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9.2 Principles of Crop Growth and Production

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Introduction

The agricultural production process, reduced to its bare essentials may be described as the conversion of solar energy into useful organic material. The ways and means used to achieve this conversion are highly diversified, depending among others on crop species, location, environmental conditions, agricultural tradition of the population and level of development. These large differences are however only of secondary importance, since many of the basic processes governing growth and production of plants, which form an essential link in the chain of events, are the same. These processes can therefore be discussed in general terms, to obtain insight into the quantitative aspects of plant production, like potential growth rates and yield capacity. Such knowledge is of prime importance since it provides a basis for assessing the possibilities for improvements in the production system, or the impact of pests and diseases.

In this paper some of the basic principles will be treated, with special emphasis on their quantitative consequences.

CO_2-Assimilation of Leaves and Crop Surfaces

The basis for any biomass production is the CO_2-assimilation of green leaves. Considerable attention has therefore been paid to this process over the years. At the beginning of this century the main factors governing the rate of CO_2-assimilation were formulated by Blackman, who showed that at low light intensities assimilation is proportional to this intensity and at high light intensities is limited by CO_2-diffusion and independent of the light intensity.

A typical dependence of the rate of CO_2-assimilation on the absorbed photosynthetically active radiation in the 400-700 nm wavelength is presented in Figure 1 for leaves of plant species referred to as C_3 and C_4 types. The main parameters used to describe these curves are the initial light use efficiency, ϵ, the respiration rate in the dark, F_d, and the maximum rate of net CO_2-assimilation at high light intensity, F_m. The greatest variation in these is found in F_m, ranging from 30-90 kg CO_2 ha^{-1} (leaf)hr^{-1} for C_4-plants and from 15-50 kg CO_2 ha^{-1} (leaf)hr^{-1} for C_3-type plants.

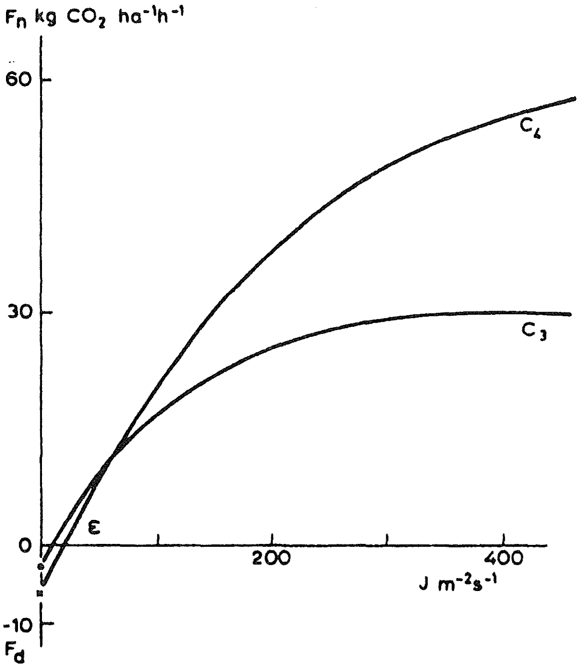

Figure 1. Characteristic net CO_2 assimilation functions (F_n) for individual leaves of C_3 and C_4 plant species

The names C_3 and C_4 refer to the length of the C-skeleton of the first stable product in the photosynthetic process. Several characteristics of the two plant types are different (Gifford, 1974). The most important ones in the present context are: (i) the main carboxylating enzyme in the C_4-plants has an affinity to CO_2 which is about twice as great as that in C_3-plants: (ii) in C_3-plants a respiratory process takes place in the light which results in a dependence of assimilation on the oxygen concentration in the air, whereas that process is absent in C_4-species. The differences in initial light use efficiency between the two species are only small however, since the energy requirements for assimilation is inherently higher in the C_4-plants.

Another important difference shows up under conditions where the CO_2-concentration in the intercellular space is regulated over a wide range of external CO_2-concentrations and light intensities through adaptation of stomatal aperture (Goudriaan and Van Laar, 1978). The level at which the internal concentration is maintained is ±210 vpm for C_3-plants and ±120 vpm for C_4-plants (Raschke, 1975;

Goudriaan and Van Laar, 1978). This difference implies that at low light intensities and normal external CO_2-concentrations the net assimilation rate of the two plant types is about the same, but the transpiration rate of C_4-plants is half that of C_3-plants. At high light intensities on the other hand the transpiration rates are about the same for both types but the net assimilation rate of C_4-species is twice as high. The result is that the transpiration coefficient, which is mainly determined by the ratio between transpiration and assimilation is about twice as high for C_3-plants as for C_4-plants over the full range of light intensities. When this regulatory mechanism is fully present, transpiration coefficients of 100 and 200 kg water per kg dry matter for C_4 and C_3 plant species may be achieved (De Wit et al., 1978). So far it has been shown, that the regulatory mechanism may be present to a greater or lesser extent in the same species under different external conditions and in different species under the same environmental conditions. These results hamper the explanation of the phenomenon, but would suggest relatively easily manipulation for one or the other trait. That is important, since under conditions of water shortage regulation may be advantageous, whereas in the greenhouse where CO_2-fertilization may be practiced, absence of regulation is desirable.

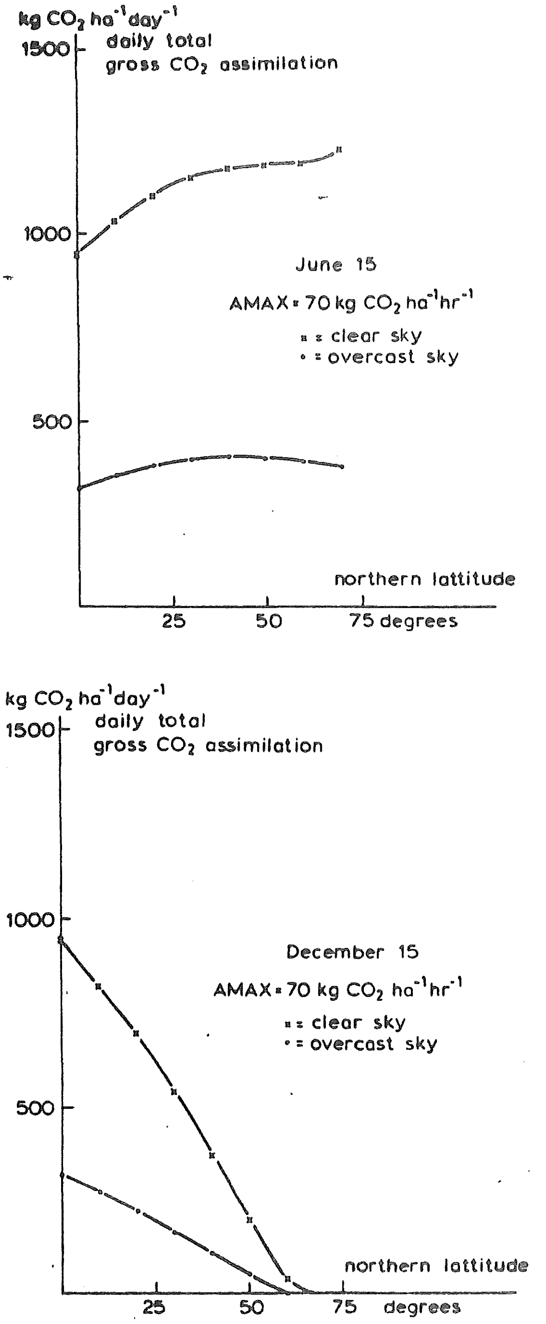

Figure 2. Daily totals of gross CO_2 assimilation of closed green crop surfaces for different latitudes on two dates

The rate of CO_2-assimilation of crop surfaces may be determined on basis of the photosynthesis light response curve of individual leaves as shown in Figure 1. Such calculations are, however, complicated, since the leaves of a crop are displayed in every direction and show widely varying illumination intensities. The problem has been tackled by the brute force of the computer, which enabled the assessment of the influence of such parameters as total leaf area, leaf angle distribution, leaf optical properties and solar height on the light distribution within the canopy (De Wit, 1965; Duncan et al., 1967; Goudriaan, 1977). Furthermore, the incoming photosynthetically active radiation at any moment is obtained as a function of solar height and the degree of cloudiness of the sky. Combination of the two, yields the assimilation rate of the canopy at any moment of the day. Integration of these rates yields the daily total amount of CO_2 fixed. In Figure 2 these totals are presented as a function of latitude for both completely clear and completely overcast skies, under the assumption of zero respiration. Potential production may be deduced from such calculations by subtracting the respiratory losses. For the latter a schematic distinction may be made between maintenance respiration and growth respiration. The former is associated with the maintenance of ionic gradients and the turn-over of structural proteins. An average value of 1.5% loss of dry weight per day at a temperature of 25°C (Q_{10} values being of the order of 2-3) and a protein content of ±20% is reasonable, but there is variation among species and cultivars (Penning de Vries, 1975). Growth respiration reflects the loss of energy associated with the conversion of primary photosynthetic products into structural plant material. Its magnitude depends entirely on the chemical composition of that material and is most conveniently expressed by means of a conversion efficiency, as is illustrated

Table 1. Conversion Efficiency of Primary Photosynthates in Various Plant Components (Penning de Vries, 1975)

Compound		Production value (g material/g glucose)
Carbohydrates		0.826
Nitrogenous compounds	from NO_3^-	0.404
	from NH_3	0.616
Organic acids		1.104
Lignin		0.465
Lipids		0.330

in Table 1 for the major plant components. These efficiencies were calculated by Penning de Vries (1975) on basis of the biochemical pathways. At higher temperatures the rate of conversion of reserves into structural material changes, but its efficiency remains constant.

On basis of the foregoing, the daily rate of increase in dry weight of a crop surface may be estimated from:

$$\Delta W = 0.7 * (PG - 0.015 * W)$$

in which Pg is the daily gross assimilation rate, 0.7 represents an average conversion efficiency, 0.015 an average maintenance respiration loss and W the standing dry matter, or the integrated value of ΔW. Such equations may be used for the calculation of potential production (Van Keulen, 1976; Van Heemst et al., 1978; McCree and Kresovich, 1978).

Potential Production and Potential Yield

Although it may justifiably be reasoned that in many parts of the world, potential growth, defined as the growth rate of a closed green crop surface, optimally supplied with water and nutrients, in a disease- and weed-free environment under the prevailing weather conditions is a far cry from reality, knowledge of this characteristic is of paramount importance, since it places the present situation in its proper perspective and provides the scope for improvements.

This potential production rate differs for species of the C_3 and C_4 plant species. In C_4-species it varies from 350-200 kg dry matter ha^{-1} day^{-1}, depending on the prevailing weather conditions (warm, sunny and dry versus cool, cloudy and humid climates). For C_3-species it is about 200 kg dry matter ha^{-1} day^{-1}, variations being mainly the result of differences in available radiant energy. The absence of significant differences in potential growth rates among species and within species of the same group may be deduced from considerable experimental evidence. This is illustrated by comparing the potential growth curves for the main agricultural crops in the Netherlands (Figure 3), all showing practically the same slope (Sibma, 1968) and by comparing the growth rate of natural grassland and that of wheat, determined in the northern Negev of Israel under near-optimum conditions (Van Keulen, 1975). Both crops exhibit growth rates of ±160 kg dry matter ha^{-1} day^{-1}, which is in accordance with calculations made on basis of the radiation climate (De Wit, 1965). These potentials have also changed very little in time, as is illustrated by comparing present-day potential production of ±20,000 kg dry matter ha^{-1} for perennial ryegrass in the Netherlands (Alberda and Sibma, 1968) with the same yield reported by Dickinson (1847) with Italian ryegrass in England, which by means of a London water cart was well supplied with water and with nutrients produced by the London population of men and animals. There seems to be very little scope therefore for increasing total biomass production through higher growth rates. An obvious alternative to achieve that goal is lengthening the period of potential growth, which may be brought about by management practices that promote early development (Sibma, 1977), or extend the period of active photosynthesis at the end of the plant's life cycle by an improved nitrogen supply and control of pests and diseases. (Sinclair and De Wit, 1975). A third possibility is provided by shortening the growth period of a species and growing more than one crop in a season.

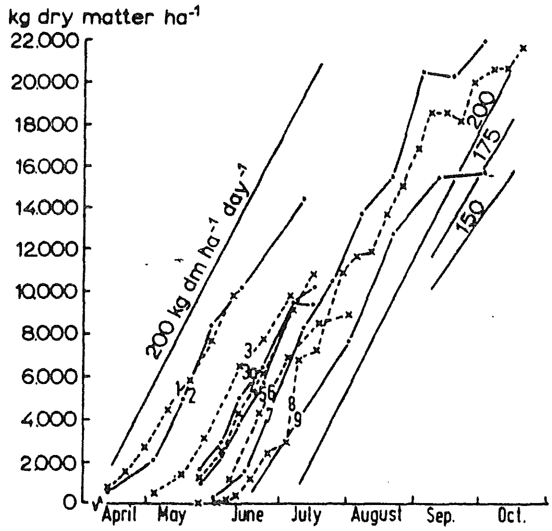

Figure 3. The growth rates of the main agricultural crops in the Netherlands under (near-) optimum conditions, compared to the curves corresponding to 200, 175 and 150 dg ha^{-1} day^{-1}. (1. grass; 2. wheat; 3. oats + barley; 4. oats; 5. peas; 6. barley; 7. potatoes; 8. sugar beets; 9. maize)

The foregoing considerations refer to total biomass production, but in many cases the interest is in only part of that biomass: the economic yield. With respect to the cereals, it is generally accepted that the carbohydrates stored in the grain are for the larger part derived from current photosynthesis during the grain-filling stage, the contribution from pre-flowering reserves being of the order of 10-20% (Austin et al., 1977; Bidinger et al., 1977; Stoy, 1965). The grain yield thus is mainly determined by the rate and duration of photosynthesis after anthesis. Many experimental data (Puckridge, 1968; Biscoe et al., 1975; Moss, 1976) show a rapid decline in photosynthesis after flowering but in most of these cases moisture or nitrogen shortage during that period cannot be ruled out. Data presented by De Vos (1975) show that during the first 30 days after flowering photosynthesis remains high, after which it declines linearly over the next 20 days. The grain yield achieved in that way is equal to 40 × 210 (that being the potential growth rate) or 8400 kg seed ha^{-1}. Adding another 1200 kg ha^{-1} from stored nonstructural carbohydrates provides a number close to the yield of 10,000 kg grain ha^{-1}, which has been obtained under these conditions.

A crucial element in this reasoning appears to be the role of the "ripening diseases". Control of these diseases permits the maintenance of a sufficiently healthy green crop surface until the end of the grain growth period. Low disease experiments carried out with a post-flowering spraying frequency, dictated only by the desire to minimize infection, regardless of economic considerations, indicate that under such conditions indeed potential grain yields may be obtained (Fig. 4, De Wit, 1975).

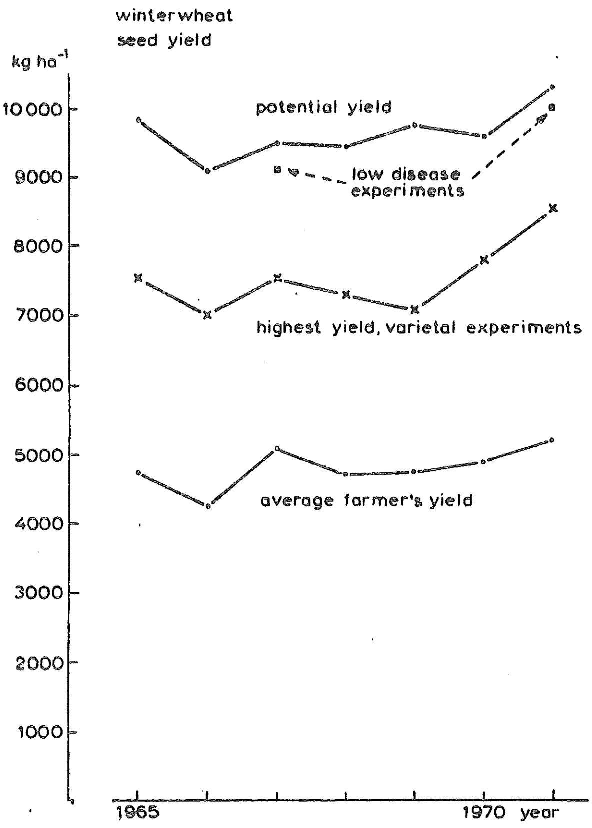

Figure 4. Various yield levels of winter wheat in the Netherlands

The duration of the grain-filling stage is influenced by temperature, higher values reducing its length. Under normal conditions however higher temperatures are concurrent with higher radiation values so that the adverse effects of temperature on the duration of the grain filling stage are compensated by higher daily growth rates (Spiertz, 1977, 1978).

The question whether sink-size may limit the yield capacity remains subject of much argument. It has been shown that grain yield is often positively correlated with kernel-number per unit area (Fisher, 1975; Gallagher et al., 1975), whereas leaf removal did not result in a proportional decline in grain yield. Under natural conditions however the discussion seems a bit trivial, since the plant obviously has a regulating mechanism for both sink and source so that the two are more or less balanced (Darwinkel, 1978). Such behavior would be suggested by the observation that in rice cultivars there is an approximate linear relation between the 1000-kernel weight and the length of its growth period. Apparently a certain carbohydrate supply per kernel and per day is necessary to avoid abortion of that kernel. Only under conditions where disastrous events either naturally or experimentally induced take place, can one of the two parameters be shown to be the sole limiting factor.

Aspects of Plant Nutrition

Potential growth rates can only be maintained throughout the plant's entire life cycle, when an adequate supply of plant nutrients is guaranteed at all stages. Therefore application of chemical fertilizers is widely practiced. To obtain higher economic yields as a result of fertilizer application the element under consideration must be taken-up by the crop and after uptake it must be used to produce useful plant material. A distinction between the two processes may be made conveniently when the results of fertilizer experiments are presented as illustrated in Figure 5 for a rice crop. In Figure 5a, the relation between grain yield and total uptake of nitrogen in grain and straw is given. Figure 5b shows the relation between the amount of nitrogen applied and the amount taken up, while Figure 5c, constructed from the other two through the elimination of uptake, gives the relation between fertilizer application and yield.

The uptake-yield curve of Figure 5a passes

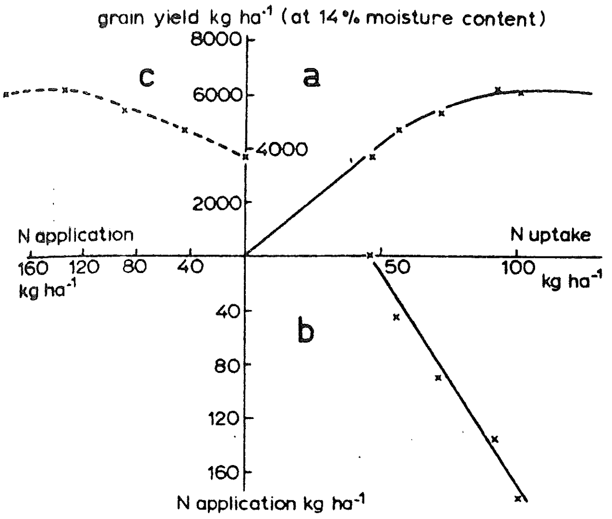

Figure 5. Relation between N uptake and grain yield (a), between N application and N uptake (b) and between N application and yield (c) for IR5 rice grown in Muara, Indonesia. Dry season 1971

through the origin and is linear at low values of N-uptake: at zero uptake no yield may be expected and under limited supply each unit of nitrogen taken up leads to an equal amount of grain being produced. The nitrogen in the tissue of both grain and straw is thus diluted to the same minimum concentration when the element is in short supply. An extensive analysis of yield-uptake curves for nitrogen on rice (Van Keulen, 1977) showed that for irrigated rice this initial efficiency is constant, irrespective of cultivar or growing conditions, and amounts to ±70 kg grain produced per kg N taken up. This value reflects minimum concentrations of ±1% and 0.4% in grain and straw, respectively, and a grain/straw ratio around unity. Also for other small grains under normal conditions the same efficiency results (Van Keulen and Van Heemst, in prep.). At higher uptake levels the curve deviates from the straight line, indicating higher concentrations of nitrogen in the harvested material. Finally a situation is reached, where some other growth factor is in short supply and increased nitrogen uptake does not result in higher grain yields. Under optimum supply of water and other nutrients ("potential growth situation") and in the absence of pest and diseases the plateau is determined by the available radiant energy.

Higher efficiencies of nitrogen utilization once it has been taken up may result from either a more favorable grain/straw ratio or from a lower minimum concentration in the plant tissue, which would mean lower protein contents in the grain, which may not be a desirable effect at all. Much more scope for improved utilization efficiency is present in the relation between application and uptake (Figure 5b). The relation given here is characteristic for the results of the majority of fertilizer experiments with nitrogenous fertilizers: a linear relation between application and uptake over the full range of applications. The intercept with the uptake axis represents the uptake without fertilizer, mainly determined by quantity and quality of the organic material in the soil, and the activity of symbiotic or free living nitrogen fixing organisms (blue-green algae, *Rhizobium* strains), while rain may contribute some atmospheric nitrogen.

The slope represents the fraction of the applied fertilizer recovered in above-ground plant material. For bunded rice, grown under normal crop husbandry practices, that is broadcast application of ammoniacal nitrogen in three split doses, at transplanting, at active tillering and at panicle initiation, the recovery appears to be low. Part of the ammonia volatilizes directly into the atmosphere and part is converted into nitrates in the aerobic environment of the water. These nitrates will enter the soil either through mass flow or by diffusion and may end up in the anaerobic environment in the soil. There the nitrates are used as electron acceptors by denitrifying microorganisms and within a very short time nitrogen is lost in gaseous form to the atmosphere. Recoveries as low as 30% are a rule under these conditions rather than an exception. The situation may be improved considerably by a different application method. Placement of the ammonium fertilizers directly into the reduced soil layer prevents the conversion into nitrates and hence the subsequent denitrification. Uptake efficiencies may at least be doubled in this way (Van Keulen, 1977). For other crops growing under "upland" conditions, the recovery fractions are in general somewhat higher around 50-60%. In that situation leaching of the nitrates is the major source of losses. Uptake by the canopy competes with the processes that cause losses. Therefore higher recovery fractions result when nitrogen is applied at later stages of crop growth, when the demand for the element is higher, due to higher growth rates. Careful management in which the rhythm of fertilizer application is tuned to the demand of the vegetation, can result in almost complete recovery. Such practices are of course more labor-intensive but they do lead to situations where fertilizers are not wasted and the environment is not unnecessarily loaded with chemicals.

For the other macro-elements, phosphorus and potassium and for other crops, similar descriptions with respect to yield-uptake curves may be set up, as shown by recent investigations (Van Keulen and Van Heemst, in prep.). The total soil stock of these elements is, however, much larger compared to the yearly withdrawal so that effects of withholding fertilizers for one growing season are far less striking than for nitrogen.

With respect to the dynamics of nutrients in the plants an important phenomenon needs attention: during the reproductive period of growth, most of the available photosynthesis products are transferred to seeds or storage organs. The conversion efficiency in terms of dry weight depends on the composition of the stored material and may be estimated on basis of that composition. Large differences between species exist: a supply of 200 kg photosynthates per ha per day results in dry matter growth rates of ±150 kg ha^{-1} day^{-1} for barley seeds and ±100 kg for groundnuts, with its much higher protein- and oil-content (Sinclair and De Wit, 1975). Nitrogen and minerals are needed also for growth of the seeds. The nitrogen demand is one-sixth of the protein growth rate and varies between 2 kg ha^{-1} day^{-1} for barley and ±6 kg ha^{-1} day^{-1} for soybeans with a protein content of ±38%. These demands are very heavy and the uptake capabilities of the root system may not be sufficient to meet them, since the energy availability is low due to the strong sink for assimilates formed by the growing seeds. Moreover, the availability in the soil may be low, either because the soil is exhausted or because the inorganic nitrogen is concentrated in the upper soil layers where water, necessary for transport is lacking. Whatever the reason, in all cases where the requirements of the storage organ cannot be met by supplies from the root system, the remainder of the nitrogen is translocated from the store in the vegetative structure, expecially the leaves. This process leads to accelerated senescence of the leaves and hence to reduced CO_2-assimilation. This self-destructive character of plants has been analysed in some detail by Sinclair and De Wit (1976) for soybeans. The results are presented in Figure 6, in terms of changes in active leaf area index during the seed-filling stage. It appears that the plant destroys itself within 20-30 days. This analysis also indicates that a lower photosynthetic capacity, causing lower seed growth rates and seed nitrogen demands, may result in higher yield through extension of the seed-filling period as self-destruction is delayed.

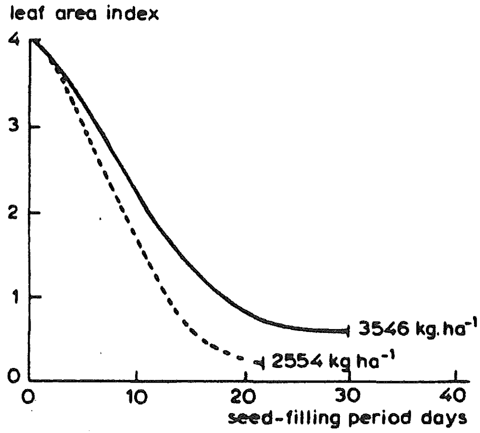

Figure 6. Simulated changes in leaf area indices with time for soya bean crops at two rates of N supply by the roots. Final seed yields in kg ha^{-1} are presented in lower right-hand side of the figure.

Synthesis

In the foregoing analysis a limited number of basic processes in crop growth and production have been considered and already the complexity presents itself emphatically. A synthesis of the various aspects within even the brightest human mind is beyond its capacity. However the development of such disciplines as systems analysis, the availability of high speed, large memory computers and their increasing accessibility through the development of suitable languages provides us with an excellent tool for this purpose. A relatively large number of computer simulation models have been developed and presented in the past decade, and despite the often justified scepticism and criticism, no other technique seems to come even near their potentialities. The consequences of our opinion about the behavior of the various elements may be compared with the results of real-world experiments and thus reveal gaps in our knowledge or wrongs in our views. Once such comparisons have yielded satisfactory results, the models may subsequently be used for simulation experiments to evaluate the consequences of changes in plant properties or in management practices and thus provide a more solid base for recommendations to breeders, agronomists and phytopathologists. As such, systems analysis and simulation provide a framework for an interdisciplinary approach of the problems connected with plant production and through that hopefully to a consistent opinion on ways and means for improvement.

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