

## 4.2 Weeds: population dynamics, germination and competition

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### 4.2.1 Introduction

Weeds are plants which interfere adversely with the production aims of the grower. These adverse influences: (1) reduce crop growth and yield, mainly due to competition for the growth-limiting resources light, water and nutrients; (2) reduce the financial value of the harvested product, mainly by contaminating the crop produce; and (3) hamper husbandry practices, especially harvesting operations, which increases the costs. Thus, weeds reduce the financial profits by lowering output (kg yield per hectare x price per kg) or increasing expenses. Weeds, therefore have to be controlled to minimize their adverse influence in the current crop ('tactics') and to anticipate these effects in future crops ('strategy').

The models presented in this Section are simple. Some summarize more comprehensive models, such as the competition models. Others, like the models of germination and seed bank dynamics are more preliminary. They are primarily instructive and directed towards providing insight into the underlying mechanisms of crop-weed interaction, and focus mainly on the biology of annual arable weeds. The models presented may also be useful for developing more effective advisory systems for practical weed management.

The long-term changes in weed seed reservoirs are discussed first. Weed infestation begins in this reservoir, from which the seeds germinate. The number of seeds and the time at which they emerge determine their starting position in competition with the crop. Germination is, therefore, the second topic to be discussed. The third section treats the modelling of crop and weed growth as determined by competition for the growth-limiting resources, providing more insight into how crop yield is reduced during the growing season and how it is affected by the various crop and weed characteristics. Attention is paid to how seed bank dynamics, germination and competition can be controlled by weeding and soil cultivation.

### 4.2.2 Dynamics of soil seed population

Changes in the soil seed population of annual, arable weeds are described using a dynamic population model, and the influence of control measures is discussed. The parameter values used here are typical for wild oats (*Avena fatua* L.) in barley, and are mainly derived from Wilson (1981) and Wilson et al. (1984). The global structure of this dynamic population model, where seed production per weed plant is treated as a constant, was also taken from these references. The model is a typical example of those applied when describing weed population

dynamics (Murdoch & Roberts, 1982; Mortimer, 1983). The model is eventually extended to include the effects of weed and crop density on weed seed production, and to estimate crop yield loss.

The sequential boxcar approach used in the preceding Sections to model the population dynamics of polycyclic diseases and pests is, in general, unnecessarily complex for weeds. Annual weeds usually accomplish only one, discrete generation a year, and plants of the same generation are quite synchronized in their development.

*A simple flow diagram* The population cycle of an annual weed is represented in Figure 53 in a simplified form. Each box denotes a state through which the seeds or plants pass during their life cycle. These state variables are expressed in numbers per unit ground area. Arrows represent transitions from one state to the other. The numbers change with the transitions and each transition is characterized by a discrete multiplication factor.

The soil seed population is exhausted by a fraction of  $P_g$  per year, so that a fraction  $1 - P_g$  survives and contributes to the soil seed population of the following year. A fraction  $P_e$  of the removed seeds gives rise to established plants, which produce, on average,  $S_N$  seeds per year. A fraction  $P_b$  of these seeds is incorporated in the soil seed population. Hence, the net annual increment of the seed population is written as:

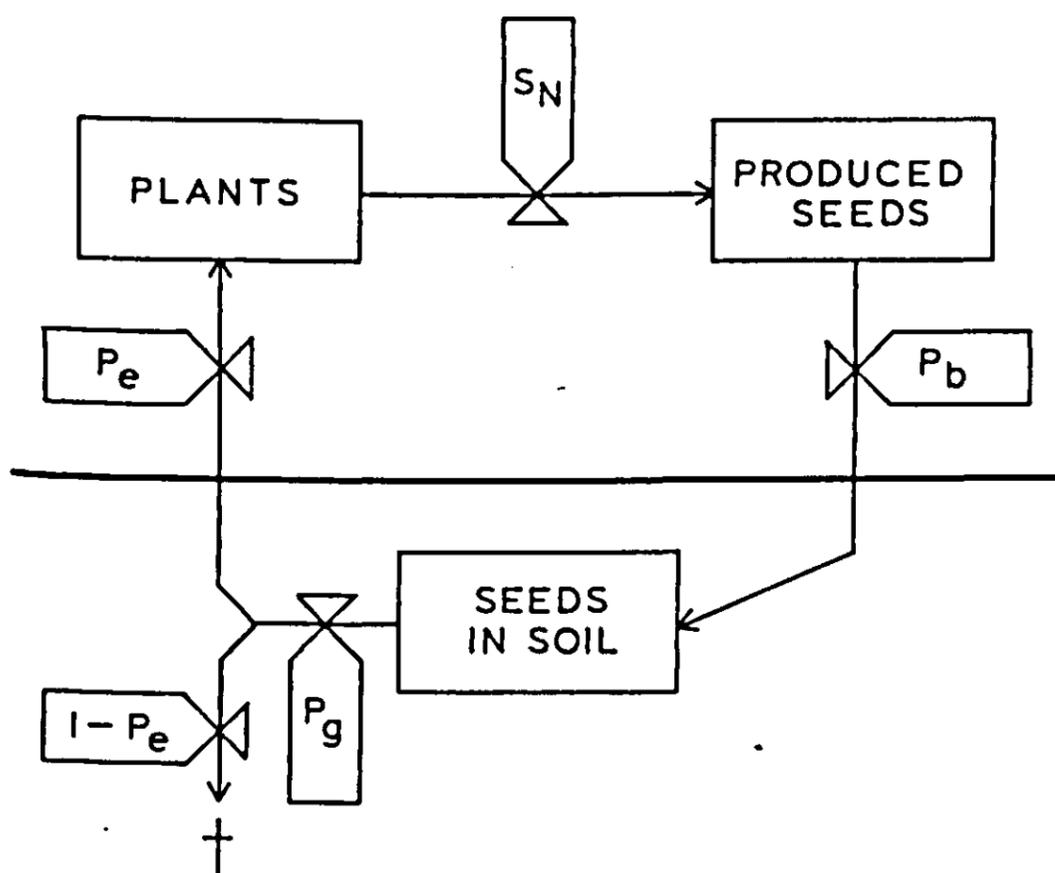


Figure 53. A simple flow diagram for the population cycle of an annual weed. The boxes represent state variables, expressed in numbers per unit area.  $P_g$ ,  $P_e$  and  $P_b$  are fractions of exhaustion, seedling emergence and seed burial, respectively ( $\text{yr}^{-1}$ ) and  $S_N$  represents the number of seeds produced per plant.

$$\Delta n_t / \Delta t = (-P_g + P_g P_e S_N P_b) n_t$$

Equation 76

where  $n_t$  is the number of seeds per unit area at time  $t$ , and  $\Delta t$  the time interval.

### Exercise 52

Make a CSMP program for the population dynamics of wild oat according to Figure 53. Typical values for wild oat are  $P_g = 0.68 \text{ yr}^{-1}$ ,  $P_e = 0.15 \text{ yr}^{-1}$ ,  $P_b = 0.60 \text{ yr}^{-1}$ , and  $S_N = 50 \text{ seeds plant}^{-1}$ . Calculate the course of the soil seed population over a period of 15 years starting with an initial density of 1000 seeds  $\text{m}^{-2}$ .

In this simple model, each parameter is independent of population size. Soil seed population increases, therefore, by a constant percentage per year, resulting in an exponential growth of the population (straight line on the logarithmic scale in Figure 54). Many models on weed population dynamics are of this simple, exponential type.

*Density dependence of seed production* The greater the plant density, the smaller the plants and the lower the average number of seeds produced per plant. Hence, the seed population increases in time according to an S-shaped curve rather than exponentially. Effects of intra-specific and inter-specific competition are often accounted for in population dynamic models using a Lotka-Volterra approach

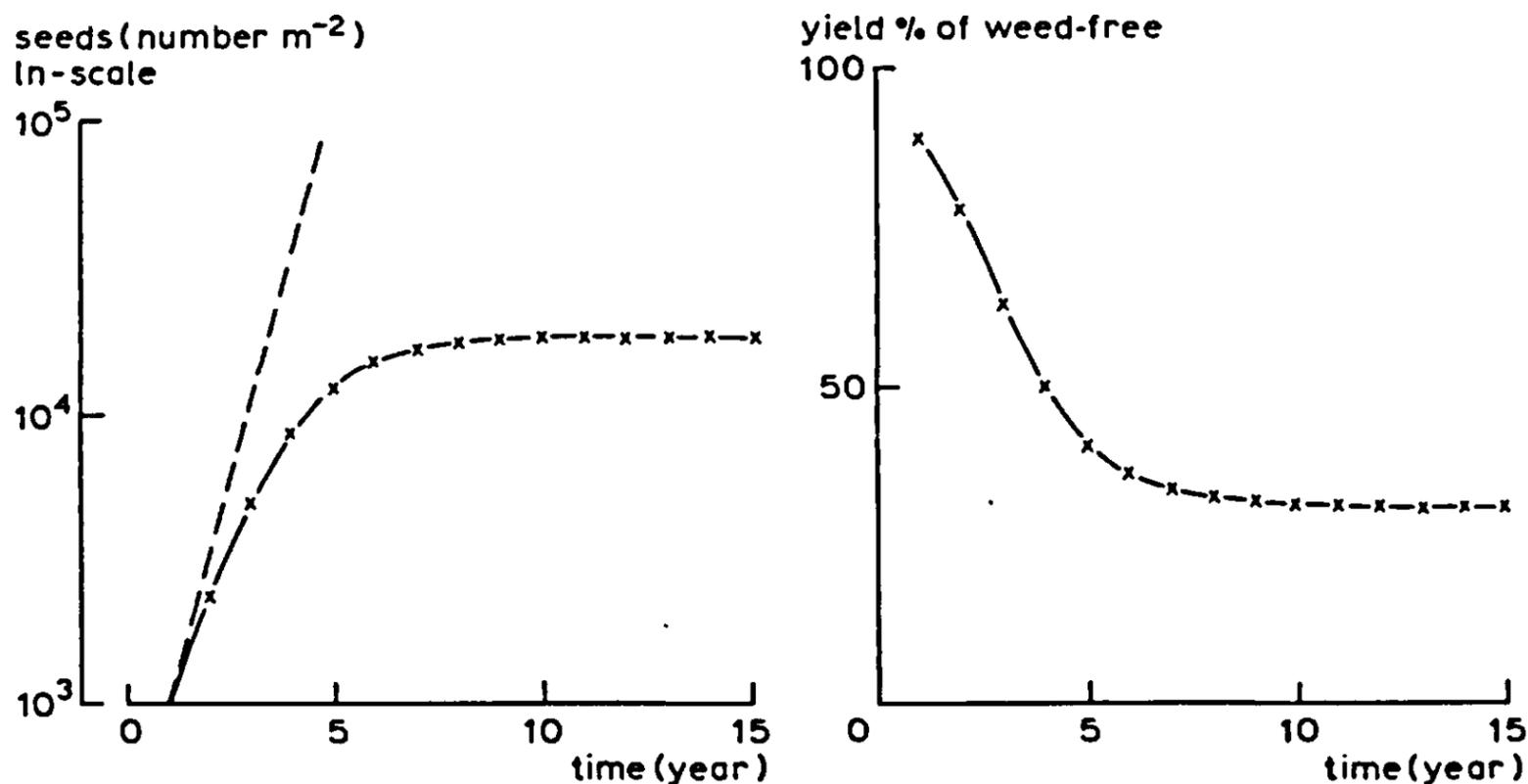


Figure 54. Simulated time course of soil seed population of wild oat, and the concomitant yield loss of spring barley. The broken line represents the exponential build-up of the seed population if density dependence of seed production is neglected. See also Exercises 52 and 53.

(e.g. Begon & Mortimer, 1981). Here, a more comprehensive model is presented where the influence of plant density is introduced by means of a descriptive competition model, based on a hyperbolic relation between biomass yield and plant density. For a review and further discussion of this type of competition model see Spitters (1983). Related descriptive equations for weed competition have been discussed by Cousens (1985). Spitters & Aerts (1983) and Firbank et al. (1984) proposed the use of this type of competition equation in models of weed population dynamics, to allow for the density dependence of weed seed production and to arrive at an estimate of concomitant crop yield loss.

The simplest form of interplant competition is that between plants of the same species. This intra-specific competition is generally characterized by a rectangular hyperbola:

$$Y = N/(b_0 + b_1N) \quad \text{or} \quad 1/W = N/Y = b_0 + b_1N \quad \text{Equation 77}$$

in which  $Y$  is the biomass yield ( $\text{g m}^{-2}$ ),  $N$  the plant density ( $\text{plants m}^{-2}$ ),  $W$  the average weight per plant ( $\text{g plant}^{-1}$ ), and  $b_0$  and  $b_1$  are regression coefficients. When  $N$  approaches zero,  $1/W$  approaches  $b_0$ , so  $1/b_0$  is the apparent weight of an isolated plant. When  $N$  approaches infinity,  $Y$  approaches  $1/b_1$ , so this quantity denotes the apparent maximum yield per unit area.

Equation 77 shows that  $1/W$  is influenced additively by adding plants of the same species. This suggests that adding plants of another species also affects  $1/W$  additively. Hence, for a crop in the presence of weeds:

$$1/W_{cw} = b_{c0} + b_{cc}N_c + b_{cw}N_w \quad \text{Equation 78a}$$

and for the associated weeds

$$1/W_{wc} = b_{w0} + b_{ww}N_w + b_{wc}N_c \quad \text{Equation 78b}$$

where the first subscript denotes the species whose yield is being considered, and the second subscript its associate. Subscript  $c$  refers to the crop and  $w$  to the weed. Adding one crop plant has the same effect on  $1/W_{cw}$  as adding  $b_{cc}/b_{cw}$  weed plants. We could say that the crop is a  $b_{cc}/b_{cw}$  times stronger competitor against itself than the weed is against the crop. The ratio  $b_{cc}/b_{cw}$  measures the relative competitive ability of crop and weed, with respect to the effect on crop yield.

If more than one weed species is involved, the term  $b_{cw}N_w$  is expanded linearly:

$$b_{cw}N_w = b_{c1}N_1 + \dots + b_{cn}N_n \quad \text{Equation 79}$$

and the term  $b_{ww}N_w$  is similarly expanded. This also provides a method for calculating long-term changes in species composition within a multi-species weed vegetation.

The competition coefficients can be estimated from Equation 78 by multiple linear regression, but this results in biased estimates because the error variance of  $1/W$  is much smaller at low values than at high values of  $1/W$ . When applying a linear regression, the data must therefore be weighted by their squared expectation value (Spitters, 1984). With the available statistical packages, however, it is

more convenient to estimate the coefficients by a least-squares procedure of non-linear regression of yield on the plant densities. To fulfil the assumption of homogeneity of variances, it is often necessary to apply a logarithmic or square root transformation of the yields when a wide yield range is covered; both sides of the equation being transformed before regression.

Usually, the crop is grown at constant plant density, so that Equation 78a simplifies to

$$1/W_{cw} = a_0 + b_{cw}N_w \quad \text{and} \quad 1/W_{cc} = b_{c0} + b_{cc}N_c = a_0 \quad \text{Equation 80}$$

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

$$Y_{cw}/Y_{cc} = a_0/(a_0 + b_{cw}N_w) = 1/(1 + N_w b_{cw}/a_0) \quad \text{Equation 81}$$

Thus, the percentage reduction of crop yield in relation to weed density is characterized by the single parameter  $b_{cw}/a_0$ . This parameter, being the initial slope of Equation 81, represents the apparent percentage yield loss caused by the first weed plant added to the crop stand. The aggregate yield reduction due to a multi-species weed infestation can be calculated, using Equation 81, from the 'damage coefficients'  $b_{cw}/a_0$  of the individual weed species  $w = 1, \dots, n$  because the effects of the different weed species accumulate additively (Equation 79). Due to the concave shape of the crop yield-weed density function (Equation 81), a non-uniform, clustered spatial distribution of the weed plants over the field gives a smaller yield reduction than a uniform distribution of the same average density.

Part of the total dry matter is invested in seeds. This ratio of seed weight to total biomass is called 'seed ratio' or 'net reproductive effort' ( $R_E$ ). Although for many species,  $R_E$  remains fairly constant over a wide range of conditions, it may be influenced by genotype, environment (e.g. de Ridder et al., 1981) and plant density. A decrease in  $R_E$  with increasing density may be accounted for by extending the equation relating weed seed yield to density, to a power function (e.g. Firbank & Watkinson, 1985). These authors also propose a descriptive equation allowing for density-dependent self-thinning of seedlings, i.e. they distinguish initial and surviving plant densities.

Seed production of the weed is obtained from its biomass production as

$$n = Y_w R_E/S_w = N_w W_w R_E/S_w \quad \text{Equation 82}$$

in which  $n$  is the number of seeds produced ( $m^{-2}$ ), and  $S_w$  the average weight per seed (g). Seed production is estimated much better in this way than by using a fixed value for the number of seeds produced per plant ( $S_N$  in Exercise 52).

It is emphasized that this simple population dynamic model uses average values for the parameters, and that these values can vary considerably from field to field and from year to year. Part of the variation is explained in relation to environmental variability by the germination model and the dynamic competition model still to be discussed.

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### Exercise 53

- a. Estimate the competition coefficients of spring barley and wild oat for the following situation. The competitive ability of plants of similar growth habits and similar times of seedling emergence, is closely related to their seed weights. Assume, therefore, that the degrees of intra-specific competition ( $b_{cc}/b_{c0}$  and  $b_{ww}/b_{w0}$ ) and inter-specific competition ( $b_{cc}/b_{cw}$  and  $b_{ww}/b_{wc}$ ) of barley and wild oat are proportional to their seed weights of 45 mg and 14 mg, respectively. Assume also that both use the available resources with an equal efficiency ( $1/b_{cc} = 1/b_{ww}$ ). The density response of barley is characterized by a curvature  $b_{cc}/b_{c0}$  of  $0.057 \text{ m}^2 \text{ plant}^{-1}$  and with the yield at a commercial density of  $250 \text{ plants m}^{-2}$  amounting to 94% of the asymptote. Assume that at this density, the weed free grain yield amounts up to  $5 \text{ t ha}^{-1}$  (85% DM) with a grain yield/biomass ratio of 0.45.
  - b. Extend the model of Exercise 52 to allow for competition effects. Use the estimated competition coefficients to calculate soil seed population and crop yields for a period of 15 years when the field is sown each year with spring barley. Reproductive effort of wild oat is 0.42.
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*Weeding (herbicides)* In the absence of control measures, the weed population builds up rapidly. Population increase is, however, strongly retarded by weeding.

In modern agriculture, weed control measures are, in general, applied early in the growing season, before the time when the weeds would significantly reduce crop growth. The efficiency of weeding can be characterized by the percentage reduction in soil cover or total leaf area of the weeds. The complementary percentage measures the degree of weed survival. Weeding operations are allowed for in the model by dividing the state variable 'plants' (Figure 53) into two state variables: 'plants before weeding' and 'plants after weeding', and by using the fraction of surviving weed plants as a multiplication factor for the transition.

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### Exercise 54

Calculate the influence of a post-emergence herbicide application – having an efficiency of 95%, and applied annually – on the system in Exercise 53. Evaluate also the effects of herbicide application once every 2, 3 and 4 years.

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In the typical situation described in Exercise 54, weeding wild oat once every second year restricted yield losses to about 5% or less (Figure 55). Thus, annual weeding resulted in yield benefits of less than 5%. In general, with yield benefits of less than 5%, the profits of herbicide application do not outweigh the costs. The present example supports the opinion that in cereals, wild oat is controlled not so

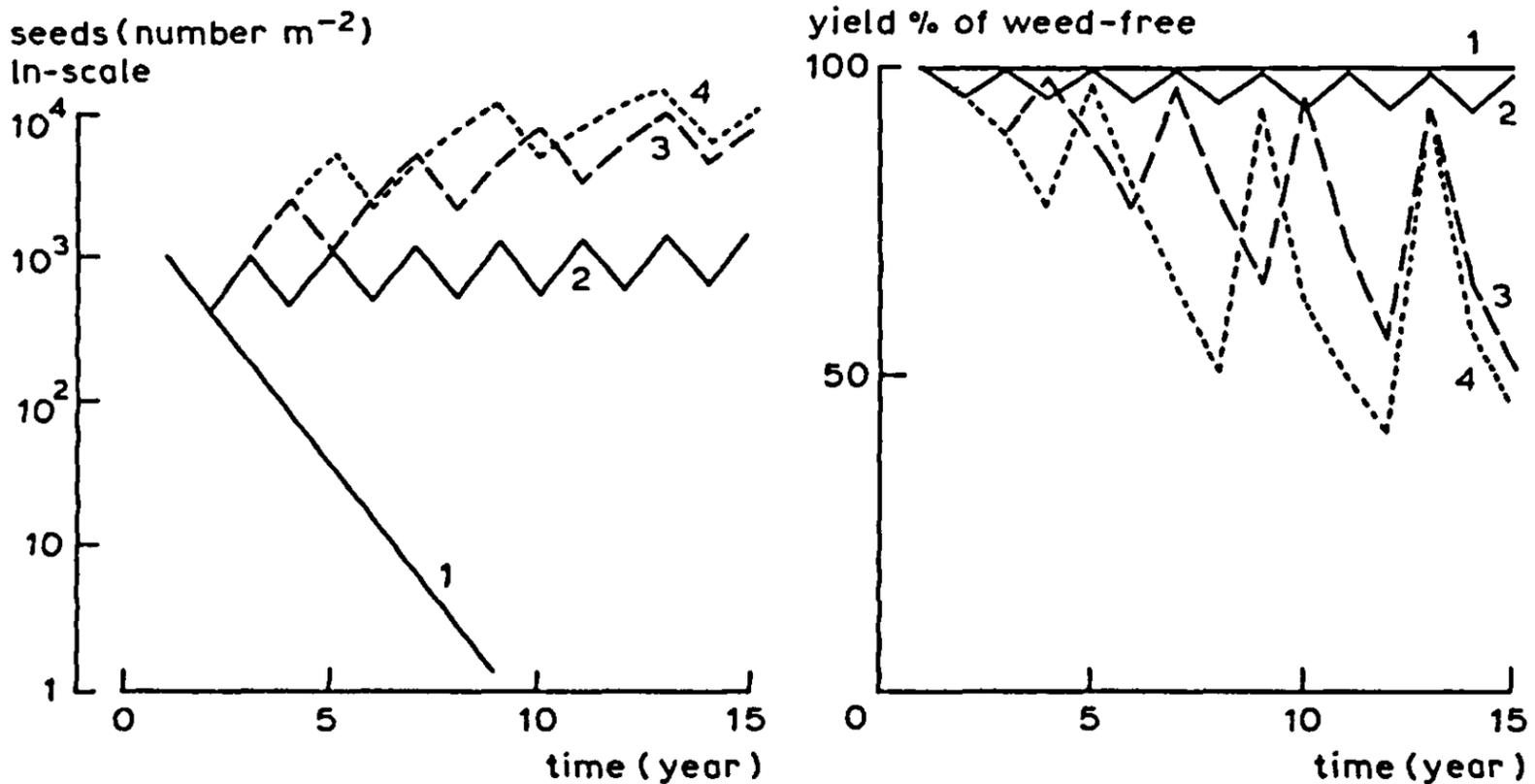


Figure 55. Simulated time course of soil seed population of wild oat, and the concomitant yield loss of spring barley. Herbicides are sprayed either annually or once every 2, 3 or 4 years.

much to prevent a yield reduction of the current crop (short-term tactics), but primarily to restrict increases in the weed seed population and thus to minimize the risks of having to take cumbersome and more expensive measures against large infestations in future crops (long-term strategy).

*Sources of seed losses* In the diagram of Figure 53, the seed population is depleted by recruitment of seedlings, losses of viability of seeds in the soil from one year to the next, and by losses prior to the incorporation of newly-produced seeds into the soil population.

Seed losses on the soil surface, the 'stubble losses', are mainly due to germination, removal by predators and attack by micro-organisms. Seeds become buried due to disturbance of the soil surface; soil cultivation being the main cause of soil disturbance in agricultural situations. After burial, seeds are lost much less rapidly: predation and parasitism are negligible; germination remains the principal factor, but is usually less than on the soil surface.

In Figure 56, a scheme is presented to introduce some more detail into calculating depletion of the soil seed population. Down to plough depth  $D_p$ , seeds are assumed to be distributed uniformly throughout the soil profile. The number of seeds below  $D_p$  is small and, therefore, ignored. Depletion of the soil seed population is primarily due to germination, either fatal or leading to successful emergence (Roberts, 1972; Murdoch & Roberts, 1982). Germination is, therefore, the only depletion process involved in the model. In Figure 56, a simple situation is represented where the probability of germination ( $P'_g$ ) is

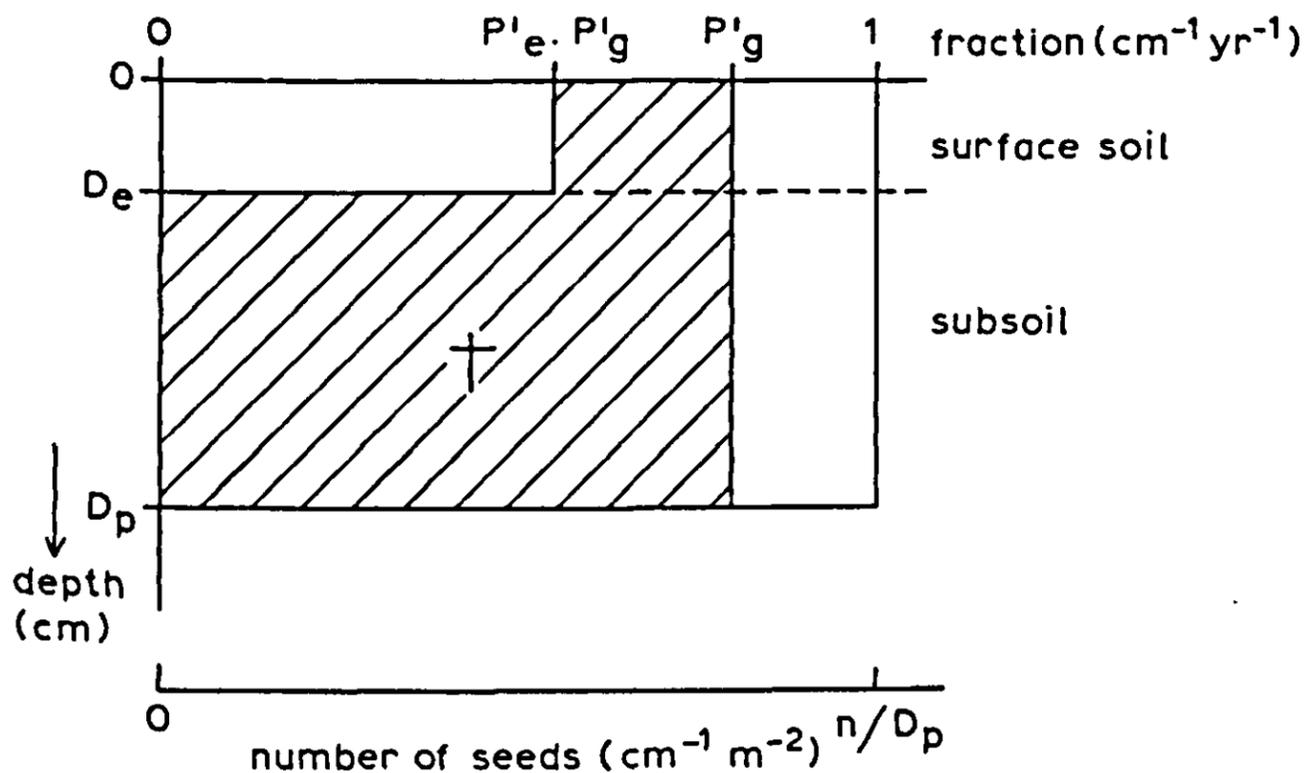


Figure 56. Fractions of germination ( $P'_g$ ) and establishment ( $P'_e$ ) in relation to soil depth. At a given depth, a fraction  $P'_g$  of the seeds germinates, of which a further fraction  $P'_e$  produces seedlings. All seeds are above plough depth  $D_p$  and successful emergence is only possible from depths less than  $D_e$ .

independent of soil depth. Successful emergence only takes place from depths less than  $D_e$ , with a uniform probability of  $P'_e P'_g$ .

The probability of seed survival from one year to the next equals  $1 - P'_g$ . The probability of emergence of germinated seeds ( $P_e$  in  $\text{yr}^{-1}$ , Figure 53) equals  $P'_e D_e / D_p$ . Alternative relations between  $P'_g$ ,  $P'_e$  and soil depth can easily be accounted for in the model. (The primed probabilities have the dimension  $\text{cm}^{-1} \text{yr}^{-1}$ , while the unprimed probabilities are cumulated over the soil profile and have the dimension  $\text{yr}^{-1}$ .)

The depth  $D_e$  from which seedlings can emerge, strongly depends on the species and is especially related to seed size. Within a species,  $D_e$  is smaller in heavier soils. Few species emerge from depths in excess of 5 cm, but large-seeded species such as *Galium aparine* are able to emerge from up to 20 cm (Froud-Williams et al., 1984). With an emergence depth of, for instance, 2 cm and a plough depth of 20 cm, only 10% of the seeds are able to emerge successfully.

Species with a transient seed bank may be distinguished from those with a persistent seed bank (Thompson & Grime, 1979). In a transient seed bank, the major part of the soil seed population is depleted each year by germination, so the soil seed population in the following year mainly consists of newly produced seeds. Grasses in particular, such as wild oat, belong to this group. In a persistent seed bank, only a small part of the soil seed population is exhausted every year by germination. Many arable weeds are of the persistent type, especially species with hard seed coats, e.g. *Chenopodium album*. Not only do persistent species show a smaller  $P'_g$ , but the  $P'_g$  of their subsoil seed bank is also usually much smaller than that of their surface soil seed bank. This greater persistence of deeply buried

seeds is due to a higher degree of dormancy. Germination of these species is strongly stimulated by light, a large daily temperature amplitude and high nitrate concentration. The intensity of these dormancy-breaking factors decreases sharply with soil depth.

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### Exercise 55

Perform a separate calculation of the changes in the surface and subsoil seed bank of wild oat in the system described in Exercise 54 with annual herbicide application. Assume an emergence depth of 4 cm and a plough depth of 20 cm. Assume that after ploughing, the seeds are distributed at random throughout the soil profile down to plough depth. Germination and emergence probabilities are 0.68 and 0.75  $\text{cm}^{-1} \text{yr}^{-1}$ , respectively. Calculate the changes also for an efficiency of herbicide application of 100%. What are the trends for a species with a persistent seed bank, characterized by a germination and emergence probability of 0.25 and 0.75  $\text{cm}^{-1} \text{yr}^{-1}$ , respectively?

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Exercise 55 demonstrates that eradication might be a possibility only for species with a transient seed bank, such as wild oat. Persistent seed banks are exhausted much more slowly, even with complete weed removal. In addition, since 100% efficiency of weed control is neither technically nor economically feasible, persistent species cannot be eradicated and containment of the species at low infestation levels is necessary (Murdoch & Roberts, 1982).

### 4.2.3 Germination

Weed infestation is recruited from the soil seed population by the processes of germination, emergence and establishment. Germination characteristics of the seeds in response to the environment, determine the initial extent of weed infestation and the timing of its occurrence. Both extent and timing are major determinants of the weeds' competitive ability, and thus of crop yield loss.

Germination accumulates over time; its rate is influenced mainly by temperature, availability of moisture, and seasonal periodicity. Periodicity of germination occurs in most weed species and is reflected in a well-defined, seasonal pattern of seedling emergence. Germination of weed seeds is often stimulated by light, daily fluctuations in temperature and high nitrate concentrations. These requirements are most intense close to the soil surface, so germination is greatest in the surface layer, and the seed bank is built up mainly in the subsoil. On the soil surface, germination may be inhibited by light (photo-inhibition) and by the low red/far-red ratio of radiation which has passed through a vegetation cover. When the seeds are buried, germination may be inhibited by a lack of stimulatory

factors (light, alternating temperature, nitrate), by a low oxygen tension or a high carbon dioxide tension, and by plant exudates.

The complex relations between seed germination and the environment have been reviewed by Heydecker (1973), Bewley & Black (1982) and Karssen (1982). In the present Subsection, the main processes of germination and seedling emergence are summarized in terms of a simulation model.

Three types of models can be distinguished for the simulation of seed germination and seedling emergence in the field. First, models in which germination is forecast on the basis of a certain average time required to germinate. Time is usually expressed as accumulated degree-days (e.g. Tamm, 1933; Bierhuizen & Wagenvoort, 1974). A second group includes models in which allowances are made for the time variation among seeds to germinate. This is done by using the cumulative frequency distribution of germination as a functional relationship in the model. Models of the third type, mimic dispersion by assuming that the germination process is composed of several arbitrary stages or boxcars. The different stages are successively passed through before reaching the final stage of visible germination (Janssen, 1974; Section 2.2). Although such a sequential boxcar approach provides a flexible model, it will often be unnecessarily complex for modelling the germination of weeds. Weed seed germination is triggered by certain, occasional events, mainly soil cultivation. In this Subsection, therefore, the second type of model is planned to simulate seed germination.

In the model, the time progression of germination and emergence is characterized by a cumulative frequency distribution function. This function is defined by three parameters. The influences of temperature, soil moisture and seed dormancy are quantified by multiplication factors for these germination parameters. The model is still in its preliminary phase, and the focus here is on its general structure. To arrive at a more accurate description of the multiplication factors, more research is needed on emergence under field conditions.

*Time course* The cumulative number of germinated seeds proceeds in time according to an S-shaped curve. Several equations have already been suggested to describe this distribution of time to germination. The model is described using a negative exponential function (Milthorpe & Moorby, 1974), being the simplest of the suggested functions. More sophisticated functions can, however, easily be substituted. In using a negative exponential, it is assumed that the seed population is depleted exponentially due to germination:

$$N_t = N_m(1 - \exp(-P(t - i))) \quad t \geq i \quad \text{Equation 83}$$

where  $N_t$  is the cumulative number of germinated seeds at time  $t$ ,  $N_m$  the maximum number of germinable seeds,  $i$  the incubation time, being the time to first germination, and  $P$  the instantaneous germination probability. Equation 83 corresponds to a boxcar approach having only one boxcar.

Differentiating Equation 83,

$$dN_t/dt = P(N_m - N_t) \quad \text{or} \quad P = (dN_t/dt)/(N_m - N_t) \quad \text{Equation 84}$$

Thus, the germination rate,  $P$ , characterizes the fraction of the remaining, but germinable seed population that germinates within a short time interval  $dt$ .  $P$  determines the dispersion of the time to germination. Constancy of  $P$  with time is a feature of an exponential depletion function. Expressing the increment rate  $dN_t/dt$  independent of time, as in Equation 84, provides a flexible model where the influence of environment can easily be quantified by multiplication factors for the germination parameters.

The germination parameters can be estimated by fitting Equation 83 to the observations of  $N_t$ , using a least-squares procedure. It is easier, however, to estimate  $N_m$  from the maximum level of the cumulative germination curve and, subsequently, to estimate  $P$  and  $i$  from the linear regression of  $\ln(1 - N_t/N_m)$  on  $t$ . The regression line has slope  $-P$  and intersects the time axis at  $i$ . The linear regression approach is, however, less accurate, because the variation around the regression strongly increases as  $N_t$  approaches  $N_m$ .

*Initialization of time* For a crop, the germination process is started at the time of sowing. For weeds, initialization is more complex. In field populations of weeds, seedling flushes appear mainly after soil disturbance (Roberts, 1984). The main reason probably being that the seeds are exposed to conditions near the soil surface which overcome dormancy and promote germination. Under arable conditions, soil cultivation is the major source of soil disturbance so, for weeds, the time is started at the time of the last cultivation.

*Temperature* The maximum germination percentage ( $N_m$ ) remains fairly constant over a wide range of temperatures (Figure 57a). The inclining sections of the temperature relation reflect the variation within the seed population in the limit temperatures for germination of the different seeds; they can be described using a cumulative normal frequency distribution (Washitani & Takenaka, 1984). For simplicity, they are approximated here by straight lines (Figure 57a). It can be derived that each inclining section embraces a temperature range of about three times the standard deviation of the population for the limit temperature.

The established temperature relation is used as a multiplication factor ( $f_T$ ) for the final germination percentage at optimum temperatures ( $N_{m,o}$ ):

$$N_m(T) = f_T N_{m,o} \quad \text{Equation 85}$$

(The stable and reproducible relationships which are usually obtained when cumulative seedling emergence in the field is plotted against accumulated degree-days, suggest that a long-term average of  $f_T$  should be used – e.g. a running average of  $f_T$  over the preceding 5 days – rather than an instantaneous effect of temperature on  $N_m$ .)

Like any metabolic process, germination is accelerated at higher temperatures. The time required to reach a certain percentage of germination, say 50%,

decreases, therefore, with an increase in temperature. Usually, the inverse of this time increases more or less linearly with temperature (e.g. Bierhuizen, 1973). Thus, the incubation rate – being the reciprocal of time to first germination – is given by:

$$1/i(T) = (T - T_b)/S = T/S - T_b/S \quad \text{for } T \geq T_b \quad \text{Equation 86}$$

where  $T_b$  is the base temperature (i.e. apparent temperature below which the germination process stops), and  $S$  the temperature sum to reach first germination ( $^{\circ}\text{C d}$ ) (Figure 57b). The linearity of the relation implies that, independent of temperature, the first seeds germinate after a fixed temperature sum,  $S$ , has accumulated. If supra-optimum temperatures are involved, effective degree-days can be defined (Subsection 4.1.3: phenological development).

Acceleration of the germination process at higher temperatures, reduces variation among the seeds in germination time, so the germination probability ( $P$ ) increases. The linear relation between the inverse of time to germination and temperature, indicates a linear increase in  $P$  with temperature (Figure 57c). The germination probability ( $P$  in  $\text{d}^{-1}$ ) on any given day is thus defined as the product of slope ( $dP_0$  in  $^{\circ}\text{C}^{-1} \text{d}^{-1}$ ) and the increase in the temperature sum over that day:

$$P(T) = dP_0 \cdot (T - T_b) \quad \text{for } T \geq T_b \quad \text{and} \quad \Sigma(T - T_b) \geq S \quad \text{Equation 87a}$$

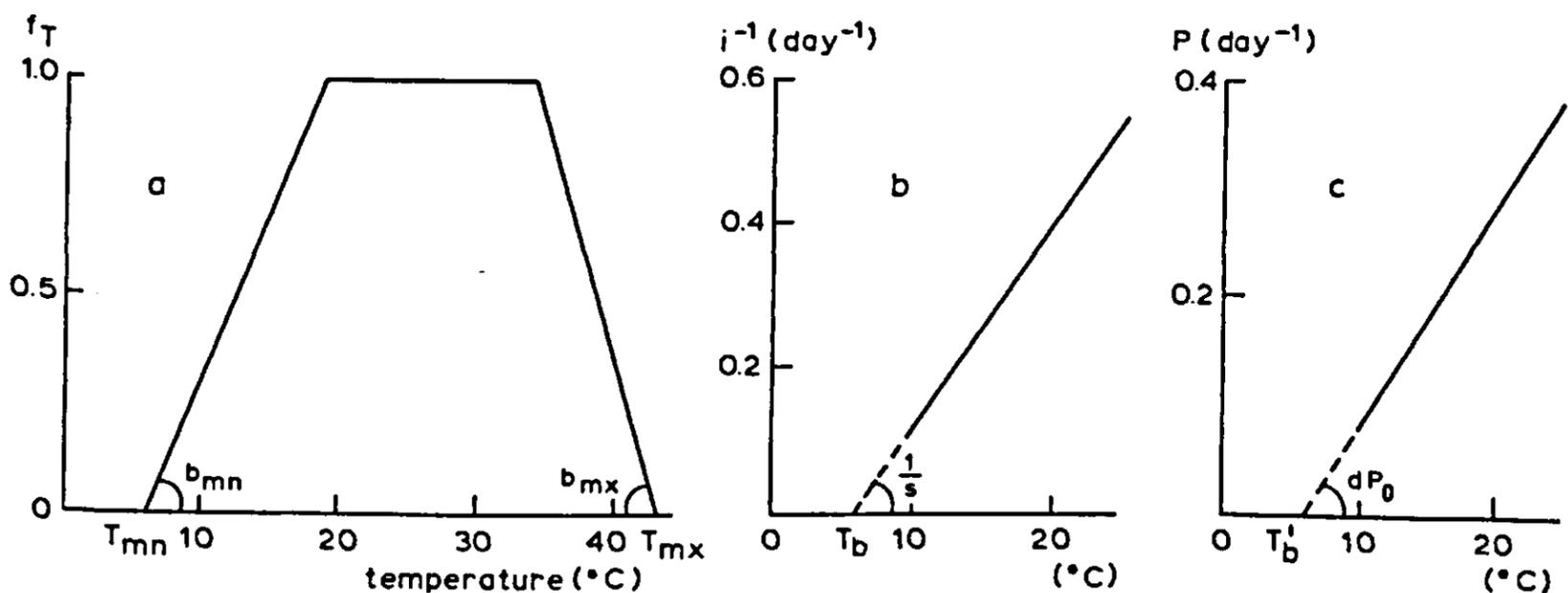


Figure 57. Influence of temperature on (a) maximum germination, represented by the multiplication factor  $f_T$  for maximum germination under optimum temperatures ( $N_{m,o}$ ), (b) incubation rate (i.e. the inverse of time to first germination) and (c) germination probability. Intercepts with the temperature axis are  $T_{mn} = 6^{\circ}\text{C}$ ,  $T_{mx} = 43^{\circ}\text{C}$ ,  $T_b = T'_b = 6^{\circ}\text{C}$  and slopes are  $b_{mn} = 0.077^{\circ}\text{C}^{-1}$ ,  $b_{mx} = -0.111^{\circ}\text{C}^{-1}$ ,  $S = 35^{\circ}\text{C d}$ ,  $dP_0 = 0.02^{\circ}\text{C}^{-1} \text{d}^{-1}$ . Relationships are based on data for field emergence in natural seed populations of *Echinochloa crus-galli* (Spitters & Graveland, in prep.).

As long as the incubation time has not yet been passed, P equals zero:

$$P(T) = 0 \quad \text{for } \Sigma(T - T_b) < S \quad \text{Equation 87b}$$

The linear regression of P on temperature is characterized by a base temperature ( $T'_b$  in Figure 57c) which may differ from that of the incubation rate.

### Exercise 56

Write a CSMP program to simulate field emergence in relation to temperature, according to the relations depicted in Figure 57. Assume an incubation time of  $35^\circ\text{C d}$  after last soil cultivation, a probability of emergence of  $0.020^\circ\text{C}^{-1}\text{d}^{-1}$  ( $T_b = 6^\circ\text{C}$ ), and 100 germinable seeds per  $\text{m}^2$ . These values are typical for *Echinochloa crus-galli*, a  $C_4$  type grass and one of world's major weeds. Assume that soil temperature increases linearly from  $10^\circ\text{C}$  at seedbed preparation to  $20^\circ\text{C}$  30 days later.

**Soil moisture** Germination requires water. Weed seedlings usually emerge from the surface soil layers only, with a maximum depth of 2 cm being typical for many weed species. The surface layers dry out rapidly, so field emergence of weeds is strongly affected by the rainfall pattern.

The average moisture content in the soil compartment from which seedling emergence takes place is tracked by a very simple model of the water balance (Figure 58). The rate of change of soil moisture (dSM) over time interval, dt, equals the infiltrated rain minus the water that percolates to deeper soil layers and the water evaporated from the soil surface:

$$dSM/dt = \text{RAIN} - \text{PERC}_d - \text{EVAP}_d \quad \text{Equation 88}$$

The soil compartment is replenished by rainfall up to, at the most, field capacity. The excess of infiltrated rain above field capacity percolates to deeper soil layers:

$$\text{PERC}_d = \text{SM}_{\text{act}} + \text{RAIN} - \text{EVAP}_d - \text{SM}_{\text{fc}} \quad \text{PERC}_d \geq 0 \quad \text{Equation 89}$$

where  $\text{SM}_{\text{fc}}$  is the amount of soil moisture at field capacity, and  $\text{SM}_{\text{act}}$  the actual amount ( $\text{kg H}_2\text{O m}^{-2}$  or mm). Field capacity ( $\text{SM}_{\text{fc}}$ ) is the amount of moisture contained by the soil after initial drainage; i.e. about 2 to 3 days after heavy rain. From standard weather data, evaporation from an open water surface is usually calculated using the Penman (1948) equation. This evaporation rate is either calculated in the model itself or obtained from a nearby weather station. (If reference-crop evapotranspiration of short grass is given, this value must be multiplied by 1.25 to obtain the value for open water.) Evaporation from moist soil is, on average, 0.75 times the Penman evaporation for open water (H. van Keulen, pers. commun.). In the model, soil evaporation is reduced by a factor ( $f_2$ ) depending on the relative moisture content of the top 2 cm of the soil. The

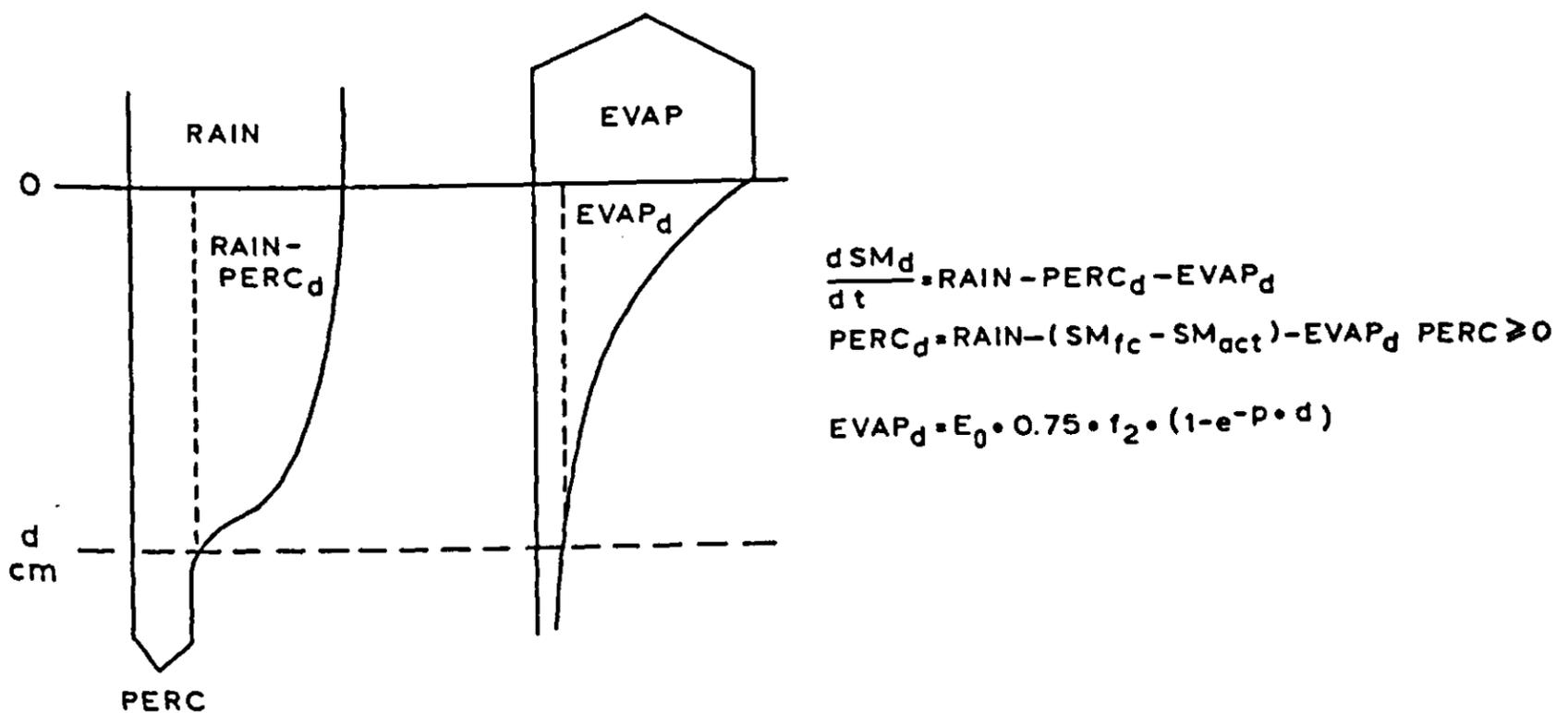


Figure 58. A simple water balance for the soil compartment of depth  $d$  from which seedling emergence takes place. The rate of change in the amount of soil moisture ( $dSM/dt$ ) equals the infiltrated rain minus the water that percolates to deeper soil layers and the water evaporated from the soil surface. Equations are explained in the text.

function used to formulate the reduction is borrowed from van Keulen & Seligman (1987) and defined in the program listing given in the answer to Exercise 57. The relative moisture content is the ratio between the amount which can actually be withdrawn by evaporation ( $SM_{act} - SM_{dry}$ ) and that which could potentially be withdrawn ( $SM_{fc} - SM_{dry}$ ). The moisture content of air-dry soil ( $SM_{dry}$ ) equals about 1/3 of that at wilting point ( $SM_{wp}$ ), the point below which plants are no longer able to withdraw moisture from the soil. The moisture content of the top 2 cm is calculated separately, but by the same procedure as that used for the compartment from which seedling emergence takes place. The procedure requires daily data of rainfall as input.

As a result of capillary rise, the evaporated water is extracted over a certain soil depth. The contribution of a soil layer is assumed to decrease exponentially with its depth (van Keulen, 1975). Thus, the amount of moisture withdrawn from a compartment by evaporation ( $EVAP_d$ ) is obtained by multiplying potential soil evaporation ( $0.75 E_0$ ) by the factor ( $f_2$ ) accounting for the drying out of the top 2 cm, and by the fraction withdrawn from the compartment:

$$EVAP_d = 0.75 E_0 f_2 (1 - \exp(-p \cdot d)) \quad \text{Equation 90}$$

where  $p$  is the extinction factor and for a sandy soil about of  $10 \text{ m}^{-1}$ , and  $d$  the thickness of the top compartment (m).

Soil moisture tension, the pF-value, is expressed logarithmically in mbars (at 100 mbar,  $pF = \log 100 = 2.0$ ). There are very few studies relating seedling emergence to soil moisture tension in the field, so the soil moisture function ( $f_{SM}$  in Figure 59) applied to the three germination parameters ( $N_m$ ,  $1/i$  and  $P$ ) is still

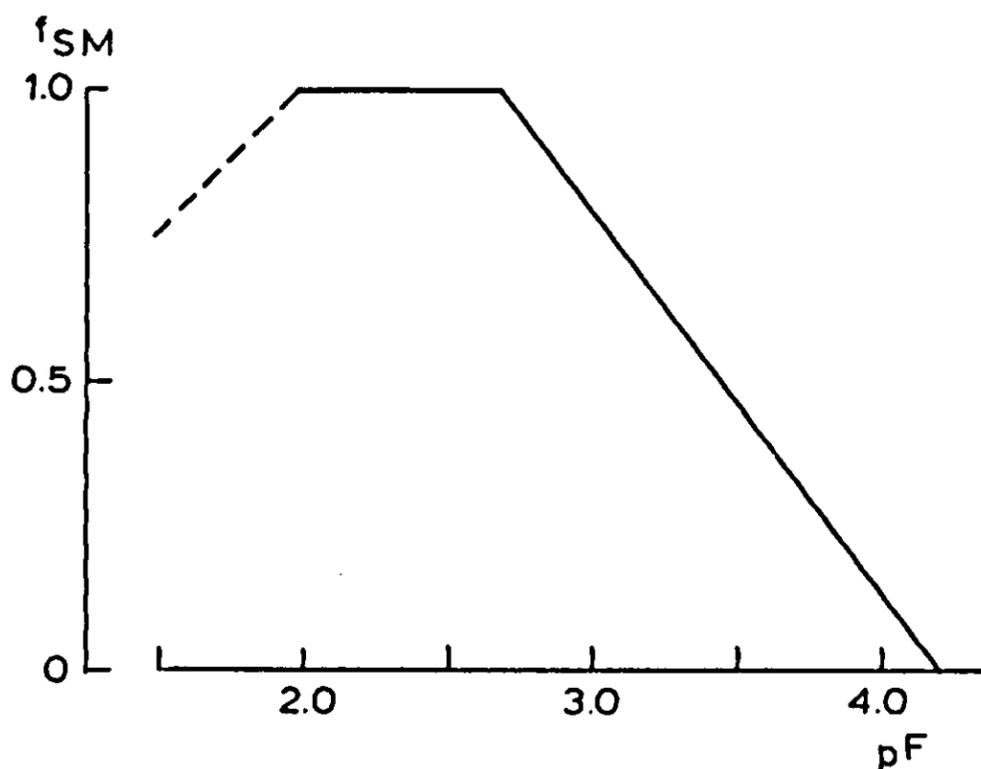


Figure 59. Influence of soil moisture tension ( $pF = \log \text{mbar}$ ) on the three germination parameters ( $N_m$ ,  $1/i$ ,  $P$ ) is characterized by the factor  $f_{SM}$  by which their values at optimum moisture supply must be multiplied. The relation presented is typical for seedling emergence in the field.

somewhat speculative. Field emergence is unrestricted at soil moisture tensions between roughly  $pF$  2.0 and 2.7 (Bierhuizen, 1973; Bierhuizen & Feddes, 1973). At lower  $pF$ -values, emergence is inhibited by anaerobiosis, whereas at higher values drought reduces emergence to zero at wilting point ( $pF$  4.2). The cardinal points depend on species and soil type.

Often, the relationship between soil moisture tension and moisture content of the soil is unknown. Then, as an approximation, the effect of drought on germination and plant growth has usually been related to the relative moisture content ( $RMC = (SM_{act} - SM_{wp}) / (SM_{fc} - SM_{wp})$ ). The linear relationship between  $f_{SM}$  and  $pF$  (Figure 59) results in an approximately linear relation between  $f_{SM}$  and  $RMC$ . This relation is remarkably consistent over different soil types, although the function relating soil moisture tension to soil moisture content varies greatly with soil type. In calculating  $RMC$ , field capacity ( $SM_{fc}$ ) is set at typical values of 1.7, 2.0 and 2.3 for clay, loam and sand, respectively. The breaking value of  $pF$  2.7 is then replaced by an  $RMC$  of 0.50.

After a rain shower following a dry spell, new seedlings do not emerge immediately. Some of the processes will have been reversed during the preceding dry period (Hegarty, 1978). Therefore, some of the germination processes in the seed, and the phase of pre-emergence seedling growth must be repeated, and a new incubation time is required. In order to allow for partial moisture stress as well, a maximum is set to the rate of recovery of  $N_m$ , which is related to the incubation rate:  $df_{SM}/dt \leq (1 - f_{SM})/i$ .

---

### Exercise 57

Extend the model of Exercise 56 to include the influence of soil moisture. *Echinochloa*, with its relatively large seeds, is capable of emerging from depths down to 12 cm. Assume that the soil has a volumetric moisture content of 0.20 at field capacity and 0.05 at wilting point. On Day 0, the soil is at field capacity. Potential evaporation amounts to  $3 \text{ mm d}^{-1}$  and rain showers of 10 mm occur on Days 3, 6 and 9, and of 15 mm at Days 22 and 25.

---

Cycles of drying and wetting reduce the number of seedlings that finally emerge. First, they promote the induction of secondary dormancy. Second, drought causes mortality among those seeds whose germination and emergence processes are too far advanced. Extent of pre-emergence mortality depends on the length of the susceptible phase and on the number of seeds in that phase. A susceptible period can be defined in terms of degree-days. Seeds at this stage, just prior to emergence, are subject to a probability of mortality ( $P_d$ ) which is presumably proportional to  $1 - f_{SM}$ . Dead seeds are then subtracted from the population of germinable seeds ( $N_m$ ).

*Dormancy* The specific, seasonal periodicity in the emergence pattern of a species is invoked by dormancy phenomena. For detailed reviews of this topic see Vegis (1964), Roberts & Totterdell (1981), Karssen (1982) and Bewley & Black (1982).

With relief of dormancy, the range of environmental conditions over which seeds are capable of germinating becomes progressively wider; while as seeds become more dormant, the range narrows again. Dormancy is a mechanism that prevents germination when environmental conditions do not provide a reasonable chance for the germinated seed to survive to reproductive maturity; e.g. in an unfavourable season or under a dense vegetation cover. By responding to environmental signals, germination can be triggered to occur in the right place at the right time.

Seeds of many species are dormant at the time they are shed from the mother plant. This primary dormancy is then released in the course of time. Such an 'after-ripening' occurs in winter annuals and postpones their germination until autumn. In summer annuals, winter cold (moist chilling or stratification) is the main dormancy-breaking factor, so that germination is in spring.

If, for some reason, hydrated seeds are prevented from germinating, secondary dormancy may be induced. In summer annuals, secondary dormancy is induced by high summer temperatures and released by winter cold, so that germination occurs in spring or early summer. The reverse holds for the autumn-germinating winter annuals. Light, alternating temperatures, and high nitrate concentrations are the other main factors leading to a release from the dormant state.

The most typical feature of dormancy is a narrowing of the temperature range over which seeds are able to germinate. The average temperature amplitude of

the population for germination can be characterized by the minimum and maximum temperatures at which  $N_m$  is reduced to half its potential value. The slopes of the temperature relationship of  $N_m$  (Figure 57a) reflect the variation among seeds in temperature amplitude. In the model, both cumulative frequency distribution functions are approximated by straight lines, so the temperature effect on  $N_m$  is characterized by:

$$N_m(T) = f_T N_{m,o} = N_{m,o} \min(b_{mn}(T - T_{mn}), b_{mx}(T_{mx} - T))$$

with  $0 \leq f_T \leq 1$

Equation 91

where  $T_{mn}$  and  $T_{mx}$  are the apparent minimum and maximum temperatures for germination, and  $b_{mn}$  and  $b_{mx}$  the slopes of the temperature relationship (Figure 57a). The minimum value of the two regression equations is used. Again,  $f_T$  is best referred to a running average of several days.

The regression coefficients change during the season with the degree of dormancy, and this periodicity can be determined empirically. To do this, seeds are buried in the field at a time coinciding with normal dispersal from the mother plant. At regular time intervals, samples are dug up and germination is tested under controlled conditions over a range of temperatures. Plotting the observed temperature amplitude against the time of sampling yields the germination window of the species (Figure 85; Karssen, 1982). Superpositioning the variation within the population on that window (Equation 91), quantifies the influence of the seasonal dormancy pattern on  $N_m$ .

### Exercise 58

Make a CSMP program for the annual course of germination of the summer annual *Ambrosia artemisiifolia* and the 'winter' annual *Lamium amplexicaule* in both dark and light. The coefficients characterizing their temperature relations were derived from data of Baskin & Baskin (1980, 1981) and are tabulated in the program listing (see answer). The annual temperature wave is depicted in Figure 85. Assume an incubation time of  $80^\circ\text{C d}$  and a germination probability of  $0.003^\circ\text{C}^{-1}\text{d}^{-1}$  at a base temperature of  $0^\circ\text{C}$ . Assume an initial population of 100 viable seeds, shed in mid-July.

The simulation results (Figure 60) clearly illustrate the effect of soil cultivation. Soil cultivation exposes a fraction of the seed population to light, and in some species an exposure of one minute or less is enough to satisfy the light requirement of the seed (Baskin & Baskin, 1980). Since the temperature window of seeds exposed to light is, in general, much wider than that of those which remain in the dark, a flush of seedlings is generated after soil cultivation. Soil cultivation can easily be introduced in the model, by shifting a fraction of the seed population to

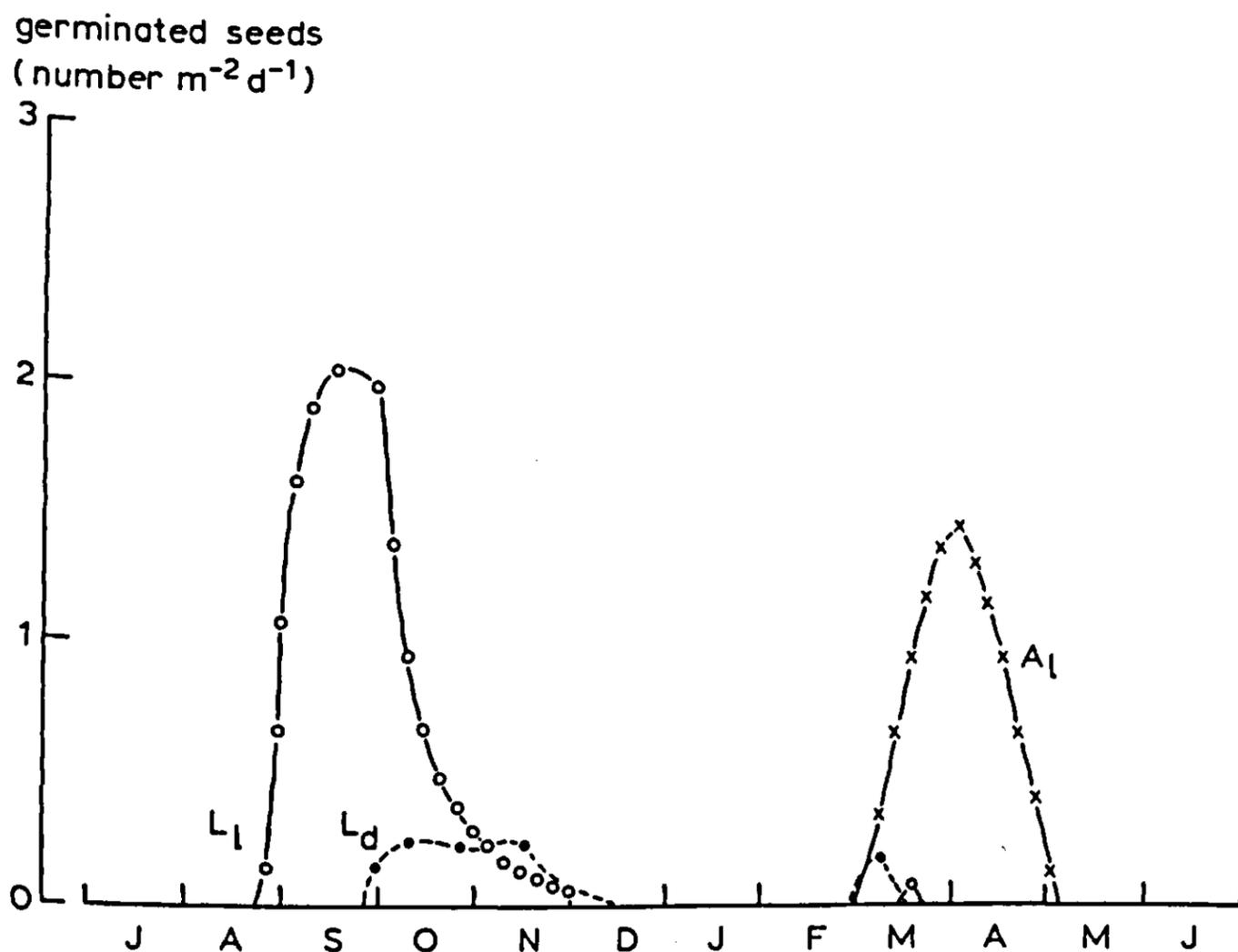


Figure 60. Simulated seasonal pattern of germination of *Ambrosia artemisiifolia* in light (x, A<sub>l</sub>) and *Lamium amplexicaule* in light (o, L<sub>l</sub>) and dark (●, L<sub>d</sub>). The model predicted that *A. artemisiifolia* was unable to germinate in the dark because the seasonal temperature wave did not overlap the temperature window of this species in the dark. *L. amplexicaule* showed little germination in spring because its seed population had already been considerably depleted in the autumn. See also Exercise 58.

a new class of 'seeds exposed to light'. These start with a new incubation time.

The above model is based on an average, observed trend over the year. Forecasting seedling flushes would be improved if more causality were introduced in the model, by storing the degree of dormancy as an integral; having the value 0 for non-dormant seeds and 1 for fully dormant seeds. This state variable changes in time according to rates of induction and relief of dormancy. These rate variables depend on the factors controlling dormancy. In addition, induction and relief of secondary dormancy are influenced by temperature, similar to other metabolic processes, for which the relation of Figure 57b may be representative.

#### 4.2.4 Competition: distributing total growth rate among the competing species

Weeds reduce yield by competing with the crop for environmental resources that are in short supply. Instead of describing these competition effects by an empirical, static regression model, as done in Equation 78, a dynamic, mechanistic model is now presented, in which distribution of the growth-limiting resources

among crop and weed, and the way each species uses the acquired resources, are simulated over time.

As an introduction, a very simple model is discussed, in which the total growth rate of the vegetation is calculated and distributed among the species composing the vegetation, according to their weighted share in total leaf area. The general crop growth model of Section 4.1 is then modified and extended to simulate competition for light, soil moisture and nitrogen.

The growth rate of a crop well supplied with water and nutrients is roughly proportional to its light interception (review by Gosse et al., 1986). The rate of crop growth can thus be estimated from intercepted light and the average efficiency ( $E$ ) with which the crop uses the intercepted light in dry matter production. Light interception is calculated from incoming solar radiation ( $R$ ) and the leaf area index ( $L$ ) of the crop. Since the light flux penetrating a canopy decreases exponentially with the leaf area, the growth rate at time  $t$  is given by:

$$\Delta Y_t = \{1 - \exp(-0.7 L_t)\} \cdot 0.5 R \cdot E \quad \text{Equation 92}$$

where 0.7 is the light extinction coefficient. The factor 0.5 indicates that only 50% of the incoming solar radiation ( $R$ ) is photosynthetically active. The light utilization efficiency ( $E$ ) is of the order of 2.5 to 3 g DM MJ<sup>-1</sup> intercepted light for ruderal C<sub>3</sub> species. For C<sub>4</sub> species,  $E$  is about 4.5 g DM MJ<sup>-1</sup> at optimum temperature.

The leaf area index ( $L$ , ha leaf ha<sup>-1</sup> ground) is obtained by multiplying the biomass ( $Y$ , kg ha<sup>-1</sup>) by the leaf area ratio (LAR, ha leaf kg<sup>-1</sup> biomass):

$$L_t = \text{LAR}_t \cdot Y_t \quad \text{Equation 93}$$

In a mixture of several species, all having an equal plant height, light interception and growth rate of each species are proportional to its share in the total leaf area. Hence, the growth rate of species 1 in a mixture becomes:

$$\Delta Y_{1,t} = \frac{L_{1,t}}{\Sigma L_t} \{1 - \exp(-0.7 \Sigma L_t)\} \cdot 0.5 R \cdot E \quad \text{Equation 94}$$

where  $\Sigma L$  is the total leaf area index of the mixed vegetation.

Crop yield is calculated by multiplying simulated final crop biomass by a fixed 'harvest index', which is the ratio between the yield of the desired parts (e.g. grains) and the total biomass of the crop.

### Exercise 59

Write a CSMP program to simulate the growth of two species growing together in a mixture. Use for incoming solar radiation a value of 14 MJ m<sup>-2</sup> d<sup>-1</sup> and for the light utilization efficiency a value of 3 g DM MJ<sup>-1</sup>. Species 1 starts with an initial biomass of 30 kg ha<sup>-1</sup> and species 2 begins with 20 kg ha<sup>-1</sup>. Assume that LAR decreases linearly from a value of 0.0015 ha kg<sup>-1</sup> at emergence (Day 0), to

zero at full ripeness (Day 101). Compute the biomass production of both species over a period of 100 days. How does the biomass ratio ( $Y_1/Y_2$ ) of the species change in time?

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Species with a higher light extinction coefficient absorb more light per unit leaf area. It can be shown that these differences are allowed for by weighting the leaf areas by their extinction coefficients ( $k$ ):

$$\Delta Y_{1,t} = \frac{k_1 L_{1,t}}{\Sigma(k L_i)} \{1 - \exp(-\Sigma(k L_i))\} \cdot 0.5 R \cdot E \quad \text{Equation 95}$$

In a mixture, a tall plant absorbs more light per unit leaf area than its shorter neighbour. In comparison to a detailed model of light competition (Appendix 7), a good approximation is obtained by setting the growth rates of the species proportional to the light intensities at half their plant heights. Extending Equation 95 gives for the growth rate of species 1 in a mixture:

$$\Delta Y_{1,t} = \frac{k_1 L_{1,t} l_{1,t}}{\Sigma(k L_i l_i)} \{1 - \exp(-\Sigma(k L_i))\} \cdot 0.5 R \cdot E \quad \text{Equation 96}$$

Assuming the leaf area of each species is evenly distributed over its plant height (Figure 61), the relative light intensity of species 1 at half its height ( $H$ ) gives:

$$l_{1,t} = \exp \left\{ - \sum_{j=1}^n \left( k_j \frac{H_{j,t} - \frac{1}{2}H_{1,t}}{H_{j,t}} L_{j,t} \right) \right\} \quad \text{where } H_j \geq \frac{1}{2}H_1 \quad \text{Equation 97}$$

---

### Exercise 60

Extend the simulation model by including the above equations to account for differences in extinction coefficient and plant height. Assume that plant height increases linearly in time from 1 cm at emergence up to 100 cm at an age of 80 days, after which time the height remains constant. Simulate first a situation where the two species are identical, and use reruns to model both monocultures. Set the total initial biomass for all vegetations to  $50 \text{ kg ha}^{-1}$ . In each subsequent simulation run, reduce one attribute value for the second species by 20% so that in any run the species differ in only a single trait. Consider the following attributes: initial biomass, plant height, leaf area ratio, light extinction coefficient, and light use efficiency. For solar radiation, use the average values from the meteorological station De Bilt, the Netherlands:

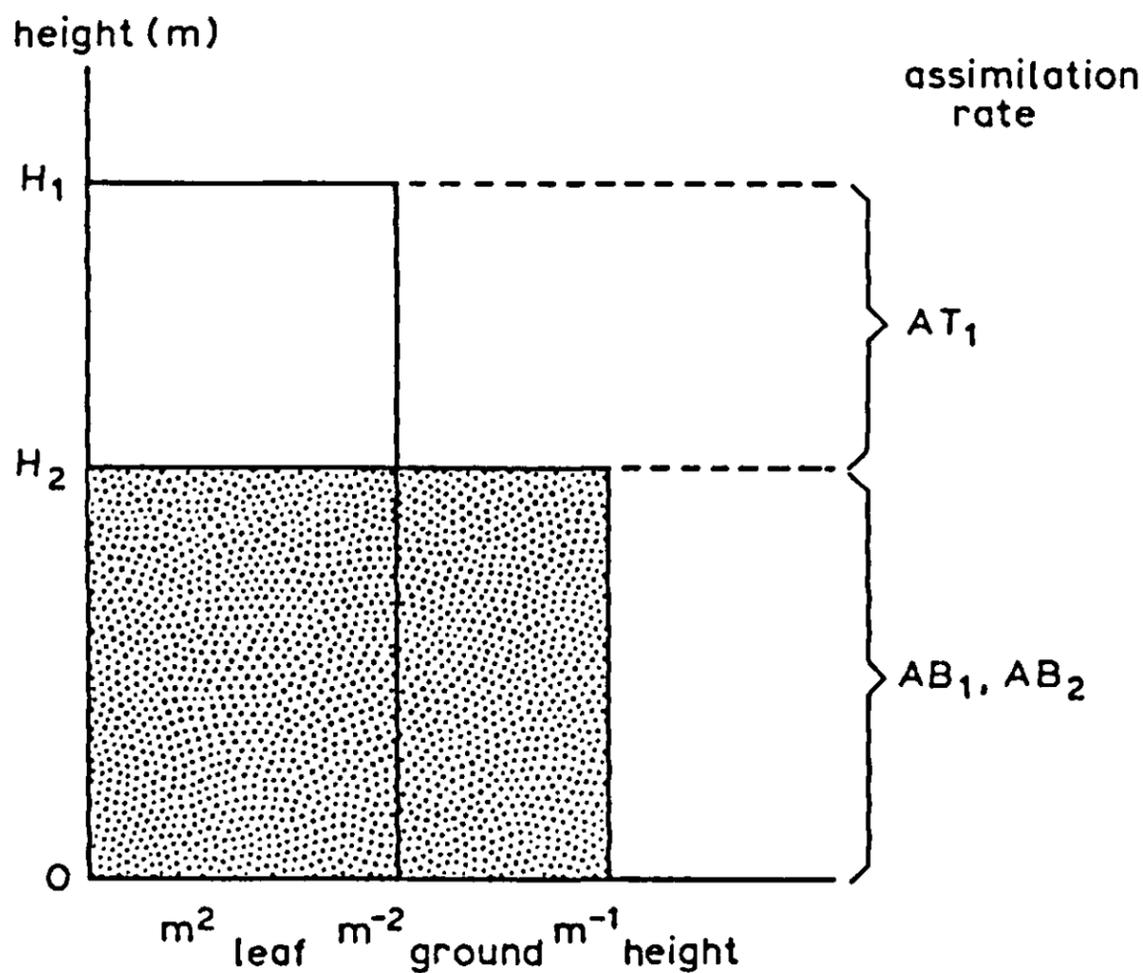


Figure 61. Schematic representation of a mixture of species 1 and 2. The canopy is divided into a top layer monopolized by the tall species 1 and a bottom layer shared by both species. Assimilation rates in the top layer (AT) and those in the bottom layer (AB) are calculated for each species separately.

Days since 1 January	105	135	166	196	227	258
Solar irradiance ( $MJ\ m^{-2}\ d^{-1}$ )	12.4	16.4	18.3	16.2	14.6	10.2
Assume seedling emergence to be at Day 120.						

The sensitivity analysis performed in Exercise 60 (Table 14) demonstrates the relative influence of the various parameters on the competitive ability of a species. The effect of differences in initial biomass shows the importance of the starting position and emphasizes the necessity for accurate initialization of the competition model (e.g. by the relative degrees of soil coverage of crop and weeds monitored in the field early in the season, when forecasting crop yield loss). The effect of plant morphology is reflected in plant height (priority for the growth-limiting factor light), leaf area ratio (pattern of dry matter allocation within the plant) and extinction coefficient (leaf angle distribution and clustering of the leaves). Physiology is reflected in the light use efficiency (photosynthesis and respiration). Stress conditions, such as shortage of water and nutrients, can be accounted for in a simplified way by multiplying the light utilization efficiency by a site index ( $0 \leq SI \leq 1$ ). This index can be estimated by calibrating simulated crop yield against the observed or expected yield level.

Table 14. Simulated effect of single attributes on the ratio in biomass production  $Y$  of two isogenic species when grown alone in monoculture or together in a mixture. For species 2, only the attribute mentioned in each line was reduced to a value of 80% of that of species 1. Monoculture yield of species 1 is  $20.2 \text{ t ha}^{-1}$ .

	$Y_{2,\text{mono}}/Y_{1,\text{mono}}$	$Y_{2,\text{mix}}/Y_{1,\text{mix}}$
Initial biomass	0.98	0.80
Plant height	1.00	0.39
Leaf area ratio	0.90	0.30
Light extinction coefficient	0.90	0.30
Light use efficiency	0.73	0.30

### Exercise 61

Evaluate the effect of the timing of herbicide application on yield, using the program of Exercise 60. Assume for both crop and weed an initial biomass of  $50 \text{ kg ha}^{-1}$  and a rate of plant height increment of  $1 \text{ cm d}^{-1}$ . Assume that the herbicide reduces biomass and plant height of the weed to 10% of their values before application.

*Herbicides* In practice, the effects of herbicide application are much more complex than is suggested by the preceding exercise. New seedling flushes of weeds may appear, especially at low leaf area index. After regrowth, the weeds may show a pattern of dry matter distribution that differs from that without spraying. The effectiveness of spraying strongly depends on the type of chemical, its dose, species composition of the weed infestation, development stage of the weeds, and weather and soil conditions. Frequently, some damage also occurs to the crop, depending on crop development stage.

Present decision making models for weed control are primarily concerned with herbicide retrieval systems, where the farmer is advised on the choice of chemical to be used. This advice is based mainly on the species composition of the weed infestation and the development stage of the crop (e.g. Aarts & de Visser, 1985).

#### 4.2.5 Calculating growth rates from absorbed light

To gain more insight into the underlying mechanisms of competition, distribution of the major growth-limiting resources over the competing species and the way each uses the acquired resources are modelled. Competition for light is discussed first.

*Growth of the crop alone* Simulation of daily growth rate of the weed-free crop is based largely on the crop growth model described in Section 4.1. For purposes of simplicity, however, a simpler procedure is used here to calculate canopy photosynthesis.

Daily totals of incoming radiation are input for the model. Daily photosynthetically active radiation (usually called 'light', 400-700 nm) is obtained as 50% of total solar radiation. The light intensity at each canopy depth is obtained from the exponential light profile:

$$I_L = (1 - \rho)I_0 \exp(-k \cdot L) \quad \text{Equation 98}$$

in which  $I_L$  is the light intensity at height  $L$ , with  $L$  counted from the top of the canopy downwards ( $\text{J m}^{-2} \text{h}^{-1}$ ),  $I_0$  the light intensity at the top of the canopy,  $\rho$  the crop reflection coefficient,  $k$  the extinction coefficient and  $L$  the leaf area index ( $\text{m}^2 \text{leaf m}^{-2} \text{ground}$ ).

Light absorption per unit leaf area at a depth  $L$  in the canopy is obtained by taking the derivative of the exponential light profile (Equation 98) with respect to  $L$ :

$$I_{aL} = -dI_L/dL = (1 - \rho)I_0 \cdot k \cdot \exp(-k \cdot L) \quad \text{Equation 99}$$

where  $I_{aL}$  in  $\text{J m}^{-2} \text{leaf h}^{-1}$ .

This concise model uses the daily average of light intensity at given canopy depth. Thus, spatial and diurnal variation in illumination among the leaves within a canopy layer are neglected. Use of averaged illumination intensities in an instantaneous assimilation-light response function of single leaves would, however, overestimate the actual assimilation rate, because of the convexity of the response function. As demonstrated by Spitters (1986), a reasonable approximation is arrived at by using the more gradual hyperbolic function for leaf photosynthesis instead of the asymptotic exponential which normally characterizes the instantaneous assimilation-light response of single leaves. Calculated crop assimilation rates deviate within  $-10\%$  and  $+5\%$  of those computed by the detailed model presented in Figure 46 ( $\text{LAI} > 0.75$ ). The rectangular hyperbola is written as

$$A = \frac{\varepsilon I_{aL}}{\varepsilon I_{aL} + A_m} A_m \quad \text{Equation 100}$$

in which  $A$  is the assimilation rate ( $\text{g CO}_2 \text{m}^{-2} \text{leaf h}^{-1}$ ). The hyperbola is used only to approximate an average assimilation rate over the day. Therefore, the values characterizing the instantaneous, negatively exponential, assimilation-light response of single leaves should be used for the initial slope  $\varepsilon$  and the saturation level  $A_m$ .

Substituting the absorbed light energy (Equation 99) into the assimilation-light response of single leaves (Equation 100) gives the assimilation rate at each depth of the canopy. Integration over canopy leaf area index  $L$  yields

$$A_d = D \frac{A_m}{k} \ln \left( \frac{A_m + \epsilon \bar{I} k}{A_m + \epsilon \bar{I} k \exp(-k \cdot L)} \right) \quad \text{Equation 101}$$

where  $A_d$  is the daily canopy assimilation ( $\text{g CO}_2 \text{ m}^{-2} \text{ ground d}^{-1}$ ),  $\bar{I} = (1 - \rho)I_d/D$  the incoming light flux averaged over the daylight period and corrected for crop reflection ( $\text{J m}^{-2} \text{ h}^{-1}$ ),  $I_d$  the daily total of incident light,  $D$  the daylength, and  $\ln$  the natural logarithm.

Typical parameter values are:  $\rho = 0.08$ ;  $\epsilon = 12\frac{1}{2} \cdot 10^{-6} \text{ g CO}_2 \text{ J}^{-1}$  (at  $20^\circ\text{C}$ , Ehleringer & Pearcy, 1983);  $A_m = 4 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$  for ruderal  $\text{C}_3$  species and  $7 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$  for  $\text{C}_4$  species;  $k = 0.72$  for a canopy with leaves randomly distributed within the canopy volume and having a spherical leaf angle distribution. Estimation of the parameter values is discussed in Subsection 4.1.4.

Assimilates are used for maintenance of standing biomass, and the remainder is converted into structural dry matter. Thus, daily crop growth rate is given by

$$\Delta Y_t = C_f(30/44 A_d - R_m) \quad \text{Equation 102}$$

where  $\Delta Y_t$  is the growth rate ( $\text{g DM m}^{-2} \text{ d}^{-1}$ ),  $C_f$  the conversion efficiency ( $\text{g DM g}^{-1} \text{ CH}_2\text{O}$ ), and  $R_m$  the maintenance requirements ( $\text{g CH}_2\text{O m}^{-2} \text{ d}^{-1}$ );  $30/44$  represents the ratio of the molecular weights of  $\text{CH}_2\text{O}$  and  $\text{CO}_2$ . The conversion efficiency of carbohydrates into dry matter is about 0.7. Maintenance requirements amount to roughly  $0.015 \text{ g CH}_2\text{O g}^{-1} \text{ biomass d}^{-1}$  (at  $25^\circ\text{C}$ ,  $Q_{10} = 2$ ) (Section 4.1).

Total daily dry matter increment ( $\Delta Y_t$ ) is allotted to the different plant organs: leaves, stems, roots and storage organs, according to empirical distribution factors which are a function of the development stage of the species. Time progression of the development stage is calculated in relation to temperature (Section 4.1).

Leaf area index is calculated as the integral of the rate of leaf area growth over time, obtained by multiplying the simulated increase of leaf dry weight with the specific leaf area ( $\text{m}^2 \text{ g}^{-1}$ ) of new leaves, assuming that leaf area growth is limited by the supply of photosynthates and thus mainly affected by irradiation. However, during the early stage of crop growth, temperature is the overriding factor due to its effect on rates of cell division and expansion. For this early stage, leaf area growth is assumed to be exponential, with the relative growth rate being a function of temperature (Section 4.1).

*Growth of crop and weed in competition* Under potential growing conditions, light is the growth-limiting factor; weeds reduce crop growth because they capture part of the incoming light flux. The procedure used to calculate the assimilation rate of the weed-free crop (Equation 101) can now be extended to allow for crop and weed growing together in competition. A mixture of two species, differing in plant height, is considered (Figure 61). The canopy is divided into a top layer, monopolized by the tall species, and a bottom layer shared by both species. The

top layer is a monospecies canopy, so the assimilation rate of the tall species in that layer is given by Equation 101.

Assimilation rates of the species in the common bottom layer are slightly more difficult to derive. The light flux passing across an arbitrary horizon of the bottom layer is

$$I = IB_0 \exp(-k_1 L_1 - k_2 L_2) \quad \text{Equation 103}$$

where  $IB_0$  is the light intensity incident at the top of the bottom layer ( $J m^{-2} h^{-1}$ ). Subscripts refer to species 1 and 2. Differentiation with respect to  $L_1$  gives the decrease in the downward light flux penetrating  $dL_1$  deeper into the canopy. Of this total amount, species 1 absorbs a fraction proportional to its share in the canopy at that horizon. The leaf areas are weighted by their extinction coefficients in order to account for differences in light absorption per unit leaf area. Hence, the amount of light absorbed by species 1 in the horizon under consideration becomes

$$\begin{aligned} I_{aL,1} &= - \frac{dI_L}{dL_1} \frac{k_1 L_1}{k_1 L_1 + k_2 L_2} = \\ &= \frac{k_1 L_1}{k_1 L_1 + k_2 L_2} I_0 \left( k_1 + k_2 \frac{dL_2}{dL_1} \right) \exp(-k_1 L_1 - k_2 L_2) \quad \text{Equation 104} \end{aligned}$$

where  $I_{aL}$  in  $J m^{-2} \text{ leaf } h^{-1}$ .

Assuming that the leaf area of each species is evenly distributed over its plant height (Figure 61),  $dL_2/dL_1$  equals  $L_2/L_1$  for any horizon of the bottom layer. Applying this simplification to Equation 104 gives

$$I_{aL,1} = I_0 k_1 \exp(-k_1 L_1 - k_2 L_2) \quad \text{Equation 105}$$

Substituting the absorption intensity into the assimilation-light response function (Equation 100) and integrating over the leaf area index of the bottom layer ( $LB_1$ ) yields the assimilation rate of species 1 in that layer:

$$\begin{aligned} AB_{d,1} &= \frac{k_1 LB_1}{k_1 LB_1 + k_2 LB_2} D \frac{A_{m,1}}{k_1} \cdot \\ &\cdot \ln \left( \frac{A_{m,1} + \varepsilon_1 IB_0 k_1}{A_{m,1} + \varepsilon_1 IB_0 k_1 \exp(-k_1 LB_1 - k_2 LB_2)} \right) \quad \text{Equation 106} \end{aligned}$$

where  $LB$  is the leaf area of the subscripted species in the bottom layer. This equation can be related directly to Equation 101 for a single-species stand, as the exponential describes the fraction of light transmitted through the bottom layer, while the first term gives the share of species 1 in the light absorption of the bottom layer.

The total daily assimilation rate of species 1 is obtained as the sum of its rates in the top and bottom strata (Figure 61):

$$A_{d,1} = AT_{d,1} + AB_{d,1} \quad \text{Equation 107}$$

in which  $A_{d,1}$  is the daily assimilation rate of species 1 ( $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ ).

Calculations for species 2 are similar. In the program listed in Appendix 6, a general formulation is used, referring to a mixture of  $n$  species with the canopy stratified into  $n$  layers bounded by the plant heights of the different species. Light absorption and photosynthesis by non-leaf organs, e.g. stems and panicles, may be treated as though these organs represented another species.

The above approach accounts, analytically, for the exponential light profile within the mixed canopy layers. A more detailed, numerical model of light competition is presented in Appendix 7. This model is an extension of the elementary crop photosynthesis model discussed in Section 4.1, and can easily be linked to the model given in Appendix 6.

*Plant height* Height increases in time according to an S-shaped curve. It is expressed as a function of development stage (or accumulated temperature) rather than chronological time. Richards (1959, 1969; Causton & Venus, 1981) defined a family of sigmoid curves. Applied to plant height:

$$H_D = H_m(1 \pm b \cdot \exp(-sD))^{-1/v} \quad \text{Equation 108}$$

where  $H_D$  is the plant height at development stage  $D$ ,  $H_m$  the maximum plant height, and  $b$ ,  $s$  and  $v$  are constants. The plus sign applies when  $v > 0$ , the minus sign when  $-1 \leq v < 0$ , while the function is not defined for  $v < -1$  or for  $v = 0$ . The rate of height increment is given by the derivative of  $H_D$ :

$$\frac{dH_t}{dt} = \frac{dD}{dt} \frac{dH_D}{dD} = \pm \frac{dD}{dt} \frac{s}{v} H_m b \cdot \exp(-sD) (1 \pm b \exp(-sD))^{-(1+v)/v}$$

$$\text{Equation 109}$$

where  $dH_t/dt$  is the rate of height increment ( $\text{m d}^{-1}$ ), and  $dD/dt$  the rate of development (stages  $\text{d}^{-1}$ ). The coefficients are obtained by fitting Equation 108 to data on height and development stage, using a least squares procedure. The logistic function ( $v = 1$ ) is often satisfactory. Sub-optimal conditions reduce plant height. As a simplifying approach, the height increment rate is then multiplied by a reduction factor which is the same as that calculated for the growth rate (Equations 113 and 117). Equation 109 assumes that a reduction of the height increment rate during a certain stage does not affect the increment rate at later stages.

In the model, height is obtained as the integral of the height increment rate.

*Initialization* In a mixture, the growth rate ( $dY_t/dt$ ) of a species tends to be proportional to its leaf area and so to its present biomass ( $Y_t$ ). This is especially true when the species differ only slightly in plant height and in the ratio of leaf area to plant weight. Thus, the relative growth rate ( $R = (dY_t/dt)/Y_t$ ) tends to be

the same for all species when grown together in a mixture. The relative differences then remain constant in time so that the competitive status of a species is fully explained by its initial leaf area (Exercise 59). This emphasizes the prime importance of a correct initialization in competition models, especially when the species show a similar plant habit.

Leaf areas of the species, as measured at an early harvest, may be used to initialize the model. This is useful when simulation is applied to interpret experiments, but it has little predictive value. For a predictive model, the species are characterized by plant density and initial leaf area per plant; the latter being estimated by logarithmic extrapolation of leaf area per plant at seedling emergence (Section 4.1).

#### 4.2.6 *Competition for soil moisture*

The above model is concerned with potential growing conditions, i.e. situations where light is the main growth-limiting factor. In the following sections, the model will be extended by simple procedures to account for growth reduction due to shortage of soil moisture and nutrients. The demand of the species is calculated by its rate of uptake with no shortage of moisture or nutrients. The degree to which the available soil stocks can cover the demand determines the actual uptake and the reduction in growth rate of the species.

*Potential transpiration* The demand for soil moisture by a species is characterized by its transpiration rate with ample moisture supply. The potential rate of transpiration of a foliage that fully covers the ground is proportional to the evaporation rate of an open water surface ( $E_0$ ), which can be calculated from standard weather data using the Penman (1948) equation.  $E_0$  is calculated in the model either by this equation or by using data of  $E_0$  from a nearby weather station. The proportionality factor, called crop factor ( $F_c$ ), is about 0.9 for  $C_3$  species (Feddes, 1987).  $C_4$  species transpire nearly half as much water per unit of produced dry matter as  $C_3$  species. In temperate climates, their growth rate is only slightly higher than that of  $C_3$  species, but in semi-arid climates their growth rate can be almost twice that of  $C_3$  species (van Keulen, 1982a; Pearcy & Ehleringer, 1984). For  $C_4$  species, therefore,  $F_c$  is set at 0.7 for temperate climates and 0.9 for warm climates.

Instead of taking the evaporation of a hypothetical water surface as a reference, one can also take the evapotranspiration rate of a reference crop, i.e. short grass, actively growing and well supplied with water ( $E_r$ ). This rate can be calculated from a modified Penman-Monteith equation (Monteith, 1965; Doorenbos & Pruitt, 1977). In the model listed in Appendix 6, a simplified expression developed by Makkink (1957) is used, which gives an accurate description for Dutch conditions (de Bruin, 1987). It has the advantage of requiring only data of solar radiation and temperature. The reference evapotranspiration of a short grass cover ( $E_r$ ) is, on average, 0.8 times the Penman evaporation of open water

( $E_0$ ). So the new crop factor ( $F'_c$ ) referring to  $E_r$  is about 1.1 for  $C_3$  species, depending somewhat on crop and climatic conditions (Doorenbos & Kassam, 1979; Feddes, 1987).

Transpiration of a crop is reduced by incomplete soil coverage. Transpiration requires energy from absorbed radiation. The rate of transpiration is, therefore, approximately proportional to the fraction of incoming solar radiation intercepted by the foliage. This fraction is calculated from the exponential radiation profile (Equation 98). All incoming solar radiation is potentially available for vapourization. Therefore, the extinction coefficient ( $k$ ) for total solar radiation (300-3000 nm) is used, which has a value of about 0.7 of that for photosynthetically active radiation (400-700 nm). In a mixed vegetation, the potential transpiration rate of each species is proportional to the radiation it intercepts in the mixture, which is calculated in a similar way to its interception of PAR in a mixture.

Thus, the potential transpiration rate of the foliage is calculated as:

$$T_{\text{pot}} = E_0 F_c (1 - \exp(-0.7 kL)) / 0.85 \quad \text{Equation 110}$$

where  $T_{\text{pot}}$  is the potential transpiration rate ( $\text{mm d}^{-1}$ ),  $E_0$  the evaporation from an open water surface ( $\text{mm d}^{-1}$ ) and  $F_c$  the crop factor ( $-$ ). The third term is the fraction of incoming radiation actually intercepted by the foliage, relative to the fractional interception at full ground coverage. At full ground coverage, LAI is about 4 and the foliage intercepts about 85% of incoming radiation. The term  $E_0 F_c$  can be replaced by  $E_r F'_c$ , where  $E_r$  is the evapotranspiration of a reference crop and  $F'_c$  the adjusted crop factor. (Note that the above references use the term 'crop coefficient' or 'crop factor' for the ratio  $T_{\text{pot}}/E_0$  or  $T_{\text{pot}}/E_r$  as a whole rather than for  $F_c$  or  $F'_c$  alone.)

*Available moisture* The amount of soil moisture is tracked using a modified version of the simple water balance model discussed in the germination section (Equations 88-90). Equation 88, however, needs to be expanded to incorporate water uptake by the vegetation. The soil compartment considered, is the depth to which the roots finally penetrate. This maximum rooting depth is often dictated by soil attributes rather than being a species characteristic. The rooted profile is, in general, of such depth that the term  $\exp(-p \cdot d)$  of Equation 90 can be neglected. Vertical root penetration proceeds rapidly: 2-4  $\text{cm d}^{-1}$ , depending on soil temperature. If substantial water shortage is expected to occur early in the season, the extended procedure of van Keulen (1986a) can be included to allow for the feature that rooting has not yet reached its final depth. Field capacity and wilting point refer to their values averaged over the rooted compartment.

To account for reduction in soil evaporation caused by the canopy cover, the term EVAP in Equation 90 is multiplied by the radiation transmission of the canopy, being  $\exp(-0.7 kL)$ . Use of the drying factor ( $f_2$ ) relies strictly upon daily data of rainfall. As a simple approximation, reduction in soil evaporation due to drying is, therefore, set linearly proportional to the relative moisture content of

the root zone rather than as a function of that of only the top 2 cm (van Keulen, 1986a).

In situations with a shallow water table and high soil conductivity, capillary rise from soil layers below the root zone substantially adds to soil moisture availability and must be taken into account; in which case, the procedure outlined by Driessen (1986a) can be used.

*Actual transpiration* When water is in short supply, plants reduce loss of water vapour from the leaves by closure of the stomata. Actual transpiration is then less than the potential value. The multiplication factor ( $f_{SM}$ ) which must then be applied to the potential transpiration rate (Equation 110) is assumed to decrease linearly from a value of 1 at a critical soil moisture content to a value of 0 at wilting point:

$$f_{SM} = (SM_{act} - SM_{wp}) / (SM_{cr} - SM_{wp}) \quad 0 \leq f_{SM} \leq 1 \quad \text{Equation 111}$$

where the critical soil moisture content is defined as

$$SM_{cr} = SM_{wp} + (1 - P)(SM_{fc} - SM_{wp}) \quad \text{Equation 112}$$

By convention, soil moisture between field capacity ( $SM_{fc}$ ) and permanent wilting point ( $SM_{wp}$ ) is considered to be the maximum quantity available for uptake by the crop. The factor  $P$  measures to what extent this maximum available soil moisture can be depleted until transpiration is reduced. At a greater evaporative demand of the atmosphere, plants rapidly fail to cover the demand by uptake of soil moisture; species differ in their reaction (Hagan & Stewart, 1972). For temperate climates, the soil moisture depletion factor ( $P$ ) varies between 0.6 and 0.4 (or pF 2.90 and 2.55) for an evaporative demand of 1 and 5 mm d<sup>-1</sup>, respectively. For climates with a high evaporative demand, the approach of Doorenbos & Kassam (1979; Driessen 1986a) may be followed. The evaporative demand decreases about exponentially with depth in the canopy. Thus, the demand is lower for a short species than for a tall species in a mixture. Evaporative demand should, therefore, refer to the values at the respective plant heights of the species in the mixture. However, this is not applied in this summary model and partly compensates for the reduced root/shoot ratio of shaded species.

The role of rooting density is discussed in the section on competition for nutrients (model listing in Exercise 62). The errors introduced in the model by neglecting the roots will usually be small, because the share of a species in the total rooting system closely correlates with its share in total leaf area, and so with its share in canopy transpiration.

*Actual growth rate* Stomatal closure with water shortage restricts not only water loss of the plant but also CO<sub>2</sub> uptake. For a wide range of environmental conditions, reduction in CO<sub>2</sub> assimilation is approximately proportional to reduction in transpiration:

$$A_{act}/A_{pot} = T_{act}/T_{pot} \quad \text{or} \quad A_{act} = (T_{act}/T_{pot})A_{pot} \quad \text{Equation 113}$$

Reduction in total growth rate, therefore, is calculated by multiplying the potential rate of growth by the reduction factor  $T_{act}/T_{pot}$ .

*Program listing of the competition model* A complete listing of the competition model is presented in Appendix 6. Parameter values are for maize and barnyard grass (*Echinochloa crus-galli* (L.)P.B. var *crus-galli*). The presented method of calculating daily assimilation rates, per species in a mixture, and the soil moisture balance, are both relatively simple, and primarily aim to illustrate the principles of competition for light and water. The description of competition for light is improved by replacing subroutine XDASSH in Appendix 6 by subroutine XDASS (Appendix 7). The latter is an extension of the model SUCROS87 described in Section 4.1 for monocultures to a mixed vegetation. The resulting model for growth of different species in a mixture is designated COMPETITOR.

#### 4.2.7 Competition for nutrients (N, P, K)

Shortage of soil nutrients reduces the rate of crop growth. The presence of weeds reinforces this reduction because they capture nutrients which would otherwise be used for crop growth.

A simple model for nitrogen competition is presented. Here, the competition model of Exercise 60, which applies to optimal growing conditions, is extended by including a procedure for N uptake. This procedure is based on the model of van Keulen (1982b) for the effect of N fertilization on crop growth. Subsequently, below-ground competition for N is introduced into the model.

*Soil nitrogen available for uptake* Mineral nitrogen (nitrate, ammonium) in the rooted profile is potentially available for uptake by the plants. To avoid the need for a complex model of the soil nitrogen balance, the amount of N actually taken up by the vegetation is tracked as a state variable in the model. Total uptake is calculated from the results of standard fertilizer trials where both yield and uptake of the crop are recorded in response to fertilizer application (Figure 62).

The amount initially available for uptake equals the uptake from unfertilized soil (intercept  $N_0$  in Figure 62). A constant fraction of the fertilizer is eventually recovered in the (above-ground) plant material (linear relation with slope  $r$  in Figure 62). Therefore, the amount of soil N at time  $t$  which is still to be taken up ( $A_{s,t}$ ) equals the initial amount ( $A_{s,0}$ ) minus the integral of rate of N uptake:

$$A_{s,t} = A_{s,0} - \int (-U_t)dt \quad \text{with} \quad A_{s,0} = A_{us,0} + rF \quad \text{Equation 114}$$

where  $A_{s,t}$  is the amount of soil N yet to be taken up at time  $t$  ( $\text{kg N ha}^{-1}$ ),  $U$  the rate of uptake ( $\text{kg N ha}^{-1} \text{ d}^{-1}$ ),  $A_{us,0}$  the uptake from unfertilized soil ( $\text{kg N ha}^{-1}$ ),  $F$  the fertilizer rate ( $\text{kg N ha}^{-1}$ ), and  $r$  the fraction of fertilizer recovered at harvest in above-ground plant material ( $\text{kg N kg}^{-1} \text{ N}$ ).

Values of the parameters can be derived from reviews of fertilizer experiments given by van Keulen & van Heemst (1982) and van Keulen (1986b). Uptake at

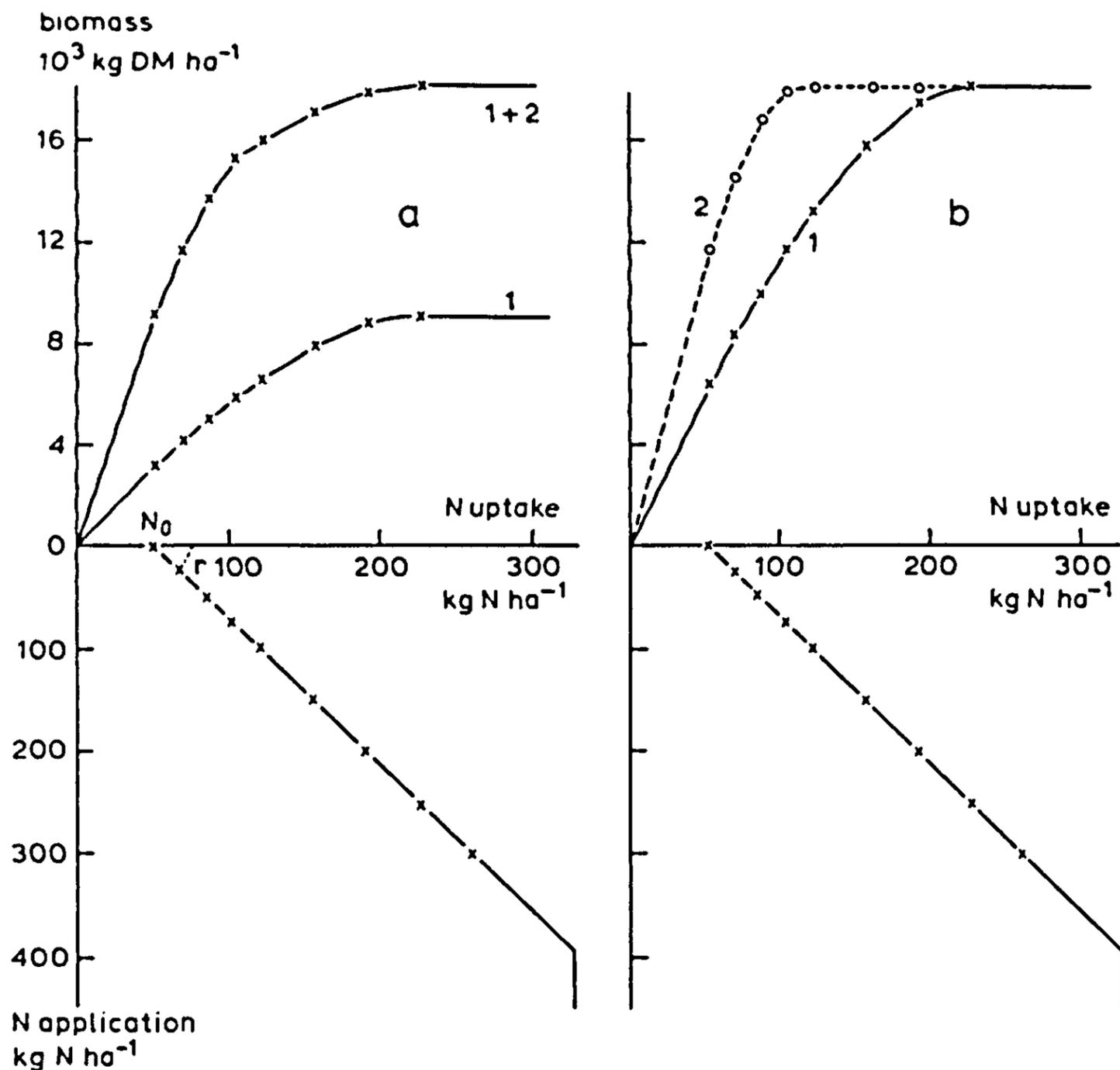


Figure 62. Simulated biomass production of two species and their total N uptake (a) in 1:1 mixture and (b) in monocultures. The lower the soil N availability the greater the relative advantage of the  $C_4$  type (species 2) over the  $C_3$  type (species 1). At low N availability, the  $C_4$  type utilizes the available N almost twice as efficiently as the  $C_3$  type because it is able to dilute the N concentration in its tissues to concentrations that are half as low. Fertilizer recovery ( $r = 0.7$ ) and N uptake from unfertilized soil ( $N_0 = 50 \text{ kg N ha}^{-1}$ ) are depicted in Figure a. See also Exercise 62.

zero application ( $A_{us,0}$ ) is mainly determined by soil characteristics. Typical values for arable lands in the Netherlands are  $70 \text{ kg N ha}^{-1}$ ,  $2.2 \text{ kg P ha}^{-1}$ , and  $40 \text{ kg K ha}^{-1}$ . The recovery fraction ( $r$ ) varies from 0.1 to 0.8 for N and from 0.5 to 0.8 for K, depending on husbandry and soil characteristics. Recovery of phosphorus seldom exceeds 0.3 (Driessen, 1986b); and the relation between P fertilizer rate and uptake often deviates from linearity. Typical recovery fractions for arable lands in the Netherlands are 0.7, 0.2 and 0.7 for N, P and K, respectively.

**Uptake** The amount of nitrogen in the plants is given by the integral of the rate of uptake. The potential rate of uptake of the vegetation is called its demand. The

demand at time  $t$  equals the maximum amount at  $t$  minus the actual amount at the previous time  $t - 1$ :

$$D_t = (NA_{mx,t} - NA_{act,t-1})/T_c = (Y_t \cdot NC_{mx,t} - NA_{act,t-1})/T_c \quad \text{Equation 115}$$

where  $NA$  is the amount of nitrogen ( $\text{kg N ha}^{-1}$ ),  $NC$  the nitrogen content ( $\text{kg N kg}^{-1} \text{ DM}$ ) and  $Y$  the biomass ( $\text{kg DM ha}^{-1}$ ). Subscripts  $mx$  and  $act$  refer to the maximum and actual values, respectively. The time coefficient  $T_c$  is introduced to account for a delay in uptake, which is of the order of 2 days (Seligman & van Keulen, 1981).

The actual uptake of the vegetation is equal to the minimum of the demand or the maximum supply by the soil:

$$U_t = \text{Min}(D_t, A_{s,t}) \quad \text{Equation 116}$$

*Growth reduction* When the N content of the vegetation decreases below a certain, critical level, the growth rate is reduced. This growth rate is assumed to be linearly related to the N content:

$$\Delta Y_{t,act} = f_N \Delta Y_{t,pot} = \frac{NC_{act} - NC_{mn}}{NC_{cr} - NC_{mn}} \Delta Y_{t,pot} \quad 0 \leq f_N \leq 1 \quad \text{Equation 117}$$

where  $Y_{act}$  and  $Y_{pot}$  are the actual and potential growth rates, and  $NC_{act}$ ,  $NC_{cr}$  and  $NC_{mn}$  are the actual, critical and minimum nitrogen contents, respectively. The actual content is obtained by dividing the actual amount ( $NA_{act}$ ) by the present biomass ( $Y$ ).

Because of stomatal control, the transpiration rate must be reduced in the same way as the growth rate when nutrients are in short supply (Goudriaan & van Keulen, 1979; Wong et al., 1985).

*Maximum, critical and minimum nutrient contents* For a given nutrient, these key values differ strongly between plant organs, decrease with development stage, and depend to a lesser degree, also upon plant species. For nitrogen, typical values for field-grown annual  $C_3$  grasses can be derived from van Keulen (1982b, p. 240). The maximum N content ( $NC_{mx}$ ) in leaves decreases linearly with development stage according to  $0.055 \cdot (1 - 0.3 \text{ DVS})$ , with 0.055 referring to the value at seedling emergence (DVS increases from 0 at emergence to 2 at maturity). Maximum N contents of stems and roots amount to about 0.35 and 0.20, respectively, of the value for leaves. The maximum N content of grass seeds decreases from 0.045 at the onset of seed filling to 0.025 at seed maturity. Critical N contents ( $NC_{cr}$ ) amount to about 0.65 of the maximum contents. Minimum content ( $NC_{mn}$ ) of the vegetative parts averages about 0.005, but is somewhat higher for the early stages. The minimum N content of grass seeds is 0.015.

Total uptake (Equation 116) is distributed among the various plant organs in proportion to their demands (van Keulen, 1982b). In the summary model of

Exercise 60, where only the total biomass of each species is considered, averaged N contents are used. The dry matter distribution pattern of annual C<sub>3</sub> grasses suggests a maximum N content of the above-ground parts that decreases from 0.050 at emergence to 0.025 at flowering, and to 0.018 at maturity; a critical content that amounts to 0.65 of the maximum content; and a minimum content of 0.008 kg N kg<sup>-1</sup> DM.

Maximum contents of C<sub>4</sub> grasses are probably close to those of the C<sub>3</sub> grasses. However, owing to the C<sub>4</sub> pathway, photosynthesis can continue at much lower contents of carboxylating enzymes (Ku et al., 1979). Critical and minimum N contents of C<sub>4</sub> species are, therefore, about 0.5 of the respective values for C<sub>3</sub> species (Penning de Vries & van Keulen, 1982; Brown, 1985). Maximum N contents of legumes are 30% and those of non-leguminous dicotyledons about 10% higher than those of grasses. Maximum contents of seeds may differ strongly between species.

Phosphorus (P) contents are coupled, to some extent, to nitrogen contents. P/N ratios vary within a range of 0.04 to 0.15 and have a value of 0.10 with ample nutrient supply (Penning de Vries & van Keulen, 1982). At very low levels of N uptake, absorption of P is restricted so that the P/N ratio does not exceed 0.15. At very low P availability, uptake of N is reduced so that the P/N ratio does not decrease below a value of 0.04. Thus, by combining these features with the N model discussed above, a simple model for P is defined.

Potassium (K) contents are of roughly the same order of magnitude as N contents, but vary greatly among plant species and according to soil cation status.

*Competition* In the case of mobile soil elements, such as water and nitrates, root density has little effect on the total uptake of these elements by the crop, when the conditions are within a normal range (Seligman & van Keulen, 1981; van Noordwijk, 1983). Thus, the total uptake of a mixed vegetation is calculated in a similar way to that outlined above for the weed-free crop.

However, when supply from the soil cannot cover demand, uptake by a species in a mixed vegetation will be related to its share in the total absorbing root length. Below-ground competition for soil elements is modelled analogously to the above-ground competition for light. Just as the fraction of light quanta intercepted by a species was related to its share in total leaf area, the fraction of water molecules or nutrient ions that is intercepted is related to its share in the total root system:

$$U_i = (l_i/\Sigma l) \Sigma U \quad U_i \leq D_i \quad \text{Equation 118}$$

where  $U_i$  is the uptake by species  $i$ , and  $\Sigma U$  the uptake summed over all species of which the vegetation is composed (kg N ha<sup>-1</sup> d<sup>-1</sup>),  $D_i$  the demand of species  $i$  (kg N ha<sup>-1</sup> d<sup>-1</sup>), and  $l$  the effective root length (m ha<sup>-1</sup>). Equation 118 shows that the relative, rather than the absolute, root lengths of the species determine their competitive ability.

A species with an extensive root system, relative to its demand, is able to meet its demand up to a lower soil nitrogen supply. In the model, at limited soil supplies, the soil nitrogen not used by such a species is distributed over the other species.

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### Exercise 62

Combine the nitrogen model with the competition model of Exercise 60. Simulate the effect of a C<sub>4</sub> grass weed on a C<sub>3</sub> cereal, assuming that crop and weed are identical except that the C<sub>4</sub> species has a critical and minimum nitrogen content which is half that of the C<sub>3</sub> species. Assume a value of 2.76 g DM MJ<sup>-1</sup> for the light utilization efficiency. Evaluate the effect of N fertilization, assuming a recovery of 0.7 and a zero uptake of 50 kg N ha<sup>-1</sup>.

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The foregoing approach assumes a limited stock of soil nitrogen, which is depleted during the course of the growing season, without periodic replenishment except from fertilizer application. This suggests that the species with the greatest demand will take up most of the nitrogen. After the available soil nitrogen has been depleted, the growth rate of a species is reduced less if it can dilute the nitrogen to lower concentrations in its tissue (e.g. a C<sub>4</sub> type), or has a low potential growth rate. The size of the root system would then be of hardly any importance. In reality, however, small amounts of mineral nitrogen become available throughout the growing season because of the mineralization of soil organic matter. The species with the greatest root capacity benefit most from this release.

Modelling the separate processes of the soil N balance is complex and falls beyond the scope of this Section (for reviews of models see Frissel & van Veen, 1981; de Willigen & Neeteson, 1985). Instead, net mineralization, i.e. the difference between mineralization and immobilization, is accounted for in a very simplified way according to Greenwood et al. (1984). Here, we consider the total mineral soil N instead of only the amount which will be taken up by the vegetation. Equation 114 for available soil N then becomes

$$A_{s,t} = A_{s,0} + \int (M_t - U_t/r)dt \quad \text{with} \quad A_{s,0} = A_0 + F \quad \text{Equation 119}$$

where  $A_0$  is the initial amount of mineral soil N (kg N ha<sup>-1</sup>),  $F$  the fertilizer rate (kg N ha<sup>-1</sup>),  $U_t$  the N uptake by the vegetation (kg N ha<sup>-1</sup> d<sup>-1</sup>) which is divided by the recovery ( $r$ ) to account for incomplete uptake of mineral soil N, and  $M_t$  the net mineralization rate (kg N ha<sup>-1</sup> d<sup>-1</sup>). Mineralization mainly depends on the amount of fresh organic material that can be easily mineralized and, therefore, on the previous crop. For UK arable soils, previously cropped with cereals, Greenwood et al. (1984) give an average of  $4.5 \cdot 10^{-5}$  kg N<sub>min</sub> kg<sup>-1</sup> N<sub>org</sub> d<sup>-1</sup> (15°C,  $Q_{10} = 2$ ) and 10 t total organic N ha<sup>-1</sup> in the rooted profile.

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### Exercise 63

Use the model of Exercise 62 to compare the soil N balance according to van Keulen (1982b) (with a zero uptake of  $50 \text{ kg N ha}^{-1}$ ) with that according to Greenwood et al. (1984) with an initial amount of  $26.4 \text{ kg N}_{\text{min}} \text{ ha}^{-1}$ . Assume a fertilizer rate of  $25 \text{ kg N ha}^{-1}$  applied in early spring, and a recovery of 0.7. Calculate the effect of a twofold difference in the root length/biomass ratio on yield and N uptake of two  $C_3$  species when grown together in a 1:1 mixture.

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In the preceding sections, the state variables referred predominantly to the whole canopy and to the whole rooted zone. For the rate variables, their daily averages were considered. The system becomes more sophisticated when the spatial heterogeneity of canopy and soil, and the temporal heterogeneity during the day is taken into account (Spitters & Aerts, 1983; Baldwin, 1976). Further detail is introduced by accounting for environmental effects on species attributes; e.g. adaptation mechanisms. This involves the effects of shade, water stress and nutrient shortage on the (re)distribution of carbohydrates within the plant, and on specific leaf area, photosynthetic capacity of the leaves ( $A_m$ ,  $\epsilon$ ) and senescence.

In Exercise 61, a simple procedure was applied to illustrate the effects of weed control. For practical purposes, however, this procedure is clearly too simple. Therefore, with respect to modelling crop-weed competition, the main subject to be enlarged upon is weed control and, in particular, to the interactions between herbicide, dose and timing of application, development stages of crop and weed, and environmental conditions.