

12 On descriptive and mechanistic models for inter-plant competition, with particular reference to crop–weed interaction

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12.1 Introduction

Species growing together in mixed stands compete with each other for growth-limiting resources such as light, water and nutrients. The study of competitive phenomena in agricultural situations started around 1900 with experiments where different species – or cultivars of the same species – were grown alone in monocultures and together in mixtures. It was found that the yield of a species in mixture, when surrounded by other species, could deviate substantially from its yield when grown in monoculture surrounded by plants of its own species. Sometimes, the higher-yielding types in monoculture were the lower-yielding types in mixture, and vice versa (Montgomery, 1912). For a long period of time, the experimental results were only presented in tables or histograms (e.g. Sakai, 1955), and the general relationships were not recognized. Measures of competitive ability – if any – were restricted to specific designs (e.g. Stadler, 1921, p. 32). General methods of analysis and experimental set-up were lacking.

This situation changed in 1960 with the publication of *On Competition*. In that paper, de Wit introduced a general experimental design (the replacement experiment) to study the effects of competition between different plant species, together with a model to analyse the results of this type of experiment. The publication was a breakthrough and in the years that followed, the replacement approach was applied in many papers.

In the 1960s and 1970s a wide variety of competition models was introduced in agronomic literature. Nearly all of them were additive in that they partitioned the yield of a species in mixture into a linear, additive combination of parameters. These parameters characterized monoculture performance and several types of competitive ability (reviews by Trenbath, 1978; Spitters 1979, pp. 27-36). Neither of these models found wide application because each of them was restricted to a specific experimental design (e.g. a competition diallel) and required relatively many parameters. With the de Wit model, in contrast, estimates from a particular experiment could easily be transposed to a different situation with another combination of the species studied. The universality of this model is based on the underlying empirical, non-linear relationship. The additive models, in contrast, rely upon an unconscious, linear expansion of the effects in purely statistical terms.

The de Wit (1960) approach is based on the replacement design. In a replacement series, a range of mixtures is generated by starting with a monoculture

of one species and progressively replacing plants of that species by plants of the other species until a monoculture of the latter is produced. All monocultures and mixtures are grown at equal plant density (Figure 74), and basically de Wit assumed a constant total density.

In weed research, however, replacing one species by another species is of less practical interest than adding plants of the weed species to a given plant density of the crop (Figure 74). Several functions have been suggested to relate crop yield to weed density in these addition experiments (review by Cousens, 1985a, b). For these models too, the tight confounding with the particular experimental design prohibited wider application.

In the early 1980s, Suehiro & Ogawa (1980), Wright (1981), Spitters (1983a, b) and Watkinson (1981, 1984), introduced models that described the competition effects over a range of populations, varying in mixing ratio and total density. These models could handle both addition and replacement experiments. Like the de Wit model, they were based on a hyperbolic equation for the relationship between the yield of a species in monoculture and its plant density.

The above models are static; they describe the results at only one time. By taking into account the time course of the model parameters, de Wit c.s. developed a dynamic competition model (de Wit & Baeumer, 1967; Baeumer & de Wit, 1968; de Wit, 1970; de Wit & Goudriaan, 1978). By comparison with the static approach, the dynamic approach has the advantage of giving a better insight into the competitive phenomena and of being more flexible. For instance, with this model Spitters & van den Bergh (1982) evaluated the effects of time and efficiency of weed control, and the importance of relative time of emergence and plant height of crop and weeds.

The aforementioned models are all empirical, as they describe the outcome of the competition process by some empirical, regression equation. They do not elucidate the underlying eco-physiological principles of the competition process itself. Recently, it has been demonstrated that the growth of plants in competition can be described by expanding existing models of crop growth to include the

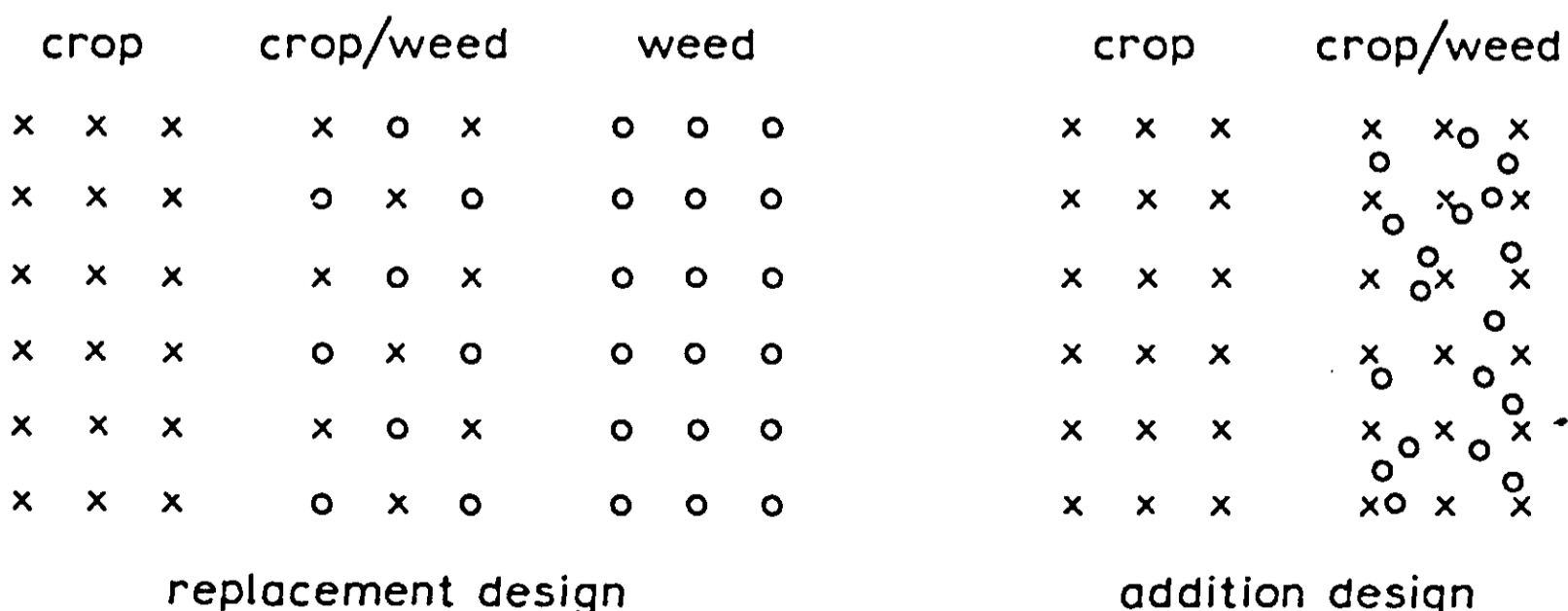


Figure 74. Replacement and addition design with crop plants (x) and weed plants (o).

simultaneous absorption of light, water and nutrients by the different species in a mixed vegetation (Spitters & Aerts, 1983; Spitters, 1984; 1989). The mechanistic approach unlocks competition research for an influx of crop physiological knowledge. In this chapter, both a regression approach and an eco-physiological approach to analyse inter-plant competition are discussed. Crop-weed interaction is highlighted.

12.2 The descriptive, regression approach

Over a wide range of densities, yield of total biomass and often also yield of a certain plant organ are asymptotically related to plant density (Holliday, 1960; Donald, 1963); the relationship being characterized by a rectangular hyperbola (Shinozaki & Kira, 1956; de Wit, 1960, 1961). This equation for intra-specific competition was expanded by Suehiro & Ogawa (1980), Wright (1981) and Spitters (1983a) to allow also for effects of inter-specific competition. Below, I will discuss this regression model, using the parameterization given in an earlier paper (Spitters, 1983a). The relationships are illustrated with results of an experiment in which maize and a natural population of barnyard grass (*Echinochloa crus-galli* (L.)P.B.) were grown in monocultures and mixtures in the field in Wageningen in 1983 (Spitters et al., 1989). The model will be applied to describe crop yield losses caused by weeds, and long-term dynamics of soil populations of weed seeds.

12.2.1 Model description

Crop yield is related to plant density, according to

$$Y = N / (b_0 + b_1 N) \quad \text{or} \quad 1/W = N/Y = b_0 + b_1 N \quad \text{Equation 45}$$

in which Y is the biomass yield (g m^{-2}), N the plant density (plants m^{-2}), W the average weight per plant (g plant^{-1}), and b_0 and b_1 are regression coefficients. The parameter $1/b_0$ is the apparent weight of an isolated plant, and $1/b_1$ represents the apparent maximum yield per unit area (Figure 75).

According to Equation 45 and Figure 75B, $1/W$ is linearly affected by adding plants of the same species. That suggests that adding plants of another species also affects $1/W$ linearly, and Figure 76B gives credence to this assumption. Hence, for a crop in the presence of weeds, the reciprocal of the per-plant weight can be written as

$$1/W_{cw} = b_{c0} + b_{cc}N_c + b_{cw}N_w \quad \text{or} \quad Y_{cw} = N_c / (b_{c0} + b_{cc}N_c + b_{cw}N_w) \quad \text{Equation 46a}$$

and for the associated weeds as

$$1/W_{wc} = b_{w0} + b_{ww}N_w + b_{wc}N_c \quad \text{or} \quad Y_{wc} = N_w / (b_{w0} + b_{ww}N_w + b_{wc}N_c) \quad \text{Equation 46b}$$

where the first subscript indicates the species whose yield is being considered, and the second subscript its associate. The subscript c refers to the crop and w to the weed. In Equation 46a, b_{cc} measures the effect of intra-specific competition, while

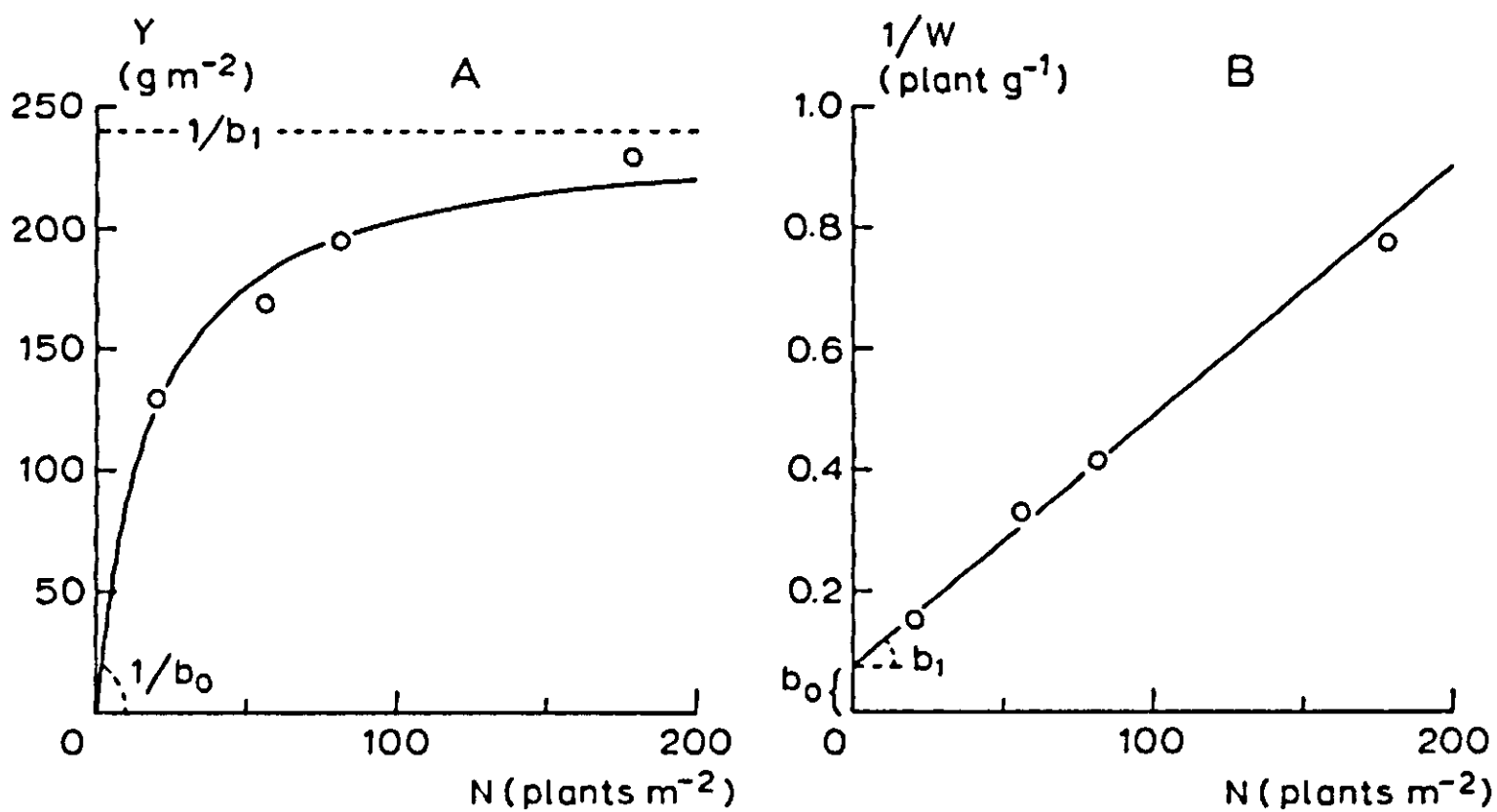


Figure 75. Density response of barnyard grass in monoculture, illustrating the meaning of the regression coefficients (b_0 , b_1). Plots of (A) biomass per unit area, and (B) the reciprocal of per-plant weight against plant density. Fitted equation: $1/W = 0.075 + 0.0042N$.

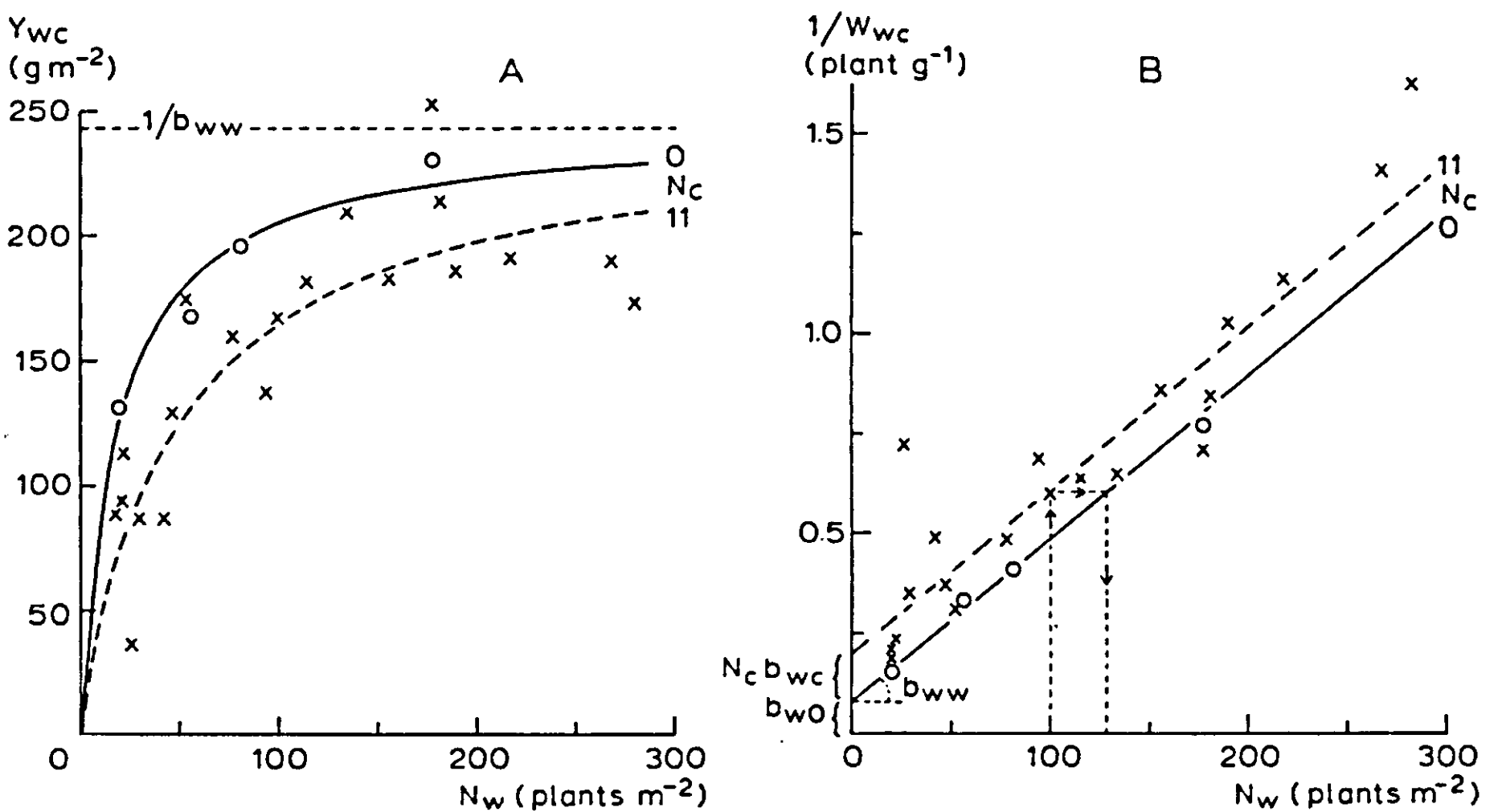


Figure 76. Density response of barnyard grass in monoculture (o, solid curves, $N_c = 0$), and in mixture with 11 maize plants m^{-2} (x, dashed curves, $N_c = 11$), illustrating the meaning of the regression coefficients (b_{w0} , b_{ww} , b_{wc}). The dotted lines indicate that addition of 11 maize plants had the same effect on the per-plant weight of barnyard grass as addition of 29 barnyard grass plants. Fitted equation: $1/W = 0.077 + 0.0041N_w + 0.0107N_c$.

b_{cw} measures the effect of inter-specific competition. The ratio b_{cc}/b_{cw} characterizes the relative competitive ability of crop and weed, with respect to the effect on crop yield. Figure 76B shows that the addition of 11 maize plants to a pure stand of barnyard grass had the same effect on $1/W$ of barnyard grass as the addition of 29 barnyard grass plants. Thus for a barnyard grass plant, the presence of one maize plant was similar to the presence of 2.6 other barnyard grass plants.

To meet the assumption of homogeneity of variances, the regression coefficients are estimated from Equation 46 by non-linear regression of Y on the plant densities. When a wide yield range is covered, the yields tend to be distributed log-normally, and the regression coefficients are therefore estimated by using non-linear regression to fit the logarithm of yield to the logarithm of the right-hand side of Equation 46 (Spitters et al., 1989).

The extension of de Wit's model to unify competition and spacing experiments was based on certain, restrictive prepositions (de Wit, 1960, p. 61; Baeumer & de Wit, 1968; Spitters, 1979, p. 83). Since these assumptions are in general not valid, analysis of competition experiments remained restricted to designs with constant total density, i.e. the replacement designs, until the introduction in the early 1980s of the generalized hyperbolic models, mentioned above. However, when in de Wit's 4-parameter model for a binary mixture, his β_1 in his Equation 8.5 is split up into β_{11} for Species 1 and β_{21} for Species 2, and similarly β_2 into β_{12} for Species 1 and β_{22} for Species 2, the result is a 6-parameter model that is equivalent to Equation 46.

12.2.2 *The special case of crop–weed competition*

A crop is usually grown at a constant plant density (Figure 74), which simplifies Equation 46 to

$$1/W_{cw} = a_0 + b_{cw}N_w \quad \text{and} \quad 1/W_{cc} = b_{c0} + b_{cc}N_c = a_0 \quad \text{Equation 47}$$

where $1/a_0$ is the average weight per plant in the weed-free crop. The yield of the weedy crop (Y_{cw}) relative to the weed-free yield (Y_{cc}) is then

$$Y_{cw}/Y_{cc} = a_0/(a_0 + b_{cw}N_w) = 1/(1 + d_wN_w) \quad \text{Equation 48}$$

where the 'damage coefficient' $d_w = b_{cw}/a_0$ characterizes the apparent fractional yield loss caused by the first weed plant added to the crop (Figure 77).

The aggregate yield reduction due to a multi-species infestation is found by expanding Equation 48 additively according to $d_wN_w = d_1N_1 + \dots + d_nN_n$ for the weed species 1 to n . The damage coefficients of the individual weed species can be estimated from separate trials with the respective weeds. Non-linear regression of crop yield on weed density, allows d_w and Y_{cc} to be estimated.

Since the damage relation is characterized by a single parameter (d), the model also facilitates the comparison of results from different experiments.

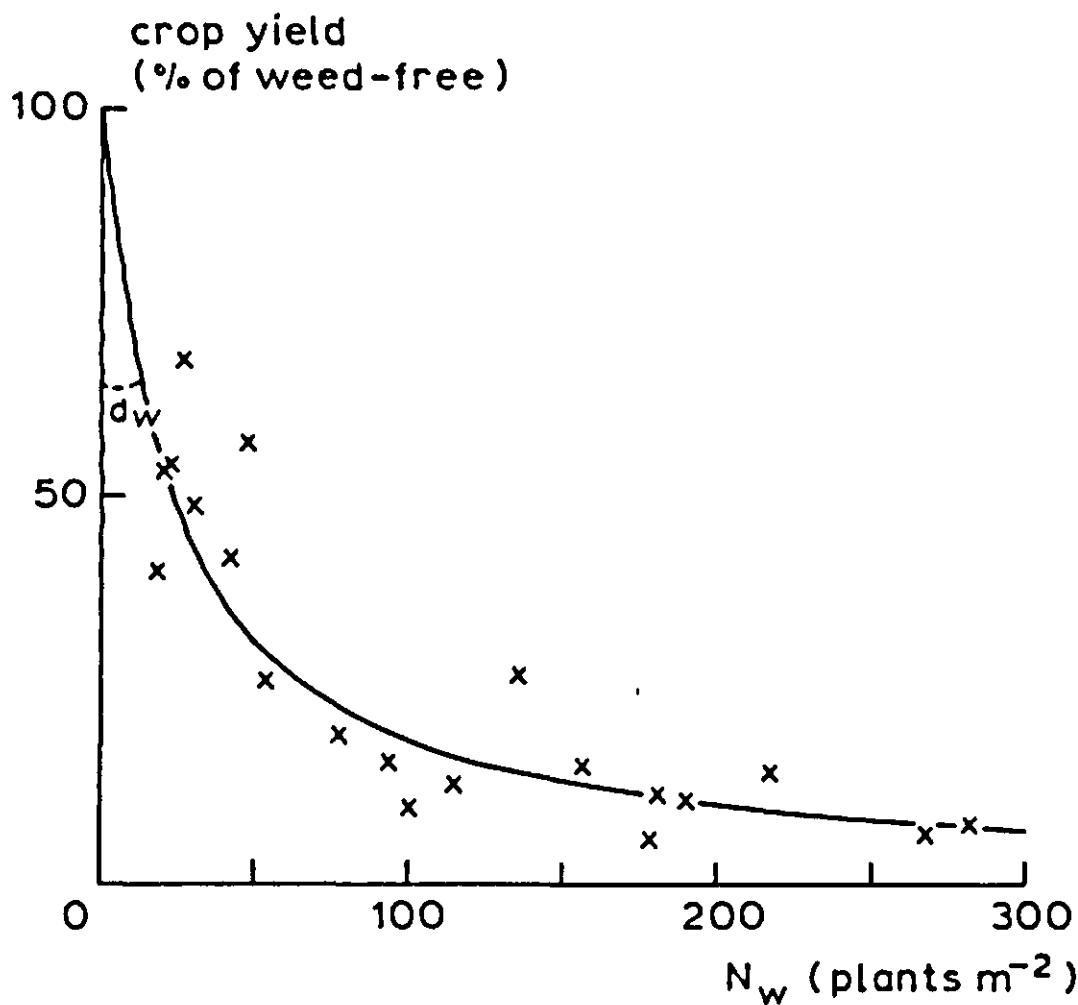


Figure 77. Yield of maize, expressed as % of weed-free yield, in relation to the number of barnyard grass plants (N_w). The damage coefficient (d_w) characterizes the apparent yield loss caused by the first weed plant added to the crop. Fitted equation: $Y_{cw}/Y_{cc} = 1/(1 + 0.044N_w)$.

12.2.3 Use in decision-support systems for weed control

Equation 48 can be used to predict the expected crop yield loss from the observed number of weed plants, and this prediction may be used in deciding whether a control measure is required. Counting the number of weed plants, however, takes time. Moreover, the relationship between crop yield loss and plant number of the given weed species varies between sites. This variation is thought to be primarily caused by the difference in time of emergence of crop and weed, which varies with the condition of the seed bed. Furthermore, within the same field, a species shows considerable variation in plant size; the big plants are more effective in competition than the small ones.

A better measure for the size of the weed infestation is derived as follows. The competitive ability of a species in mixture is strongly determined by its leaf area at the moment inter-plant competition starts (Subsection 12.3.3). Spitters & Aerts (1983) concluded, therefore, that the leaf area index of a weed species (L_w) early in the season, relative to that of the crop (L_c), will be a better action criterion for weed control than plant number. It can be derived that in Equation 48, N_w has to be replaced by L_w/L_c and the damage coefficient has to be expressed on a leaf area basis. This new damage coefficient $d'_w = d_w N_c 'L_c / L_w$, where $'L_c$ and $'L_w$ are the initial per-plant leaf areas of crop and weed, respectively. During early growth, the ratio L_w/L_c usually changes relatively little because differences in early leaf area are mainly caused by differences in starting position rather than by differences in relative growth rate (Equation 57). Use of the total leaf area index for each

species accounts for the large variation in plant size within the species and for the difference in time of emergence between the species.

In the aforementioned experiment, 50% plant emergence of maize was two days later than that of barnyard grass. Three weeks after emergence of maize, the ratio between the per-plant leaf areas of maize and barnyard grass was 5.4. Thus, at the density of 11 maize plants per m², the value of 0.044 m² plant⁻¹ for the damage coefficient (Figure 77) can be replaced by a value of $11 \times 5.4 \times 0.044 = 2.6$ on a leaf area basis.

A practical measure of the effective leaf area of a species is its percentage of ground coverage. This can be estimated visually; or more precisely from photographs taken vertically above the vegetation or by viewing the vegetation through a frame divided into a large number of gridsquares and counting the gridsquares that are more than half-filled by the species (Burstall & Harris, 1983; Steven et al. 1986). Ground coverage of the weed species, relative to the crop, can be monitored in the field and can be the basis for a decision-support system for weed control (Feyerabend et al., 1976; Marx, 1980).

12.2.4 Dynamics of soil seed population

Weeds are not only controlled to minimize their negative effects in the current crop, but also to anticipate for these effects in the future crops. This type of strategic control is directed towards minimization of the soil population of weed seeds.

A simple model to keep track of the seed bank of an annual weed is depicted in Figure 78. The seed population is depleted annually by a fraction of P_g . A fraction P_e of the removed seeds succeed in establishing, and the established plants produce S_n seeds per plant, a fraction P_b of which is incorporated in the soil seed population. Thus, the net annual increment of the seed population is

$$\Delta n_t = (-P_g + P_g \cdot P_e \cdot S_n) \cdot n_t \quad \text{Equation 49}$$

The early models of seed population dynamics of arable weeds assumed a constant seed production per plant, i.e. a constant value of S_n , irrespective of weed density (Cussans & Moss, 1982; Murdoch & Roberts, 1982; Wilson et al., 1984). Use of Equation 46, however, introduces the effect of weed density on the seed production per plant and, moreover, it gives an estimate of the concomitant yield reduction of the crop (Spitters & Aerts, 1983; Firbank et al., 1984).

To obtain a measure more or less independent of the fertility level of the site, weed seed production is expressed relative to the apparent maximum number of seeds produced per m², when grown in competition with the crop

$$Y_{wc}/Y_{wc}(N_w = \infty) = c \cdot N_w / (1 + c \cdot N_w) \quad \text{Equation 50}$$

where $c = b_{ww} / (b_{w0} + b_{wc} N_c)$ and $Y_{wc}(N_w = \infty) = 1/b_{ww}$. The influence of a second weed species (x) is introduced by expanding the denominator of the expression for c by the term $b_{wx} N_x$. In Equation 50, Y is expressed in number of seeds produced

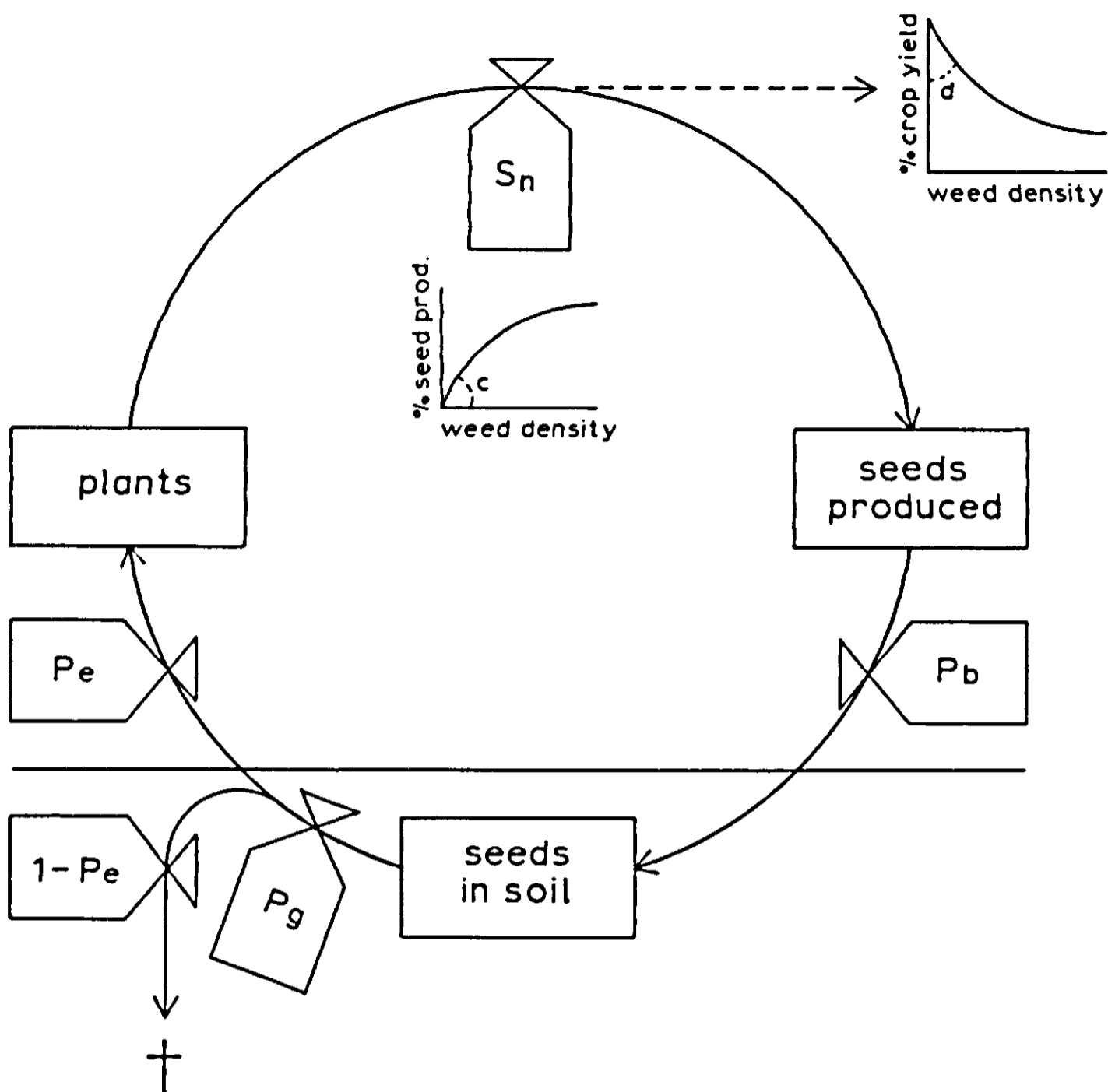


Figure 78. A flow diagram for the population cycle of an annual weed. The boxes represent state variables (numbers m^{-2}); P_g , P_e and P_b are fractions of depletion, seedling emergence, and seed burial, respectively (yr^{-1}); S_n is the number of seeds produced per plant.

per m^2 , rather than in biomass, by taking into account the seed/biomass ratio of the weed and the average seed weight. The parameter c characterizes the initial slope of the density response and c/b_{ww} the seed production per plant at low weed density in the crop. Actual weed seed production is estimated by multiplying Equation 50 by the apparent maximum seed production ($1/b_{ww}$), which is set proportional to the predicted or observed weed-free crop yield.

Parameter values typical for wild oat (*Avena fatua* L.) in barley are $P_g = 0.68$, $P_e = 0.15$, $P_b = 0.60$, $c = 0.00124$, $d = 0.00116$, $1/b_{ww} = 30120$ seeds m^{-2} at a weed-free yield level of 5000 kg ha^{-1} (85% d.m.) (references in Spitters, 1989). In Figure 79, the effect of a post-emergence herbicide, killing 95% of the emerged weed plants, is illustrated in relation to the application frequency. In this situation, controlling wild oat once every second year restricted yield losses to 5% or less. Such a control strategy would then be sufficient because with yield benefits of less than 5%, the benefits of the application usually do not outweigh the cost. The long-term population dynamics are, however, sensitive to the percentage of weed plants surviving the control measure. This also stresses the importance of reliability of control, particularly to avoid control failures, as was shown by Vleeshouwers & Streibig (1988).

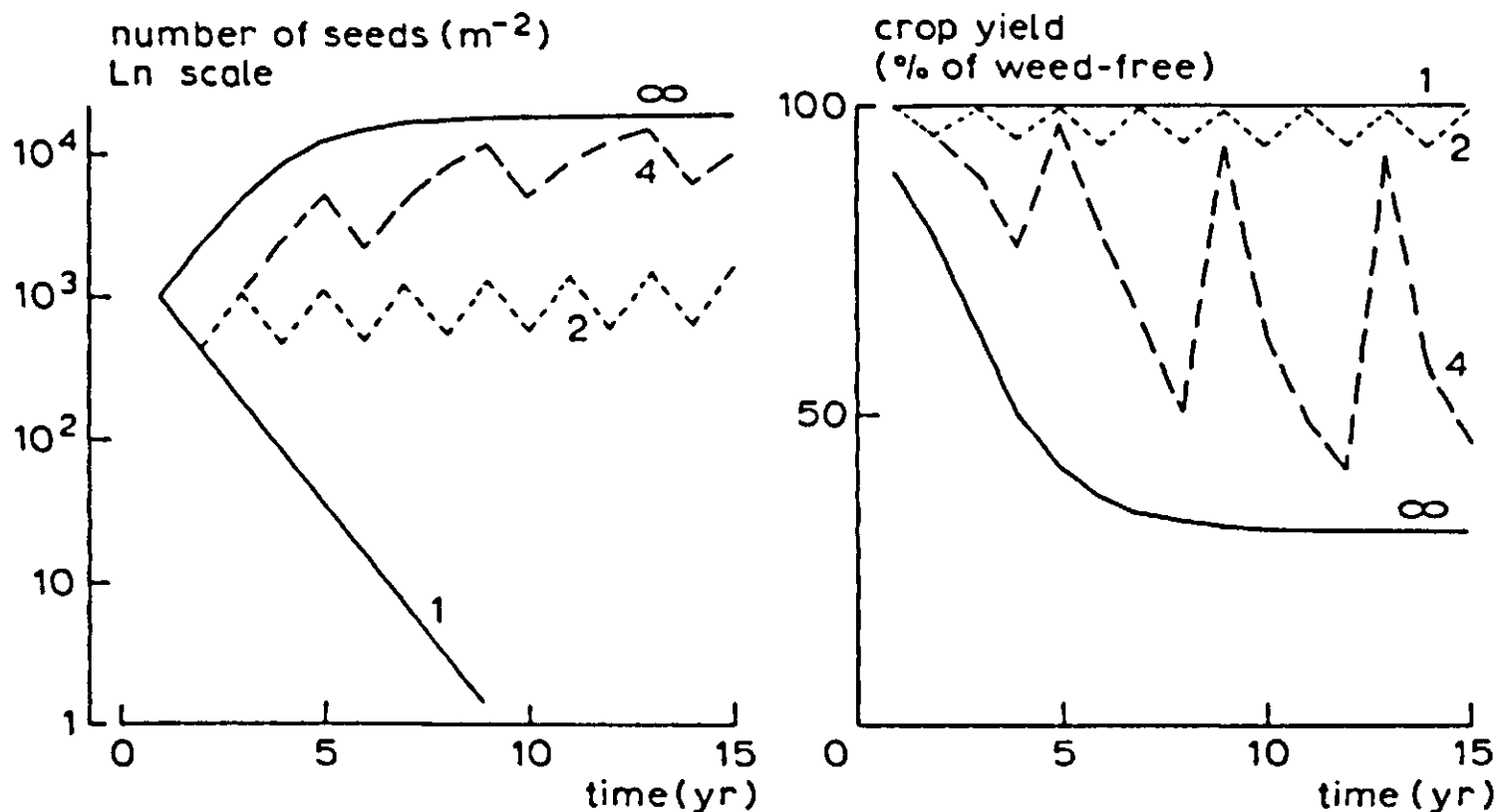


Figure 79. Simulated time course of soil seed population of wild oat, and the concomitant yield loss of spring barley. Herbicides were applied either annually, once every 2 or 4 years, or not at all. Herbicide application killed 95% of the weed plants.

12.3 The eco-physiological approach

Inter-plant competition can be defined as that interaction between the plants in which they restrict each other's growth by capturing growth-limiting resources from one another. Weeds reduce crop yield mainly because they absorb light, water and nutrients that would otherwise be used for crop growth. The competition process can therefore be described in terms of the distribution of the growth-limiting factors over the species in mixture and the way each species uses the amounts acquired in dry matter production. I will illustrate this eco-physiological approach with a very simple model of competition for light (Figure 80; Spitters, 1984). More detailed simulation models have been published elsewhere (Spitters & Aerts, 1983; Spitters, 1989).

12.3.1 A very simple model of competition for light

The growth rate of a canopy is more or less linearly related to its light interception (review by Gosse et al., 1986). Since light interception is exponentially related to total leaf area, the growth rate of the canopy is

$$\Delta Y = (1 - \exp(-k \cdot L)) \cdot PAR_0 \cdot E \quad \text{Equation 51}$$

in which ΔY is the daily growth rate ($\text{g m}^{-2} \text{d}^{-1}$), L the leaf area index ($\text{m}^2 \text{ leaf m}^{-2} \text{ ground}$), k the extinction coefficient, E the average light utilization efficiency (g d.m. MJ^{-1}), and PAR_0 the incoming photosynthetically active radiation ($\text{MJ m}^{-2} \text{d}^{-1}$). Incoming PAR (wave bands 400-700 nm, 'light') amounts to 50% of total incoming solar radiation (300-3000 nm).

In a mixture of identical species, each species intercepts an amount of light that

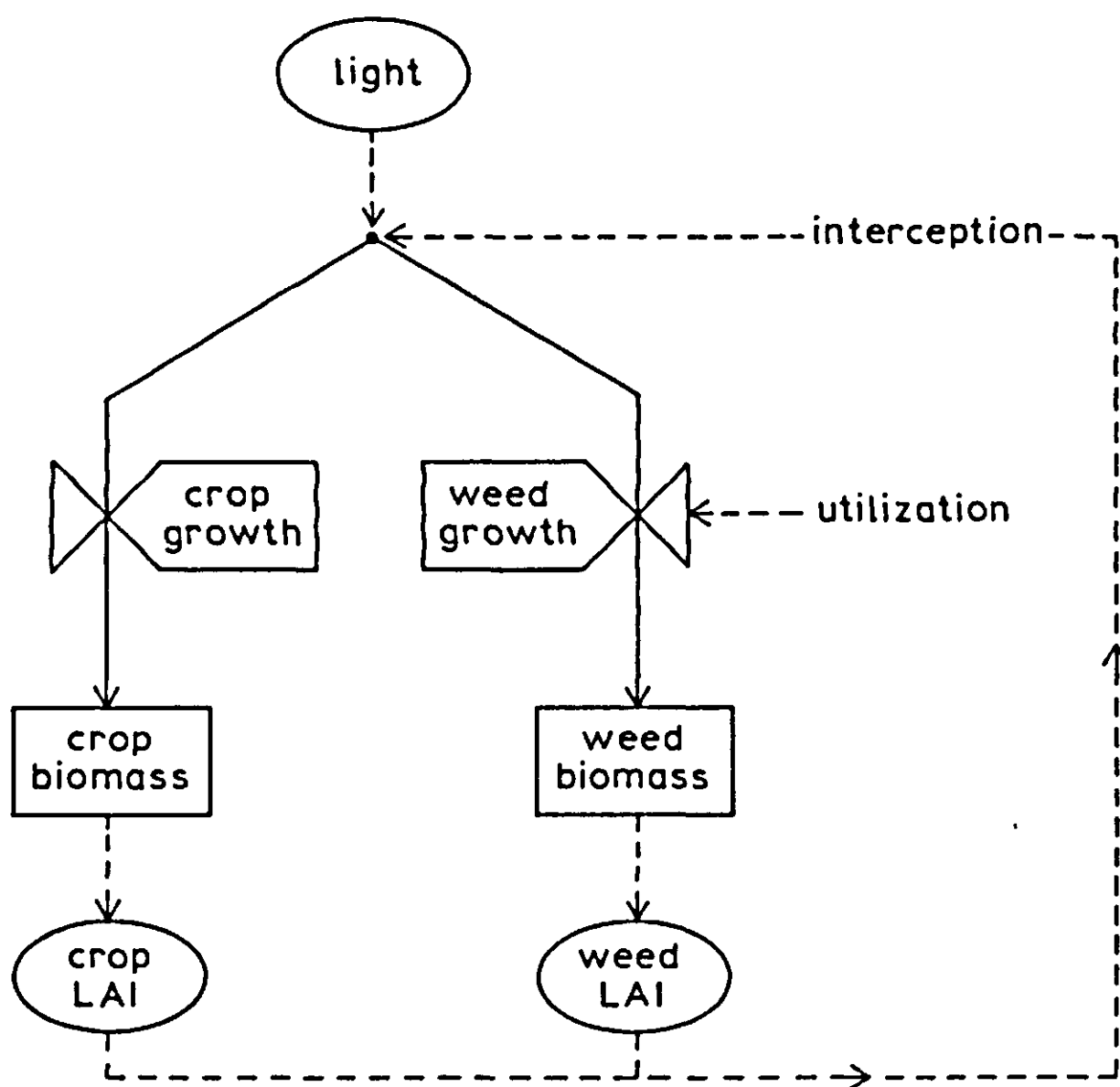


Figure 80. Simplified scheme for the simulation of competition between crop and weed for light.

is proportional to its share in the total leaf area. Following the proportionality between growth and light interception, Equation 51 gives for the growth rate of Species 1 in mixture with Species 2

$$\Delta Y_1 = \frac{L_1}{L_1 + L_2} (1 - \exp(-k \cdot L_1 - k \cdot L_2)) \cdot PAR_0 \cdot E_1 \quad \text{Equation 52}$$

where the subscripts refer to Species 1 and 2, respectively.

The share of a species in total growth increases, however, when it intercepts more light per unit of leaf area. This is achieved with a greater extinction coefficient, e.g. because of a more horizontal leaf angle distribution, and with a greater plant height. In the distribution term of Equation 52, the leaf areas are then weighted according to their respective light absorption. In a mixture of short and tall species, the light interception is set proportional to the light intensities at half of the plant heights. For Species 1

$$\Delta Y_1 = \frac{l_1 \cdot k_1 \cdot L_1}{l_1 \cdot k_1 \cdot L_1 + l_2 \cdot k_2 \cdot L_2} (1 - \exp(-k_1 \cdot L_1 - k_2 \cdot L_2)) \cdot PAR_0 \cdot E_1 \quad \text{Equation 53a}$$

Assuming the leaf area of a species evenly distributed over its plant height (Figure 81A) gives the following for the relative light intensity of Species 1 at half of its height (H_1)

$$l_1 = \exp(-\frac{1}{2}k_1 \cdot L_1 - \frac{H_2 - \frac{1}{2}H_1}{H_2} k_2 \cdot L_2) \quad H_2 > \frac{1}{2}H_1 \quad \text{Equation 53b}$$

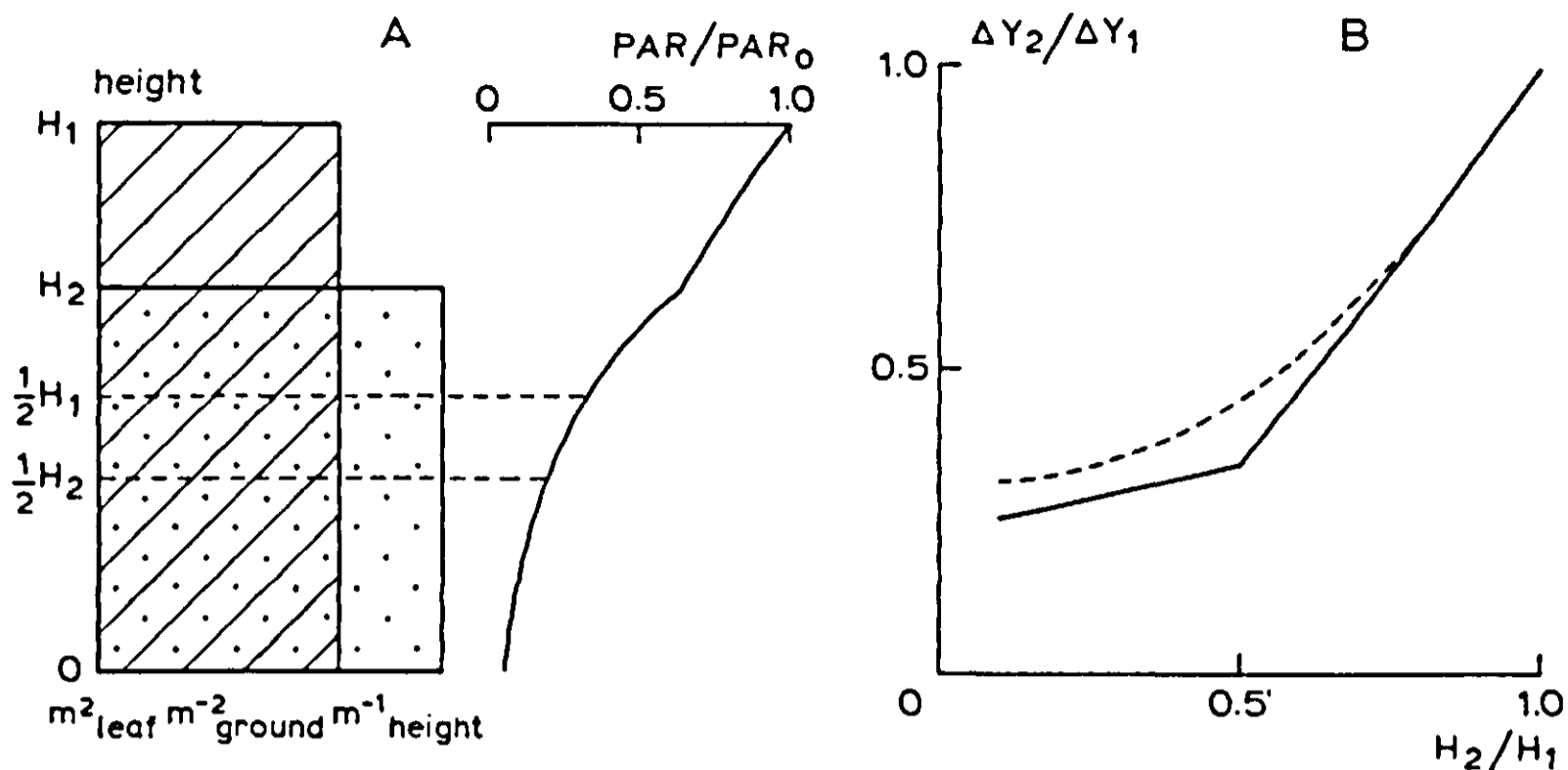


Figure 81. Schematic representation of the summary model of competition for light. A: In the summary model, the share of each species in total light interception is assumed to be proportional to its leaf area, weighted by the light intensity at half of its plant height. This intensity is calculated from the exponential light profile (PAR/PAR_0), assuming a uniform distribution of leaf area over plant height (H) for each species. B: The ratio between the growth rates of the two species in mixture ($\Delta Y_2/\Delta Y_1$) simulated by the summary model (solid curve) and by a detailed model (dashed curve). Each of the two species had a leaf area index of 2.

Compared with a detailed model of competition for light, Equation 53 gave a good approximation (Figure 81B).

In the detailed approach to competition for light, the light profile within the canopy is simulated and light utilization is calculated for each canopy layer separately (Figure 82; Spitters & Aerts, 1983; Spitters 1989). For that, the canopy is stratified into various, horizontal height layers. The illumination intensity at the various heights is derived from the exponential light profile. This is done for sunlit and shaded leaf area separately, taking into account the profiles of both the diffuse and direct light flux. From the photosynthesis–light response of individual leaves, the rate of CO_2 assimilation per unit leaf area is calculated for each species and for each layer separately. Multiplication by the leaf area of the species in the layer gives its assimilation rate in that layer. Summation over the various canopy layers and over the hours within the day gives the daily assimilation rate of each species in the mixture. After subtraction of respiration losses, the daily growth rates are obtained.

In the simple model, leaf area is calculated by multiplying the accumulated biomass at time t (Y_t) by the leaf area ratio (LAR_t , $m^2 g^{-1}$) at that time

$$L_t = LAR_t \cdot Y_t \quad \text{Equation 54a}$$

This assumes that leaf area growth is limited by dry matter growth. Before canopy closure, however, leaf area growth is usually restricted by the potential rates of cell division and expansion, which depend on temperature rather than on the

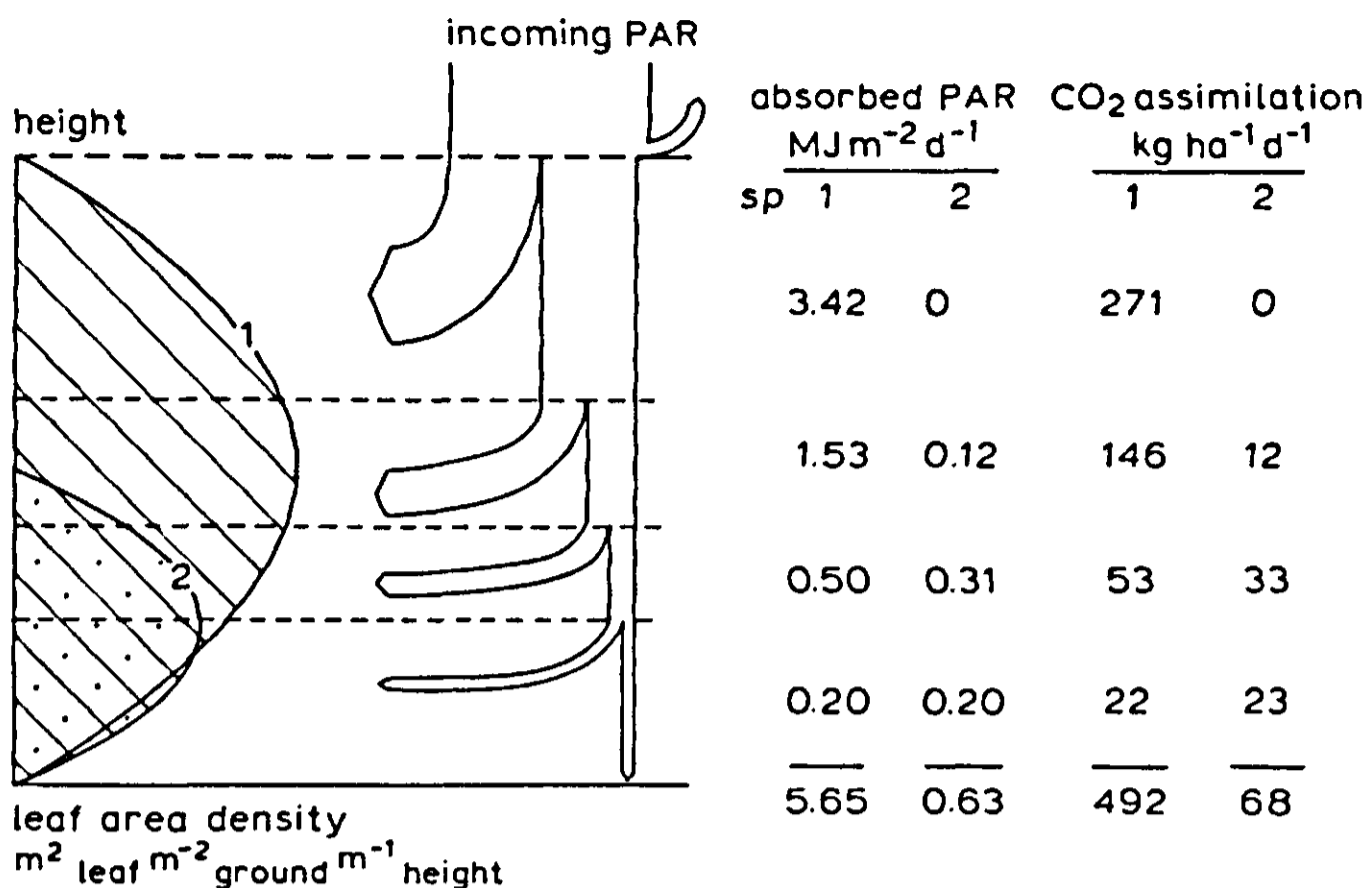


Figure 82. Schematized calculation of light absorption and CO₂ assimilation of a tall and a short species in mixture. In the simulation, calculations were performed for each of 20 horizontal canopy layers at selected moments of the day, and these results were accumulated to daily values for each of the four layers shown. The tall (1) and short (2) species had leaf area indices of 3 and 1, respectively. Incoming *PAR* was 7.07 MJ m⁻²d⁻¹.

supply of photosynthates. In this early phase, leaf area growth is more or less exponential. As will be discussed later, the competitive ability of a species is strongly determined by its early growth. Therefore, a more accurate procedure is followed in which leaf area is assumed to increase exponentially until the beginning of mutual shading at a total *LAI* of 0.75

$$L_t = N \cdot L_0 \cdot \exp(R \cdot t) \quad L_1 + L_2 < 0.75 \quad \text{Equation 54b}$$

where *N* is the plant density (plants m⁻²), *L*₀ the apparent leaf area per plant at emergence (m² plant⁻¹) found by logarithmic extrapolation of leaf area data, *R* the relative growth rate of leaf area (m² m⁻² d⁻¹) and *t* the time in days after plant emergence.

The relative growth rate (*R*) is strongly affected by temperature and the early growth is therefore described with time expressed in accumulated degree-days rather than in days. Both leaf area ratio (*LAR*) and plant height (*H*) are a function of phenological development, which is mainly driven by temperature. Both are therefore given as a function of degree-days after emergence. Under adequate moisture supply, germination and plant emergence are also approximately linearly related to temperature. Germination of weeds is triggered by soil cultivation, and thus weed emergence is calculated by a certain temperature sum after last cultivation, i.e. seedbed preparation. Crop emergence is calculated from sowing date, using a fixed temperature sum.

In the detailed model, the total daily growth rate is partitioned to leaves, stems,

roots and storage organs, according to keys that are a function of the development stage of the species. Leaf area growth is calculated from the dry weight increment of the leaves and the specific leaf area of the new leaves, and the decrease in leaf area as a result of senescence is also taken into account. Simulation of specific leaf area and senescence rate in response to shading need special attention, because leaf area is of paramount importance for competitive ability, including during full ground coverage (Equation 52). Simulation of early leaf growth is further improved by calculating leaf area per plant from leaf appearance rate and the final size of the successive leaves (e.g. Sinclair, 1984).

In the simple model, crop yield is obtained by multiplying the simulated final biomass of the crop by a fixed harvest index, which is the ratio between the yield of the desired plant organs and the total biomass.

In the foregoing, competition for light was discussed. Stress conditions are accounted for by using a multiplication factor for the light utilization efficiency (E). The multiplication factor takes a value between 0 and 1, depending on the degree of stress. Many models have been published to describe the effect of drought and nutrient shortage on crop growth. Most of the simple approaches can easily be attached to the competition model to describe the growth reduction of the mixed stand as a whole. However, when soil moisture or nutrients are in short supply, uptake of these elements by an individual species in the mixture will be related to that species' share in total root length. When the competing species differ markedly in their leaf area to root length ratio it is especially important to account for these differences, elsewhere (Spitters, 1989) a simple model was presented for this.

If the nature of the stress is unknown, the light utilization efficiency may be calibrated against the observed or expected yield level of the crop.

The various versions of the model have been validated against results from field experiments with mixed stands of maize and barnyard grass (Spitters & Aerts, 1983; Spitters, 1984), and sugar beet and fat hen (Kropff, 1988).

12.3.2 Sensitivity analysis

The model described above can be used to illustrate the effect of various morpho-physiological attributes on the competitive ability of a species. For this, two isogenic species were assumed to grow in an $\frac{1}{2} : \frac{1}{2}$ mixture and in monoculture. Total stand density was 200 plants m^{-2} , and both species started with a leaf area of 1 cm^2 per plant at emergence. The relative growth rate of leaf area during the juvenile phase was $0.15 d^{-1}$, while the leaf area ratio decreased linearly from a value of 150 cm^2 leaf area per g plant weight at emergence to zero at full ripeness, 100 days after emergence. The light extinction coefficient was 0.7 and the light utilization efficiency was 3 g of dry matter formed per MJ of intercepted light. Plant height increased from 1 cm at emergence to 1 m, 80 days later. Incoming PAR averaged $8 MJ m^{-2}d^{-1}$.

In subsequent simulation runs one attribute value for the first species was

increased by 20%, so that in any run the species differed in only a single characteristic. Only LAR and R were simultaneously changed. To study the effects of fertility level, the simulations were also performed for an environment with a 20% higher light utilization efficiency.

The results of the sensitivity analysis are depicted in Figure 83. All attributes affected the yield of the species much more when it was grown in mixture than when it was grown in monoculture. In mixture, the advantage of a 20% greater leaf area at plant emergence was maintained over the whole growing period, whereas in monoculture it had a much smaller effect. In mixture, the biomass production of a species increased disproportionately after increasing its light absorption per unit leaf area – either by having taller plants or a greater extinction coefficient – or after increasing its utilization of the absorbed light, or its leaf area formed per unit plant weight.

The 20% increase in fertility level of the site resulted in a 27% higher yield for the reference crop. In contrast to this large effect on total production, the competitive relations were hardly influenced (Figure 83). Only the effect of plant height became more pronounced as a result of increased shading, invoked by a greater total leaf area index.

In the next section the effects will be explained using the classical growth analysis.

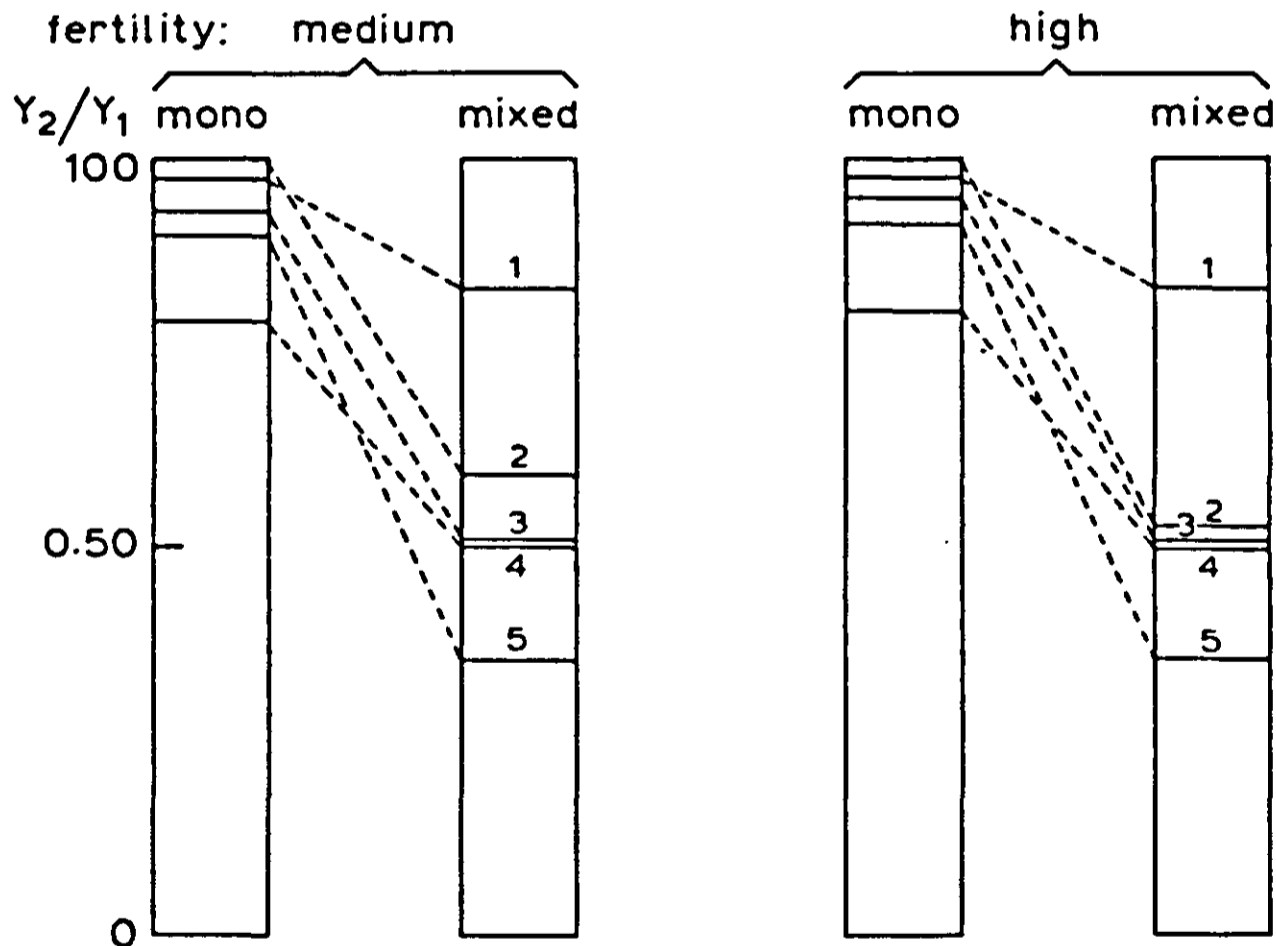


Figure 83. Simulated effect of single attributes on the ratio in biomass production of two isogenic species (Y_2/Y_1), grown at two fertility levels in monocultures and in mixture. For Species 1, the attribute in question was enhanced to a value of 120% of that of Species 2. Attributes: 1) initial leaf area per plant, 2) plant height, 3) extinction coefficient, 4) light utilization efficiency, 5) leaf area ratio. The simulated biomass yields of the reference type in monoculture were 15.6 and 19.8 t ha⁻¹ under medium and high fertility, respectively.

12.3.3 Classical growth analysis

In experiments to study the growth pattern, the stand is normally harvested at intervals and at each harvest, leaf area is measured and the dry weights of the various plant organs are determined. Apart from using a simulation model to analyse the experimental results, we can partition the observed growth rates into various components. In the classical growth analysis the relative growth rate is considered; it is defined as the dry matter increment (dY/dt) per unit of biomass present (Y). This relative growth rate (RGR , in $g g^{-1} d^{-1}$) is split up into the growth rate per unit leaf area (net assimilation rate, NAR in $g m^{-2} d^{-1}$) and the leaf area to plant weight ratio (leaf area ratio, LAR in $m^2 g^{-1}$)

$$RGR = NAR \cdot LAR \quad \text{Equation 55}$$

The leaf area ratio is partitioned into the fraction of total dry matter allocated to the leaves (leaf weight ratio, LWR in $g g^{-1}$) and the leaf area per unit leaf weight (specific leaf area, SLA in $m^2 g^{-1}$)

$$LAR = LWR \cdot SLA \quad \text{Equation 56}$$

This approach is only sensible when growth rate is proportional to leaf area; NAR being the proportionality factor. This is approached during the juvenile phase when plants are still standing free and light interception is proportional to leaf area. It does not hold when the foliage fully covers the ground. Incoming light is then fully intercepted and additional leaf area does not contribute to additional light interception. Then, growth rate per unit ground area, rather than growth rate per unit leaf area, tends to be constant. When studying crop growth, therefore an analysis in terms of light interception per unit ground area and growth per unit intercepted light (Equation 51) should be used, rather than the classical growth analysis. In mixture, however, the growth rate of a species tends to be proportional to its leaf area over the entire period of growth (Equation 52) and so the classical growth analysis is appropriate.

In Figure 84, the simulation results obtained with the simple model described above are presented. In the first situation (solid curves), the species were only differentiated in their starting position. On a logscale, the distance between the curves remained the same over the whole growth period (Figure 84A), i.e. the biomass ratio of the species (Y_1/Y_2) was constant. Consequently, the absolute difference ($Y_1 - Y_2$) increased rapidly in time (Figure 84B).

The leaf area at an early time t is defined by the exponential equation

$$L_t = N \cdot L_0 \cdot \exp(R \cdot (t - t_e)) \quad \text{Equation 57}$$

Thus, a species acquires a favourable starting position by having a large plant number (N), a great apparent leaf area per plant at emergence (L_0), a high relative growth rate of leaf area during the juvenile phase (R), and an early emergence (t_e). For instance, in an isogenic mixture, an advantage in emergence of only a single day will give, at $R = 0.15 d^{-1}$, a 16% better starting position and so a 16% greater

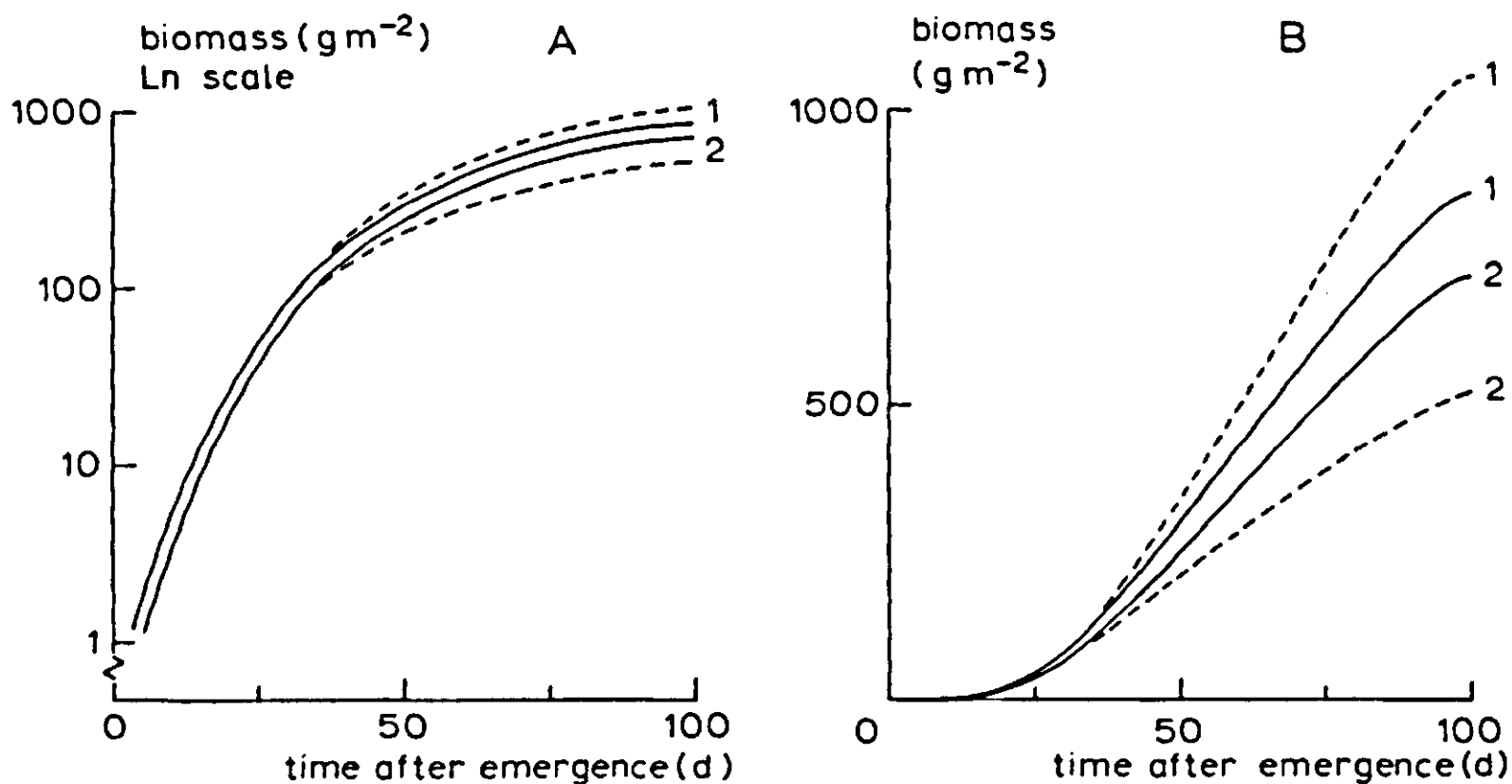


Figure 84. Seasonal course of simulated biomass of two species growing in mixture. Species 1 started with a 20% greater leaf area than Species 2, and was either of the same height (solid curves) or 20% taller (dashed curves) than Species 2.

final yield. This emphasizes the paramount importance of the starting position for the competitive ability of a weed and the importance of accurate initialization in competition models.

In the second situation (dashed curves in Figure 84), the species were also differentiated in plant height. On logscale, the distance between the curves changed with time, indicating a shift in the biomass ratio (Y_1/Y_2) and thus differences between the species in relative growth rate (RGR). From the exponential growth equation it can be derived that the change in Y_1/Y_2 over the time interval Δ equals

$$\frac{Y_{1t+\Delta}/Y_{2t+\Delta}}{Y_{1t}/Y_{2t}} = \exp((RGR_1 - RGR_2) \cdot \Delta) \quad \text{Equation 58}$$

This enables analysis of changes in relative abundance in mixture in terms of the growth analysis components RGR , NAR and LAR (Equation 55).

The net assimilation rate can be partitioned into the light absorption per unit leaf area ($\text{MJ m}^{-2}\text{d}^{-1}$) and the efficiency with which the absorbed light is used for dry matter production (g MJ^{-1}). In mixture, a greater light absorption per unit leaf area is achieved with a greater plant height, because light intensities are greater at the top of the canopy, and with a foliage architecture such that a greater extinction coefficient is obtained. More efficient use of the absorbed light can be the result of a greater photosynthetic capacity of the leaves and a smaller whole-plant respiration rate per unit leaf area. A greater LAR is obtained with a relatively greater allocation of assimilates to leaves (LWR) and with thinner leaves (SLA).

In conclusion, if the species do not differ in relative growth rate, their relative differences in mixture will be maintained over time. Differences in RGR , invoked by variation in morpho-physiological characteristics, change the relative abun-

dances of the species in mixture. The fertility level of the site primarily affects the total production of the vegetation, but in agricultural situations it has a much smaller effect on the inter-species distribution of the dry matter produced.

12.4 What kind of model should be used?

Two types of competition models have already been discussed: the regression models in which the competition effects are described by some empirical equation; and the mechanistic, simulation models in which the competition process is explained from the underlying eco-physiological principles.

Skoog's statement (1955, cited by Loomis et al., 1979) that 'we can claim to understand the plant when we can express it all in a mathematical model' is an incentive to develop very comprehensive models. Constructing such physiologically detailed competition models is primarily a way of doing research. For people other than the modeller himself and perhaps an inner circle of colleagues, the detailed model tends, however, to be a black box, whose simulation results cannot be verified and, therefore, do not convince. To achieve a wider application, we would probably do better to follow Simberloff & Boecklen (1981, p. 1224), who stated that a more complicated theory is a *panchreston*, a concept that, by attempting to explain everything, explains nothing. In terms of Ockham's razor: 'multiplicity ought not to be posited without necessity' (William of Ockham, 14th century). Indeed, the simple model for light competition already clarified the main principles of competitive interaction between plants. The simple physiological approach may also offer a frame to analyse the results of competition experiments; the model version that is to be used must be adjusted according to the aims of the researcher. The regression approach can also be useful in this respect, as it summarizes the observed experimental results with a minimum number of parameters.

A weak point of the physiological models is usually their lack of precision. They contain many functions and parameters, each having its own uncertainty. These errors accumulate in the simulated final crop yield. Practical weed management, however, requires reliable predictions, deviating from the actual yields by not more than a few per cent. The regression models seem to be better suited for this purpose, in particular when their variables have a causal basis, and their parameters are estimated from many experiments carried out in the conditions under which the model has to perform.

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