 'which form of intensification and where to improve the situation in a sustainable way?'. De Wit has argued in favour of intensifying agriculture on the most favourable soils (de Wit, 1972; Chapter 17) on the grounds that under those conditions inputs are used most efficiently, and hence production is most economic. Recently, de Wit (1988) demonstrated that such developments have indeed taken place in the European Community and that this leads to marginalization of the less endowed regions, which requires, at least, social programmes that may include stimulation of agricultural activities to prevent complete destruction of such societies (de Wit et al., 1987). I agree that the efficiency of inputs increases superproportionately with increasing production potential of the land (Figure 87), but I do not conclude that therefore agricultural development should necessarily only be promoted in those areas. Several arguments can be used against such a policy.

- Although the negative influence of intensive agriculture on the natural resources will be lowest per unit of product, for the time being it is the highest per unit area (de Wit, 1988).
- The observed yield increases are strongly governed by the socio-economic conditions under which production takes place, which in developing countries are far less favourable. In addition, if environmental costs, associated

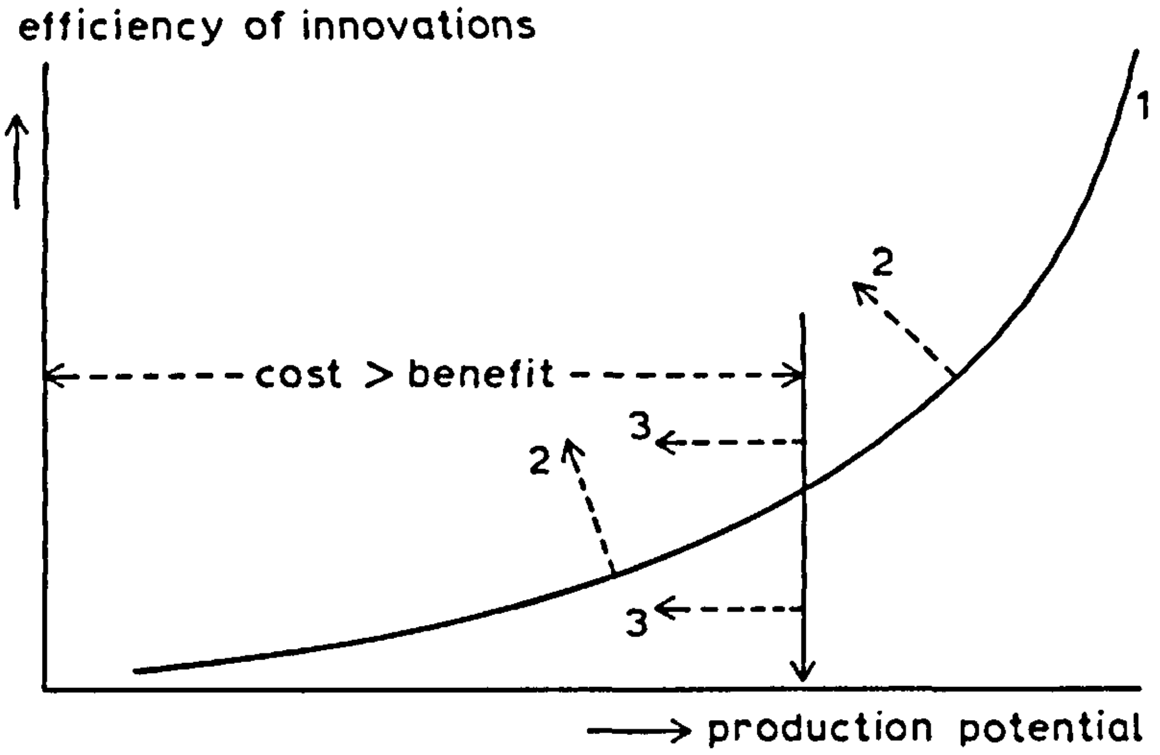

Figure 87. The most probable relationship between the efficiency of innovations from private efforts in a liberal environment (1) and the production potential of land (determined by the natural environment in its socio-economic context) and the direction to be given to agro-ecological research (2) and socio-economic policies (3), to avoid marginalization of people, regions or countries by these innovations.

with intensive production would be taken into account, the costs of production may well be higher than in less intensive systems, where more natural functions of the environment are still vigorous. In addition, increased skills will be required of the farmer, leading to higher labour costs.

- It will be difficult enough to have the suggestion accepted within a country or within the European Community the level to which de Wit et al., (1987) address themselves. The market where producers operate also limits the region where solidarity is maintained. This is the EC as a whole for the EC-countries but for many developing countries it is the country as such. 'Less favoured' and 'better-endowed' regions are relative notions, as the best conditions in one country may be equal to the worst in another.
- Supporting subsistence agriculture may be the cheapest social measure for marginal areas, especially when also considering the additional social benefits for society as a whole, e.g. the slowing down of urbanization.
- Social measures imply dependence, a notion incompatible with well-being, and the more so the more direct this dependence is.

It is therefore worthwhile to also pay attention to less favoured regions, and to investigate at least the possibilities for appropriate agricultural intensification. That implies that socio-economic research and measures must aim at pushing the break-even line in Figure 87 to the left. The cost-benefit ratio could be influenced directly by national policies or international agreements and support, or indirectly by influencing the input/output ratio through proper incentives in areas such as tenure systems.

An original agro-technical option to reach the same goal was de Wit's idea to use zeppelins to distribute phosphates which, in terms of Figure 87, is equivalent to shifting the x-axis to the right. In general, agro-ecological research and interventions should try to make the curve in Figure 87 less concave. That is not equivalent to suggesting 'natural alternatives' for intensive agriculture (Table 23) for the poor farmers in the Third World, even though such suggestions seem attractive because of the high costs of inputs for intensive agriculture, the growing dependence on using them and the existence of fascinating local alternatives based on effective use of natural resources (e.g. Franke, 1987). However, the potentials of these alternatives are often overestimated, because the constraints presented by the current situation are ignored, and their costs in terms of capital and labour are underestimated (Breman, 1987).

To properly judge the scope for improvements, research should at least be directed towards optimum use of inputs like fertilizers and irrigation, not only for cash crops but also for crops cultivated primarily for subsistence. That requires an improved research methodology: instead of the single dose–effect experiments yielding time- and site-specific results only, modelling and simulation techniques should be used to increase insight in the underlying processes so that the results

Table 23. Indications of environmental conditions that guarantee optimum efficiency for agricultural elements regarded as 'natural alternatives' for intensification through the use of external inputs.

Production systems	Soil						Climate		
	fertility			water-holding capacity			water availability		
	low → high			low → high			low → high		
increased availability of water and/or nutrients:									
• manure			+	+					+
• legumes	+				+			+	
• agro-forestry	+			+			+		
decreased losses of water and/or nutrients:									
• agro-forestry			+	+					+
• erosion control:									
– wind			+	+			+		
– water			+		+				+
• water harvest			+	+			+		
• mixed cropping									
– pest control			+		+				+
– drought		+		+				+	
• adapted varieties	+			+			+		+

can be used for extrapolation and prediction (van Keulen & Wolf, 1986). For instance, results from PPS (Penning de Vries & Djitèye, 1982), SAFGRAD (PIRT, 1986) and the Agro-Meteorological Service of Mali (Traoré & Konaté, 1989) clearly show that data used to estimate the returns on fertilizers (Annual reports of the Department for Farming Systems Research) are not realistic. Rather, they show lack of insight in the conditions of the zone and the basic processes.

16.3.4 Integrated agriculture

When trying to develop methods to intensify agriculture in sub-optimum zones, it is dangerously naive to copy the Western example. The latter developed without serious incentives for economizing on the use of inputs like fertilizers and pesticides and without general awareness of the environment. But disregarding the production potentials of the Western example would also be unwise, in view of the still growing demands for food. Mixtures of elements of intensive agriculture and 'natural alternatives' might lead to a more favourable shape of the curve of Figure 87.

To make this plausible, an attempt has been made to break down the *x* axis of Figure 87 into its basic elements: the suitability of a region for intensive agriculture depends on soil fertility, soil water-holding capacity and water availability as dictated by climate. Their rough relation with the efficiency of intensive agriculture is presented in Figure 88.

The optimum conditions for natural alternatives are not necessarily identical to those for intensive agriculture. Some of the 'plusses' in Table 23 are self-evident, other were chosen rather subjectively and could probably be questioned by specialists.

Given that for some of the conditions the optimum for natural alternatives is different from that for intensive agriculture, combinations of both, so-called integrated agriculture, may have optimum conditions different from those for intensive agriculture alone. At least the range of conditions under which potential production can be realized is extended (Figure 89). Hence, the curve resulting from a combination of the relations for soil fertility, water-holding capacity and water availability will be less concave than that of Figure 87.

The intensified system presented in Table 21 uses only some tens of kg ha^{-1} of N in the form of manure and fertilizers. Half the amount is probably unnecessarily lost by runoff, leaching and erosion. Programmes like those of the anti-erosion project in the zone (Hijkoop & van der Poel, 1988) require investments in human efforts and capital that are not profitable in the average system, in which only 8 kg ha^{-1} of N is lost (Table 21). Hence, the more intensive the system, the greater the profitability of such measures.

The proportion of legumes in the rotation decreases with 'intensification' (Table 20), though the Department for Farming Systems Research recommends cultivating cowpea to improve the diet of draught oxen. Berckmoes et al. (1988)

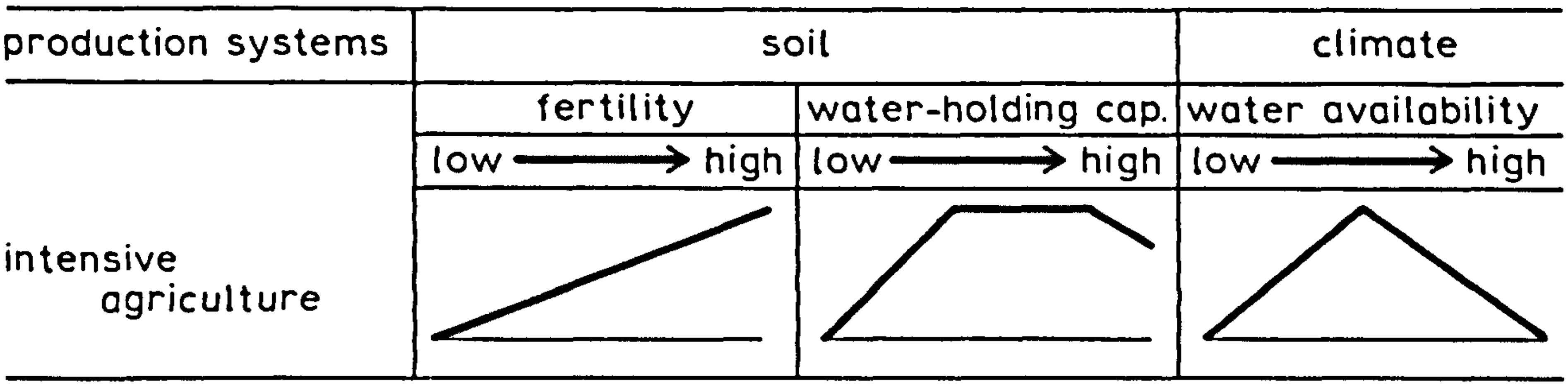

Figure 88. The production efficiency of intensive agriculture in relation to the potential of the environment, specified for soil and climate parameters.

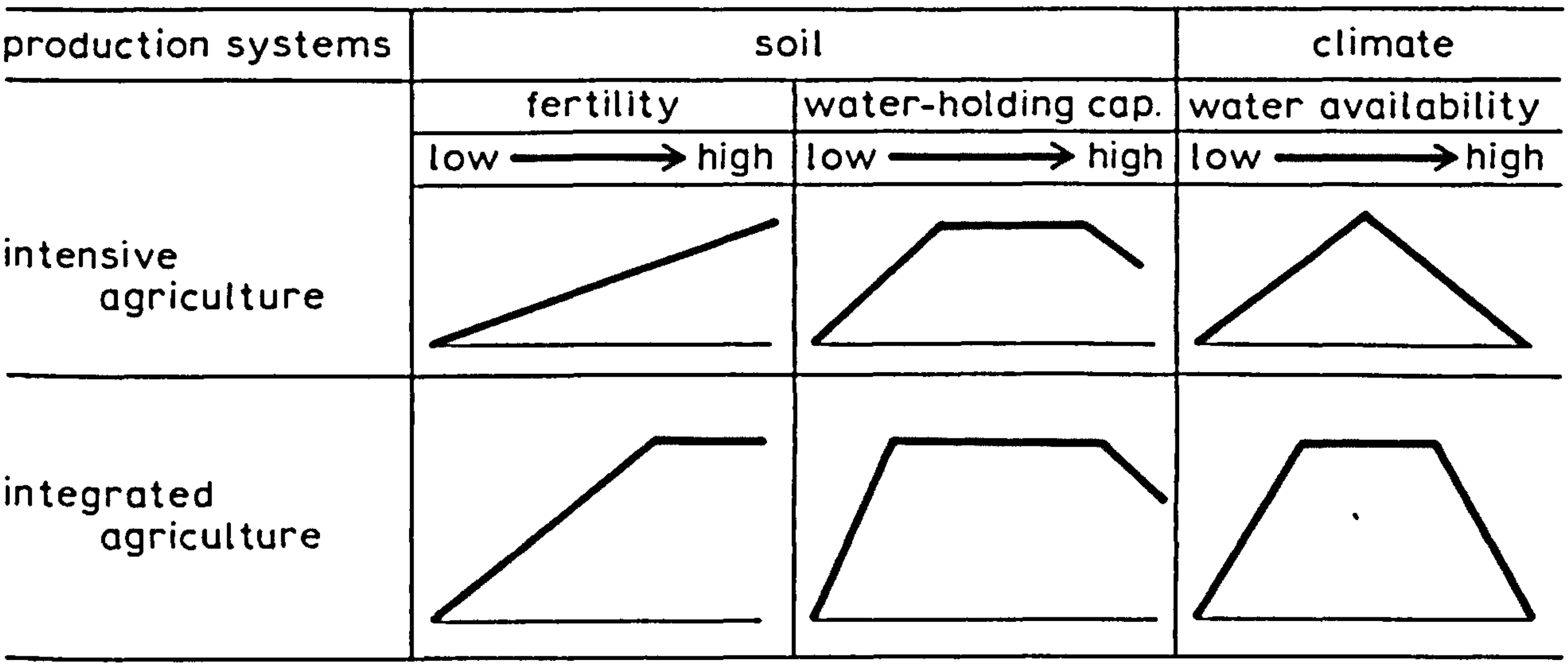

Figure 89. The production efficiency of intensive agriculture in relation to the potential of the environment, compared with such a relation for integrated agriculture.

suggest that the decline in area of this crop is due to its low yield and the low price of cotton cake. The low yield is rather self-evident. Generally, recommending cultivation of legumes is still not automatically linked to recommending the use of P fertilizers, despite ample evidence of P deficiency and its negative consequences for the production of legumes (Penning de Vries & Djitèye, 1982). In addition, labour productivity is low and there is a shortage of labour in parts of the cropping season (Brossier & Jager, 1984). A yield of 1000 kg ha^{-1} dry matter of cowpea fodder is then unacceptable; using P it can be several times higher!

Experience in monsoonal northern Australia suggests that legumes alone could probably improve the natural rangelands in southern Mali, but with insurmountable management problems. Application of P fertilizers could partly alleviate these problems and might increase the production of animal protein 5-fold (Breman & Traoré, 1987).

16.4 Concluding remarks

I hope that the suggestions put forward in this chapter wil provoke de Wit and his school to extend their models for various production situations (potential production, production with limited water supply, and production with limited supply of water and nutrients) by introducing forms of integrated agriculture at the various levels. Such models would be useful tools in agro-ecological research to identify appropriate innovations with less concave relations than the curve of Figure 87, without unnecessary trial and error.

Development of integrated agricultural production systems could lead to improved prospects for marginal areas. However, populated areas with conditions characteristic of those to the left of the break-even point in Figure 87, will remain. Only social measures can guarantee sustainability of life there. Once overpopulation is a reality in such areas (Figure 86B), social measures are to be preferred above giving 'stones for bread', by condemning cash crops and advocating natural alternatives only.

Situations exist where interdependence is preferable above independence. It may be a prerequisite for an increased independence of the country as a whole that the Sahelian region remains dependent on the savannah zone, and it may be a prerequisite that farm sizes increase in the latter zone. Charity begins at home.

In this chapter I have attempted to demonstrate the usefulness of systems analysis in development cooperation. If I have succeeded, this implies that the methodology has to be taught in developing countries that may want to decide unilaterally the position of the break-even line (Figure 87) and its dynamics. Hopefully, an increasing number of scientists will follow this line of thought and use the tools initiated and strongly advocated by de Wit, joining me in the song:

'O, I takes the gospel, when ever it's possible but with a grain of salt'.

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17 International agricultural research for developing countries*

C.T. de Wit

Most of us are familiar with pictures like that of a little black boy sitting in the dusty sand with a belly swollen by hunger, oblivious to the flies running over his face, and looking wide-eyed into the camera lens. Such images of hunger and deprivation are necessary to keep up the level of our charitable donations to organizations which, often with great effort, make their own contribution to alleviate acute poverty.

These images also provided us with a vision of the Third World as a world of backwardness and stagnation and thus condemned to a permanent dependence on our dynamic, ever-changing First World. However, this is a distorted picture. Of course there are far too many poor and it is true that development is stagnating in a number of countries, but other countries have been laying their own foundations for development and growth, and some have achieved a level of prosperity comparable to that in the West in the 1950s. In contrast to the disheartening expectations at that time, the medical doctor did not steam ahead of the agriculturist. This is not because the Law of Malthus had finally been proved to be true, but because agricultural production has kept abreast of the strongly increasing demand for food.

Despite a threefold increase in Third World population, global food shortages have been averted, and the occurrences of famine have been reduced in both number and size. These have been limited to regions under pressure from war or natural disasters or that have been exposed to instability and political adventurism, as in Sudan at the end of the 1980s and in China during the 'great leap forward', at the end of the 1950s. Even a country such as Bangladesh, confronted with massive food shortages at the beginning of the 1970s, has become almost self-supporting thanks to its record rice and wheat harvests. The fact that the catastrophic flooding in 1988 did not result in enormous actions for food aid six months later, indicates that the country has built up a remarkable resilience.

Agricultural research has contributed a great deal to these unexpectedly favourable post-war developments. In the second half of the 1950s it became clear not only that the agricultural techniques that had been developed in temperate zones were also indispensable in the tropics, but also that attempts to achieve the necessary transfer would be doomed to failure if no appropriate research was conducted in the tropics themselves. The Rockefeller and Ford Foundations had the means and flexibility to provide the necessary momentum to this research.

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* Address on the occasion of leaving the post of extraordinary Professor of Theoretical Production Ecology at Wageningen Agricultural University on 17 February 1989.

Partly continuing the activities started in the colonial era, the institutes they financed were rapidly successful in bringing about a change in Asia, parts of Latin America and several regions in Africa. This has since become known as the 'green revolution'. These days, 20 years later, it has become clear that as far as food production is concerned this revolution did indeed bring about necessary changes for the good, but, as in every revolution, also devoured some of its children in the process of rapid change.

The necessary research efforts soon proved too much for these Foundations. At the beginning of the 1970s, the Food and Agriculture Organization (FAO), the United Nations Development Fund (UNDP), the World Bank and a number of donor countries therefore united to form the Consultative Group on International Agricultural Research, or CGIAR for short (Baum, 1986). In the expansive 1970s, this organization grew to form a system of international research in which 13 autonomous institutes, together with about 30 donor countries share the responsibility for a yearly research budget of over 200 million US dollars [1].

Despite its spectacular growth, this international research constitutes no more than 5 % of the total agricultural research in developing countries. This is because national agricultural research organizations have likewise been growing considerably over the past 25 years, as appears from numerous studies of the International Service for National Agricultural Research (ISNAR) in the Haque. At the same time, the effectiveness of research in Asia and Latin America has been improved by transferring the management of the research to institutions that function at some distance from governments and their respective departments of agriculture, and in which the researchers themselves contribute to research policy and management. The opposite is true in Africa. Here, many bilateral research projects, in which the donor countries and their executors seize the chance to blow their own trumpets, obstruct the potential for developing national research policies. This is not a call to suspend bilateral aid, but it is a plea to apply this aid in such a way that the research systems of the countries themselves are strengthened instead of being trampled underfoot.

International agricultural research will be able to fulfil an essential innovatory and complementary role, particularly within a network of strong national research organizations. Their programming should then be directed at problems that extend across the borders of the individual countries, and should be led both by scientific possibilities and by problems recognized in the field. International research can only continue to function at some distance from the national political arenas and as a consequence only at some distance from the daily problems of the farmer. Therefore, national organizations should play a central role in the identification of the demands for applied international research and for adapting its results at the farm level. Proper dove-tailing requires that the influence of research organizations of developing countries on control, management and execution of international research has to be increased at the expense of the donors and their agents. Transfer of responsibilities to non-governmental organizations of development assistance (NGOs) is no help, because these have their constituency in the affluent West and cherish, like donor governments, their own ideologies. Changes are overdue, but if made in time there will be a role for multilateral international research in agricultural in developing countries for years to come.

There is enough to be done (CGIAR, 1987). Firstly, there is the population increase. In view of the young age of population, this will continue for the time being, even in those countries making efforts that are beginning to control the problem. Secondly, there is urbanization, which will exceed 50% in many developing countries at the beginning of the next century. Thirdly, there are increasing incomes and levels of aspiration, which express themselves in Western ways of life and a craving for consumer goods which we ourselves are also so fond of, such as cars, motorbikes, transistor radios and bread, meat and vegetables, preferably stacked in the form of 'Big Macs'.

For agriculture, this means that production needs to grow considerably above a level necessary to fulfil the need of the rural areas, and that its composition has to be adjusted to the food demands of an urban population. Furthermore, this food must also be cheap enough to contribute to the alleviation of hunger as a result of poverty. This kind of development is only possible under two conditions. The section of the population that does not participate in agriculture should provide the external means of production that are necessary to increase the productivity of labour and soil, and economic relationships should be such that self-amplifying interactions between agriculture and other sectors of the economy are supported.

Both the political basis and the natural resources are missing for a pastoral development of simplicity and self-sufficiency to keep the malevolent world at bay. On the other hand, it has become evident, particularly in Africa, that policies directed at urban development and at the expense of rural areas, grind to a halt. This is as a result of increasing imports of agricultural produce, increasing problems of marketing industrial goods which do not correspond to the taste and quality requirements of Western society, and an increasing foreign debt. More self-reliance is imperative, and this requires that in most countries most of the internal demand for agricultural products be met by domestic production. Any research policy that does not strengthen the interaction between urban areas and their hinterlands is doomed to failure.

Agro-ecological research carried out over the past 20 years[2] has demonstrated that most countries have large enough regions where the soils and climate enable adequate agricultural production, providing that external means of production are available, and this without further assaults being made on fragile ecosystems[3].

This is also true for Africa, even though the increase in agricultural production to date lags a long way behind that of Asia and parts of Latin America. But, in the same way that it was impossible to transfer the technical developments of the Western world to the irrigated regions of Asia without research, it is also impossible to transfer the technical developments on other continents to the rain-dependent agriculture in the tropical rain areas and the savannah regions of Africa without research.

These areas require the development of new agricultural systems that enable a greater productivity of soil and labour than the traditional systems. For this purpose, crops other than rice and wheat need to be adjusted to more productive environments than the present. Although such crops, for example maize, millet and cassava, are traditionally consumed in rural areas, they may require new methods of conservation, storage and processing to keep them acceptable for an urbanizing population. Cattle are a necessary component of these agricultural systems to provide draught power, and permanent ground cover is necessary to limit the ever-present threat of erosion from wind and water. Moreover, these systems have to enable efficient use of natural and industrial fertilizers. Many lessons should also be learned from the sometimes disastrous mistakes that have been made elsewhere in attempts to control of diseases, pests and weeds by means of biocides. And finally, it should be taken into account that rapid urbanization may lead to such a shortage of labour in rural areas that some forms of mechanization are needed and herbicides have to be used to lessen the burden of weeding. However, there is still a large gap between what in principle might be done and what happens in reality. The international institutes are in a position to contribute significantly to bridging this gap.

Exports are needed to pay for necessary imports for production and consumption. Therefore cash crops have to be incorporated into some of the agricultural systems and incentives have to be created to make their cultivation worthwhile for the farmer. But rich countries display a disconcerting lack of interest in reforming their egocentric trade policies in favour of the developing countries. Lack of foreign exchange, lack of reserves, the necessity to use scarce external means of production efficiently and the need for cheap food, oblige developing countries to further develop those areas that are better off agro-ecologically and infrastructurally. In many situations, this makes it also necessary to direct development efforts at labour-intensive, family-run farms. Seed stock, industrial fertilizer and biocides can be traded in small amounts, so that, in areas where application of the new techniques is attractive, the smaller enterprises will eventually follow the lead of the larger ones. However, this is of little or no consolation to the smallest farmers. In spite of increasing yields, these cannot maintain their aspired level of income, because they are caught between falling prices for their products and an increasing general level of prosperity[4].

Policies that are geared towards the survival of enterprises that are too small to make a decent living, put the cart before the horse, since they drain away the financial resources for creating permanent employment. Therefore, an important task of policy-oriented research is to show potentials for regional development by improving infrastructure and promoting industrial activities and services. At first, such regional development is likely to be driven by agricultural development but in the course of time it should develop its own momentum. This should stimulate geographically distributed urban development instead of the present uncontrolled growth of mega-cities. John Mellor, the director of the International Food Policy Research Institute (IFPRI, Washington) has written many papers on this theme.

The explicit recognition of the necessity to develop well endowed regions, implicity involves the recognition of the existence of other regions where development lags behind. This is a relative distinction: agro-ecological and infrastructural situations that are considered poorly endowed in one country may be the best there is in other countries. Futhermore, there are less endowed regions that might be carried over the threshold by relatively simple means, such as correcting the soil acidity, adding micronutrients, building some roads or providing extension. In other cases, more elaborate investments are needed, such as for drainage, terracing or irrigation. Comparative, international agro-ecological research may contribute considerably to a rapid and efficient evaluation of potentials.

However, in every country, there are always regions where structural improvements do not justify their costs, because even with them the production level will be too low, the risks too high and the use of external means of production too inefficient. The problems of these marginal areas are even larger if, as a result of developments elsewhere in the country, the prices of agricultural products come under pressure. The traditional response is emigration of the young and the able to regions with more promising possibilities for agriculture, to cities or to other countries. The remaining population is then forced to sacrifice the limited long-term possibilities for production for the purpose of eking out a short-term meagre existence. Overexploitation as a result of poverty forms the most serious threat for the environment in developing countries.

Therefore, a number of donors of the CGIAR stress that research should focus particularly on improving agriculture in these least endowed regions. However, many problems in these regions are not very different from those in regions that are better off; they are only more severe. Accordingly, much of the agricultural research that is particularly directed towards these least endowed regions, is more readily applied elsewhere [5], so that their comparative advantage is not increased and their marginalization continues. This is one reason why the contribution of research towards mitigation of inequity is so often disappointingly small. The structural development of poorly endowed regions requires much more substantive collective efforts than research, but the chance that developed countries will be willing to contribute their share is remote. As it is, they grossly neglect their own less endowed regions. And this the more so under the influence of a neo-conservative ideology, which has itself reconciled with the existence of inequity. Nothing suggests that the developing countries have any original ideas on the distribution of power and wealth, and therefore hunger and poverty in the midst of relative prosperity will persist. But this is not a reason to neglect agricultural research that is primarily directed at the increase of production, since problems of distribution can never be solved in situations where absolute food shortages prevail.

There are at least two other good reasons why research directed towards growth and production is still appropriate at a time when, in the shadow of the year 2000[6], so many of the well-to-do are so concerned about unintended consequences of their prosperity. In the first place, the development of farming systems that are so productive that indiscriminate reclamation of virgin lands can be avoided is a necessary condition to control further degradation of the surface of the earth and destruction of natural ecosystems. In the second place, those countries that have little to lose but poverty and see some silver lining at last, are going to forge ahead anyhow. And as long as I am drinking wine, I am not going to preach that others drink water.

Notes

1 Membership of the Technical Advisory Committee (TAC) of the CGIAR is reshaping my opinion on development research, but not to such an extent that TAC should be blamed for the views expressed in this address.

2 Production potentials were estimated by P. Buringh et al. (1979). Their paper may be considered to be a reaction to the pessimistic view of the Club of Rome. A more recent study was done by FAO (1984).

3 The agricultural production process in low-yielding situations, where many, partly unknown factors interact, is not very well understood and therefore difficult to manage, whereas high-yielding situations require that growth is better controlled and understood, so that inputs may be better timed and adjusted to demand. Accordingly, although more inputs per unit area are needed in high-yielding situations, less of most inputs are needed per unit product. Hence, for the same total production, fewer external inputs are required and wasted, less land is needed for agriculture and more natural ecosystems can be spared. On the other hand, the increased use of inputs on the land that is in use for agriculture may cause environmental and health problems. This is especially the case in developed countries, where external inputs such as industrial fertilizers and biocides are relatively cheap and thus used over-abundantly (see de Wit, 1988).

4 This occurred in all developed market economies, with the exception of Japan. But there the policy of shielding the small farmer has resulted in prices that are about 3–5 times higher than elsewhere.

5 The PPS project (Penning de Vries & Djitèye, 1982) is an example. The objective of the research was to better understand the factors that determine the Primary Production in the Sahel, to benefit the semi-nomads. However, the knowledge gained is increasingly being used in more southern regions that are better endowed with water and infrastructure so that potential pay-offs of interventions are more promising. The International Livestock Centre for Africa (ILCA, Addis Ababa) has also been shifting from the Sahel to greener pastures.

6 'Millenarism' appears to be a breeding-ground for doomsday-like expectations in the Western world, as it was at the end of the first millenium. Because of its biblical and apocalyptic roots (Dasberg, 1980), its impact in developing countries may turn out to be smaller.

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Simulation Monographs 34

This book gives an impression of the field of Theoretical Production Ecology, its development and its position as an interdisciplinary subject. Revised versions of the papers presented at the symposium *Theoretical Production Ecology: hindsight and perspectives,* organized on the occasion of the retirement of Professor C.T. de Wit from Wageningen Agricultural University, are presented. Professor de Wit's valedictory address is included.

The contributors are either former students of Professor de Wit (most of whom work at Wageningen Agricultural University and the Centre for Agrobiological Research) or academics from overseas who have collaborated with de Wit.

The papers have been arranged according to the four scientific themes covered by the Department of Theoretical Production Ecology: soil and climate; plant growth and development; pests, diseases and weeds; agricultural production systems. During his scientific career of more than 40 years, Professor de Wit made substantial innovative contributions in each of these four areas. Together the papers give an overview of the major developments during de Wit's inspiring involvement in production ecology and indicate the directions in which it may proceed in the years to come.

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