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COMPETITION FOR RESOURCE CAPTURE IN AGRICULTURAL CROPS

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Introduction

Interplant competition for capture of the essential resources for plant growth i.e. light, water and nutrients, strongly affects the performance of natural, semi-natural and agricultural ecosystems. Ecologists have studied competition to understand the diversity and stability of plant communities, succession patterns of vegetation, and to help define management strategies for semi-natural ecosystems. Agroecologists have studied competitive phenomena to optimize plant densities of crops, to optimize intercropping systems and to quantify crop–weed interactions to improve weed management systems with minimum herbicide inputs. Similar approaches have been used to study interplant competition in natural and disturbed systems. However, because of the complex nature of interplant competition, it has taken a long time to develop generalized concepts and theories.

The first systematic approaches for studying competitive phenomena were developed in the 1960s. For monocultures, much of our current understanding is based on the work of a Japanese group (e.g. Shinozaki and Kira, 1956) whereas de Wit (1960) developed the first systematic approach to study competition in mixtures. He introduced an experimental design (the replacement series in which the mixing ratio varies, but total density remains constant) with a model to analyse the results. These approaches were based on a hyperbolic relationship between plant density and yield, and have been used extensively in agricultural and ecological sciences to study competition between plants, plant population dynamics, and component contributions of intercropping systems (see reviews by Trenbath, 1976; Harper, 1977; Radosevich and Holt, 1984; Grace and Tilman, 1990). Recently, several papers discussed the disadvantages and pitfalls of the replacement series approach, such as its total density dependence (cf. Connolly, 1986; Taylor and Aarssen, 1989). Only in the early 1980s, approaches were developed to describe competition over a range of population densities with varying mixing ratios and at a range of total densities, generally also based on the hyperbolic yield–density relationship (Suehiro and Ogawa, 1980; Wright, 1981; Spitters, 1983a, b; Cousens, 1985; Spitters, Kropff and de Groot, 1989). Similar approaches have been developed using the neighbourhood approach, in which the number of neighbours of an individual plant in a predefined area is related to the weight of the central plant (Silander and Pacala, 1985; Firbank and Watkinson, 1987; Pacala and Silander, 1987). However, a great deal of plant size frequency remains unexplained by the spatial arrangement of the plants alone (Firbank and Watkinson, 1990). All these approaches have a phenomenological character: the outcome of competition is described at a given moment, but no explanation is given of the process. The extrapolation domain of these descriptive approaches is often limited; they only account for the effect of plant density on the competition process. This results in a variation of model parameters from year to year and site to site (Firbank and Watkinson, 1990). Also, these descriptive approaches cannot help identify the mechanisms for evolution of species traits or for the structure and dynamics of populations, communities and ecosystems (Tilman, 1988), and they cannot help in explaining the mechanisms for variation in competition effects between seasons and sites (Kropff, 1988).

In the 1980s, more mechanistic approaches were developed to quantify interplant competition by taking into account the temporal dynamics of competition. Spitters and colleagues developed ecophysiological models for interplant competition, based on ecophysiological models for monoculture crops (Spitters and Aerts, 1983; Kropff *et al.*, 1984). They focussed on competition in weedy crop situations. Several other groups developed similar approaches to quantify crop–weed interactions (Graf *et al.*, 1990; Ryel *et al.*, 1990; Wilkerson *et al.*, 1990), competition between grassland species (Rimmington, 1984), and competition in row crops (Hodges and Evans, 1990). In ecology, mechanistic models for interplant competition have been developed with a focus on competition for nutrients and succession in more complex semi-natural plant communities (e.g. Tilman, 1988; Berendse, 1985). In these long-term studies, the approach is vastly different from the approach taken in the crop–weed interaction studies where instantaneous processes are taken into account.

The actual mechanisms of competition for resource capture by plants are complex. Plants are morphologically and physiologically extremely plastic in their response to their environment, making generalization of plant responses difficult. This chapter reviews currently used approaches to the quantification of effects of interplant competition in monoculture crops, intercrops and weedy crops. Available descriptive as well as mechanistic approaches will be discussed.

Approaches to describe the effect of competition on resource capture in agricultural crops

COMPETITION WITHIN MONOCULTURES

Competition in monocultures has been studied extensively by agronomists conducting density experiments to optimize harvestable yield and minimize seed inputs in the system. Montgomery (1912, cited by de Wit, 1960) reported the yield density response of oats, showing that yields increased with reduced spacing until a maximum yield level was reached. In the 1960s, a group of Japanese scientists identified the major effects of competition in monocultures and developed approaches to mathematically describe relationships that appeared to be consistent (Kira, Ogawa and Sakazaki, 1953; Shinozaki and Kira, 1956; Yoda *et al.*, 1963). They related plant size and plant survival (self-thinning) to competition effects as a result of differences in plant spacing. De Wit (1960) also discussed the issue of competition in monocultures, used the hyperbolic equation for the

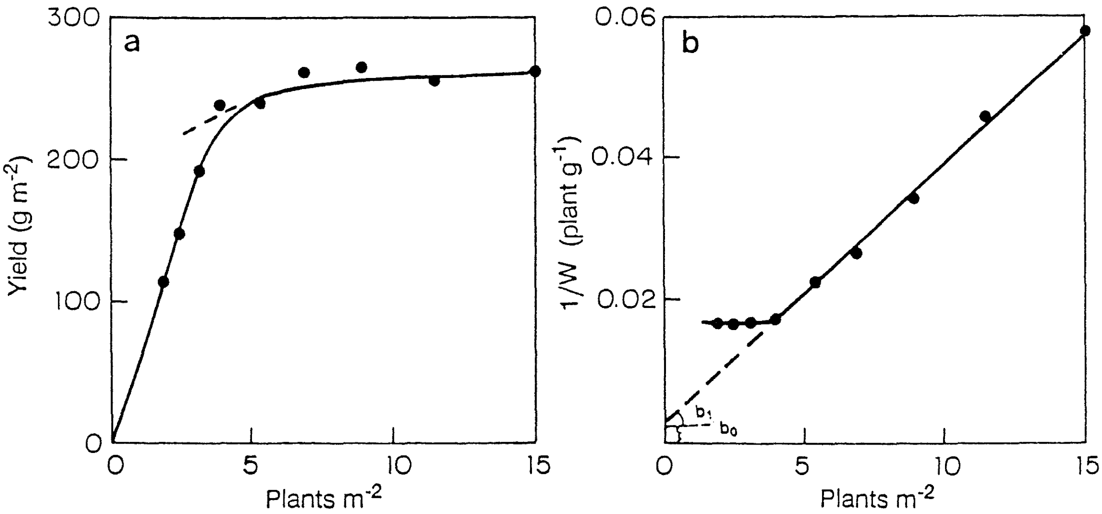

Figure 13.1 Density response of maize. Plots of (**a**) biomass per unit area and (**b**) the reciprocal of per-plant weight versus plant density. (After: Spitters, 1983a)

yield density response and discussed differences with the approach introduced by Shinozaki and Kira (1956). The most widely used approach to describe the density response is a rectangular hyperbola (e.g. Shinozaki and Kira, 1956; de Wit, 1960) (*Figure 13.1*):

$$Y = N \,/\, (b_0 + b_1 N) \qquad \text{(1a)}$$

where Y is the yield of the crop in monoculture in g m^{-2}, N is the plant density of the crop in numbers per square metre, and b_0 is the intercept and b_1 is the slope of the relationship between N/Y and N. The reciprocal per plant weight then is a linear function of plant density:

$$1/w = N/Y = b_0 + b_1 N \qquad \text{(1b)}$$

where w is the weight per plant (g plant^{-1}). The intercept b_0 is the reciprocal of the virtual biomass of an isolated plant. It deviates from the real biomass of and isolated plant, because at wide spacings, without interplant competition the biomass is density independent and does not decrease with density as the hyperbola suggests. This is illustrated in *Figure 13.1* where the relation between $1/w$ and density levels off at low densities. The parameter b_1 is the reciprocal of the maximum biomass per unit area e.g. the asymptote in *Figure 13.1a*.

This relationship can be used to describe the response of total dry matter production of crops to density reasonably well except for extremely low densities (Figure 13.2). For harvestable yield, however, a very narrow optimum density has been observed for several species. This is illustrated in *Figure 13.2* for some crops that respond differently (de Wit, van Laar and van Keulen, 1979). In cereals, seed yield and total dry matter production are constant over a wide range of densities in which the crop is able to form a closed canopy. These plants have the characteristics of a determinate growing point that terminates in an ear or panicle for every tiller that survives. Interplant competition determines

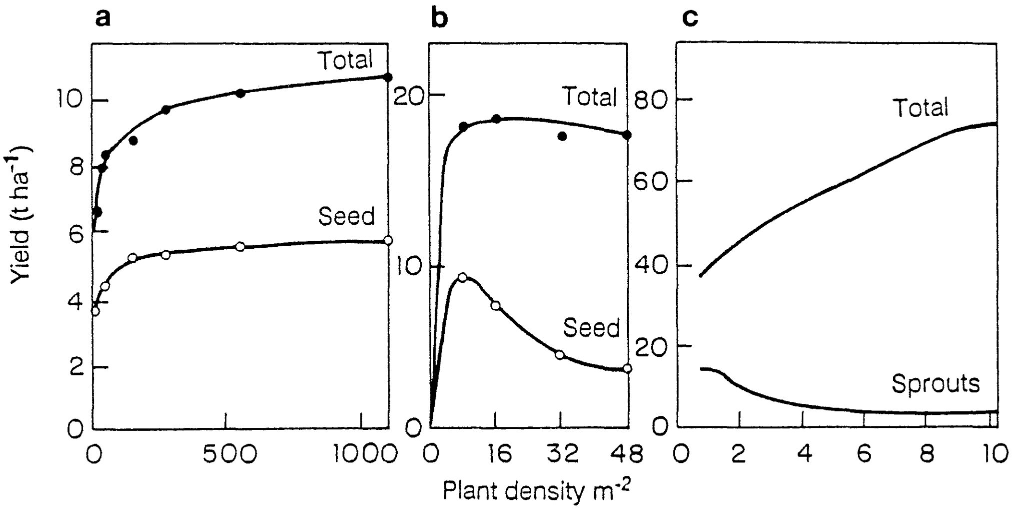

Figure 13.2 Relation between plant density and yield (total and harvestable) for barley (**a**), maize (**b**), and Brussels sprouts (**c**). (After: de Wit, van Laar and van Keulen, 1979)

tiller survival and not so much the size of the ears or panicles. Therefore, the number of tillers per unit of area in cereals is relatively constant over a wide range of densities (for wheat: Darwinkel, 1978; for rice: Yoshida, 1981). However, optimum spacing may differ between varieties. For rice it was found that early maturing varieties need a higher density than late maturing varieties to form a dense canopy (Yoshida, 1981).

In indeterminate plants such as Brussels sprouts, the growing point remains vegetative and the harvestable yield is formed by axillary leafy buds that have to reach an appropriate size. If interplant competition is too strong, the amount of resources captured by a single plant is too small to produce enough assimilates for the main and secondary growing points. For harvestable yield of Brussels sprouts, the optimum density is very low (almost free growing plants are needed), whereas total dry matter production per unit of area continues to increase with plant density, because the crop as a whole captures more resources. For maize, an intermediate situation has been observed. The cob emerges also from axillary buds, and when plant density is higher than the plant density needed to form a closed canopy for optimum resource capture, total dry matter production remains constant, but harvestable yield decreases (*Figure 13.2*). If the relationship between harvestable yield and density shows a maximum, an alternative model has to be used. Spitters (1983b) added a quadratic term to Equation 1:

$$1/w = b_0 + b_1N + b_2N^2 \qquad (2)$$

Watkinson (1980) introduced a power term to account for optimum shape of responses:

$$w = w_m \, (1 + aN)^{-b} \qquad (3)$$

where w_m is the weight of an isolated plant.

In plant monocultures, interplant competition may result in mortality of the least competitive plants. This phenomenon is known as self-thinning, which was first described by Yoda *et al.*, 1963. They found a close relationship between the number of plants per unit area that survived and the weight per plant. Their so-called 2/3 power law describes the dynamics of the system i.e. how density declines as mean weight per plant increases in a single stand in time. This relationship is intensively used in forestry, to determine thinning rates for tree stands, to optimize timber production. For a detailed discussion of these approaches refer to Firbank and Watkinson (1990).

Another aspect of competition in monoculture stands is the variation in individual plant size. Firbank and Watkinson (1990) showed evidence that the variability in individual plant weight increases with increasing density i.e. competition. Differences in individual plant weight and size are caused by differences in starting position of the individual plants (moment of germination, seed size) and genetic variation in growth parameters. In general, relative differences remain the same throughout the season.

COMPETITION IN INTERCROPPING SYSTEMS

Intercropping is intensively practiced in the tropics. These systems range from complex systems in which farmers fill up all space with crop plants that are needed for subsistence, to agroforestry systems, where tree species are combined with annual crop species. The most commonly used systems are: (1) mixed intercropping – growing two or more crops simultaneously, without a specific spatial arrangement; (2) row or strip intercropping – growing two or more crops simultaneously where one or more crops are planted in rows or strips; (3) relay intercropping – growing two or more crops simultaneously with only a partial overlap of the growing cycle.

The agronomic aspects of these systems have been thoroughly reviewed by Willey (1979a, b) and Vandermeer (1989). These systems can have several advantages over monoculture systems, of which the potential higher efficiency of resource use is the most important one studied. The advantage of intercropping over monoculture systems is generally expressed using the LER (Land Equivalent Ratio) (Willey, 1979a, b):

$$\text{LER} = Y_{1,\text{mix}}/Y_{1,\text{mono}} + Y_{2,\text{mix}}/Y_{2,\text{mono}} \quad (4)$$

where $Y_{1,\text{mono}}$ and $Y_{2,\text{mono}}$ are the yields of the species in monoculture and $Y_{1,\text{mix}}$ and $Y_{2,\text{mix}}$ are the yields in mixture. When LER=1, the same yields can be obtained with monoculture, using the same area of land. When LER>1 a larger area of land is needed to produce the same yields in monocultures as in the mixture. Often LER values are reported that are much higher than 1 (Willey, 1979a, b). However, in these standard mixed cropping trials, the individual crops in mixture are grown at the same density as in the respective monocultures. In many situations where high values for LER are reported, the advantage could therefore also be obtained by growing the crop in monoculture at a higher density. The replacement series approach developed by de Wit (1960), is much more suitable to address questions related to the real yield advantage of intercropping over monoculture cropping. The relative total density is the same in mixtures and monocultures.

The yield of a species is expressed relative to its yield in monoculture. The sum of the relative yields is the RYT (Relative Yield Total). If RYT>1, there is a true advantage of mixed cropping. However, in the replacement series design, some pitfalls exist as well (Connolly, 1986).

An alternative approach was developed by Spitters (1983a, b). This approach starts from the same principles as the approach of de Wit (1960). The starting point in the derivation of the model is the response of crop yield to plant density, which can be described by a rectangular hyperbola (Equation 1). The effect of other species can be introduced in this equation in an additive way (Suehiro and Ogawa, 1980; Wright, 1981; Spitters, 1983a):

$$Y_{12} = N_1 / (b_{10} + b_{11}N_1 + b_{12}N_2) \quad (5a)$$

The reciprocal per plant weight then equals:

$$1/w_1 = b_{10} + b_{11}N_1 + b_{12}N_2 \quad (5b)$$

where Y_{12} is the yield of species 1 in a mixture with species 2, and N is the number of plants. The parameter b_{11} measures intraspecific competition between plants of species 1 and the parameter b_{12} measures interspecific competition effects between the species. A similar equation can be derived for species 2. *Figure 13.3* demonstrates the shape of such a relationship for groundnut and maize (Spitters, 1983a). This approach allows the analysis over a range of total densities and mixing ratios. The parameter values can be used to derive indices for the relative competitiveness of the species (b_{12}/b_{11}) and niche differentiation: If the ratio $(b_{11}/b_{12})/(b_{21}/b_{22})$ exceeds unity, there is niche differentiation and a RYT>1, indicating that the mixture as a total captures more resources than the respective monocultures. This can be the case when species have different

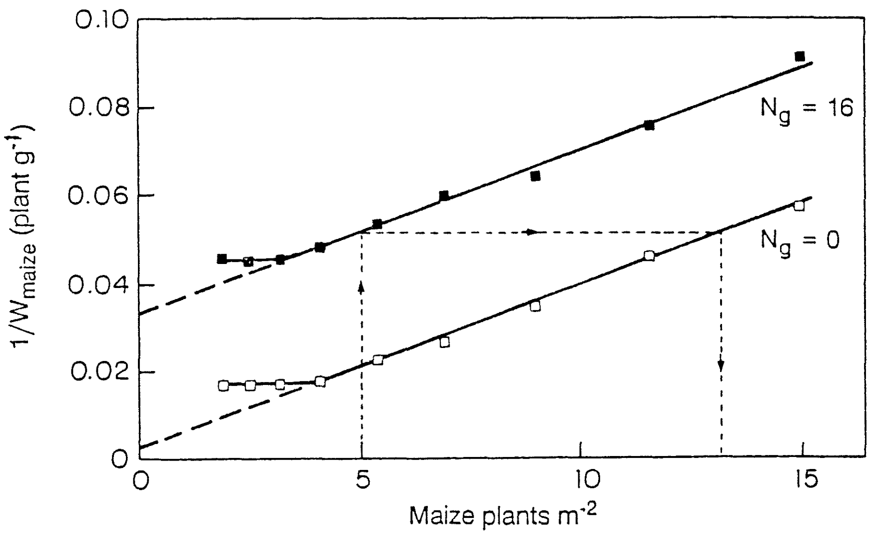

Figure 13.3 The effect of adding 16 groundnut plants (N_g =16) to a monocrop of maize (N_g=0) had the same effect on maize biomass as adding eight maize plants. (After: Spitters, 1983a)

rooting systems, exploiting different compartments of the soil or in the situation of legumes, intercropped with other crops that can use the N fixed by the Rhizobia. The parameters can be estimated using non-linear regression techniques on the logarithm of both sides of the equation because the yields are distributed log-normally.

For harvestable yield, Spitters (1983b) derived a parabolic equation based on Equation 2, to account for the effect of strong competition on harvestable yield.

COMPETITION IN WEEDY CROPS

The hyperbolic yield density equation for the description of yield loss in relation to weed density is the most widely used regression model to describe effects of competition at one point in time (Cousens, 1985; Spitters, van Keulen and van Kraalingen, 1989). Based on the general formulation of Spitters (1983a) (Equation 5), a one parameter hyperbolic function can be derived for the effect of weeds on crops (Spitters, Kropff and de Groot, 1989):

$$Y_L = a\ N_w \ / \ (1 + a\ N_w) \qquad (6)$$

where Y_L gives the yield loss relative to the weed-free crop, N_w is the weed density and *a* describes the yield loss caused by adding the first weed per square metre. In this one-parameter regression model, maximum fractional yield loss is 1 (or 100%) at high weed densities.

The approach described by Cousens (1985) involves an additional parameter which permits a maximum yield loss of less than 100% (*m*):

$$Y_L = a\ N_w \ / \ (1 + a/m\ N_w) \qquad (7)$$

These hyperbolic yield–density equations fit well to data from experiments where only the weed density is varied (Kropff *et al.*, 1984; Cousens, 1985; Weaver, Smits and Tan, 1987; Spitters, Kropff and de Groot, 1989; Kropff, Weaver and Smits, 1992). However, the parameters *a* and *m* may vary strongly among experiments due to the effect of other factors on competition processes. An example demonstrating the large difference in effects of *Echinochloa crus-galli* (L.) P. Beauv. on maize in two subsequent growing seasons is given in *Figure 13.4*. In this situation, the extra parameter for a limited maximum yield loss (Equation 7) was not needed to obtain a good fit of the model. In other situations, a very clear maximum yield loss smaller than 100% was observed at high weed densities (Weaver, Smits and Tan, 1987). Because variation in the yield loss–weed density function is often largely determined by differences in the period between crop and weed emergence, (Håkansson, 1983; Kropff *et al.*, Cousens *et al.*, 1987; Kropff, Weaver and Smits, 1992), precise prediction of yield loss on the basis of early observations should be based on both weed density and the period between crop and weed emergence. An additional variable in the hyperbolic yield–density equation to account for the effect of differences in the period between crop and weed emergence was introduced by Håkansson (1983) and Cousens *et al.* (1987). However, in practice, weeds often emerge in successive flushes, making it difficult to apply a descriptive model that accounts for the effect of both weed density and the relative time of weed emergence because every flush has to be regarded as

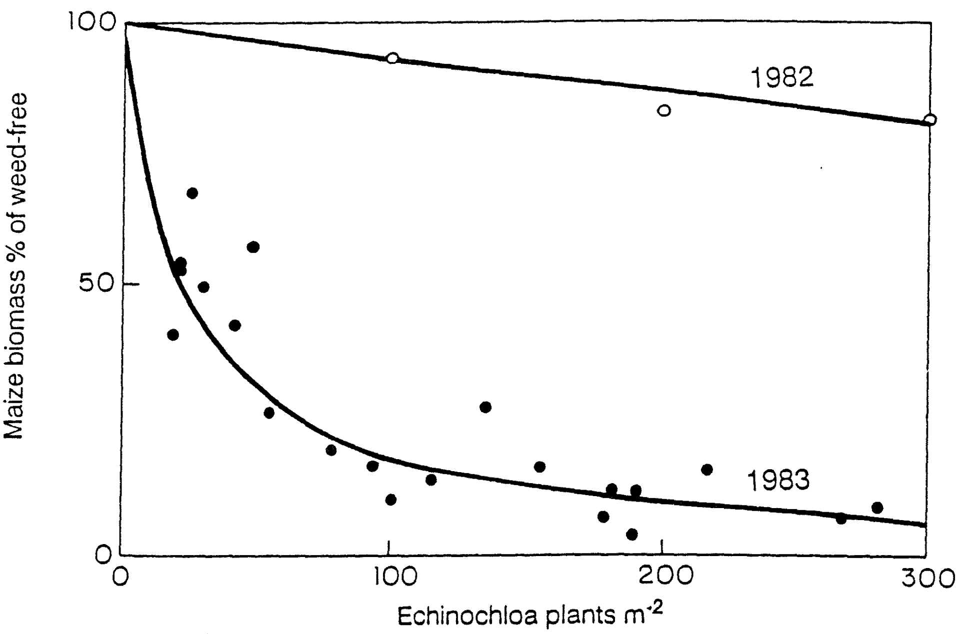

Figure 13.4 The effect of different densities of *Echinochloa crus-galli* L. on maize yield in 2 years at the same site in Wageningen, The Netherlands. (After: Kropff *et al.*, 1984)

a different weed species. Therefore alternative approaches are needed to predict yield loss by weeds for use in weed management systems.

Toward a mechanistic understanding of competition for resource capture in agricultural crops

The approaches previously discussed are all descriptive at the system level and do not explain competition effects at the process level. To improve the productivity and resource use efficiency of crop plants by varietal improvement and optimization of crop management in various competition situations, quantitative insight in the mechanisms of competition and the role of morphological and physiological plant traits is needed. Relationships between morphological and physiological characteristics of species and their competitive strength have been widely studied (cf. Pearcy, Tumosa and Williams 1981; Ampong-Nyarko and De Datta, 1989). Pearcy, Tumosa and Williams (1981) found a close relationship between competitive ability and photosynthetic responses of *Chenopodium album* L. (C_3 plant type) and redroot pigweed (*Amaranthus retroflexus* L., C_4 plant type). However, causal relationships should include processes related to resource capture and not only resource use efficiency. The complexity of relationships between morphological and physiological characteristics and competitive ability of plants in mixtures has been recognized by many researchers.

Ecophysiological models for interplant competition for the resources light, water and nutrients can be used as a tool to study these complex relationships. These models are based on the assumption that competition is a dynamic process which can be understood from the distribution of the limiting resources between the competing neighbouring plants and the efficiency with which each plant uses the resources captured. Such a mechanistic approach provides insight into the processes underlying competition effects observed in (field) experiments and may so be of help in searching for ways to manipulate competitive relations, like those between crop and weeds.

Most effort to simulate interplant competition using ecophysiological models has been on crop–weed interactions (Spitters and Aerts, 1983; Kropff *et al.*, 1984, Kropff, 1988; Graf *et al.*, 1990; Ryel *et al.*, 1990; Wilkerson *et al.*, 1990; Kropff and Spitters, 1992). A few attempts have been made to develop ecophysiological models for interplant competition in intercropping systems (e.g. Caldwell and Hansen, 1990). Because of the complexity of these systems, ecophysiological models may help to optimize the systems and to suggest optimum plant densities, planting dates, cultivar combinations, crop management practices, seeding rates, etc. Detailed data from field experiments, however, will be required to parameterize, calibrate and validate the models. Ecophysiological models for monoculture crops, generally do not simulate the growth of individual plants that compete for resource capture. A simple preliminary model for competition between individual plants was developed by R. Stokkers, M.J. Kropff, J. Goudriaan and J.A. den Dulk, Wageningen Agricultural University, unpublished), using a simulation model for interplant competition that is based on the assumption that the leaves are distributed homogeneously over an area. The model simulates competition for light for every individual plant by taking into account the leaf area and height of its neighbours. Preliminary results demonstrated the principle that relative differences between plants remain the same throughout the growing season. Hodges and Evans (1990) developed a model for the effect of row spacing on maize yield. They added to the CERES-Maize model (Jones and Kiniry, 1986) a light distribution model, only based on distribution of direct radiation. Their model accurately predicted effects of differences in spacing and plant density on yield.

An ecophysiological model that was developed to simulate crop–weed interactions (see later) developed by Kropff and Spitters (1992) was used to analyse the effect of shading by panicles in rice at different positions in the canopy (Kropff, Cassman and van Laar, 1993). The model demonstrated that the existing variation in panicle height caused differences in light interception resulting in more than 15% differences in daily photosynthetic rates during the grain filling period, assuming that the panicles do not photosynthesize.

AN ECOPHYSIOLOGICAL MODEL FOR INTERPLANT COMPETITION

In the past three decades, many mechanistic or ecophysiological simulation models for crop growth and production have been developed. These models simulate crop growth on basis of the response of physiological processes to the environment (cf. de Wit *et al.*, 1978; Penning de Vries and van Laar, 1982; Jones and Kiniry, 1986; Jones *et al.*, 1989). The approach taken to simulate the growth of a mixture of species is very similar to the approaches used in simulation of the growth of monoculture crops. The single difference is the calculation procedure for resource capture. Thus, competition for resource capture is also simulated on a per area basis in these models. They account for vertical heterogeneity in the canopy, but it is assumed that the leaves are horizontally homogeneously distributed. The general structure of the modelling approach to simulate competition for light and

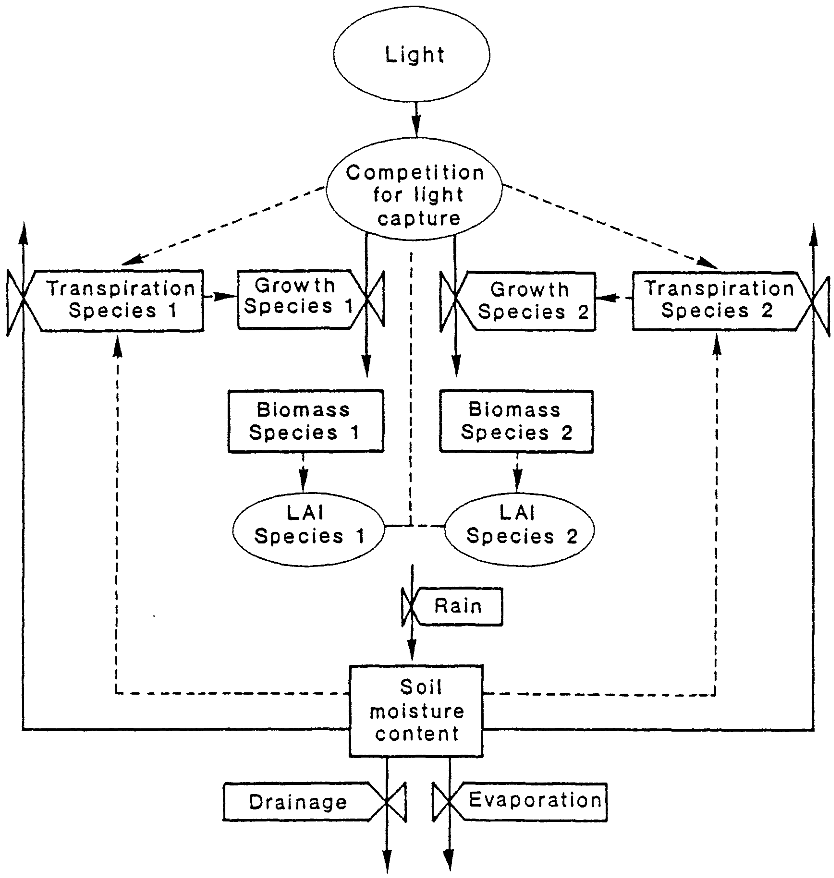

Figure 13.5 General structure of the ecophysiological model for interplant competition (INTERCOM)

water is given in *Figure 13.5*. Under favourable growth conditions, light is the main factor determining the growth rate of the crop and its associated weeds. From the leaf area indices (*LAI*) of the species and the vertical distribution of their leaf area the light profile within the canopy is calculated. In these functions, it is assumed that the leaves are distributed over the total height of the plants according to a parabolic function. In a canopy with a mixture of species, the net light flux at height h can be calculated from:

$$I_h = (1 - \rho)\, I_0 \exp(-\Sigma\, (k_j\, L_{h,j})) \qquad (8)$$

where

I_h is the net flux (PAR) at height h (J m^{-2} ground s^{-1}),
I_0 is the flux at the top of the canopy (J m^{-2} ground s^{-1}),
$L_{h,j}$ the cumulative leaf are index of species j above height h (m^2 leaf m^{-2} ground),
ρ the reflection coefficient of the canopy, and
k_j the extinction coefficient of species j.

The leaf areas ($L_{h,j}$), weighted by the extinction coefficients (k_j), are summed over the $j = 1 \ldots n$ plant species in the mixed vegetation.

The light absorbed by species *i* at a height *h* in the canopy ($I_{a,h,i}$, J m^{-2} leaf s^{-1}) is obtained by taking the derivative of Equation 8 with respect to the cumulative leaf area index:

$$I_{a,h,i} = - \mathrm{d}I_{h,i} / \mathrm{d}L_i = k_i (1 - \rho) I_0 \exp(-\Sigma (k_j L_{h,j})) \qquad (9)$$

The same equation is used to calculate the radiation absorbed by stems and reproductive organs, i.e. these organs are regarded as different species. The diffuse and the direct flux have different extinction coefficients, resulting in different light profiles within the canopy for diffuse and direct radiation. Therefore, three different radiation fluxes are distinguished: the component of direct light, the total direct flux and the diffuse flux.

The CO_2 assimilation-light response of individual leaves follows a saturation type of function, characterized by the initial slope (the initial light use efficiency) and the asymptote (A_m) and is described by the negative exponential function (Goudriaan, 1982):

$$A_h = A_m (1 - \exp(-\epsilon I_a / A_m)) \qquad (10)$$

where
A_h is the gross assimilation rate (gCO_2 m^{-2} leaf s^{-1}),
A_m the gross assimilation rate at light saturation (gCO_2 m^{-2} leaf s^{-1}),
ϵ the initial light use efficiency (gCO_2 J^{-1}), and
I_a is the amount of absorbed radiation (J m^{-2} leaf s^{-1}).
From the absorbed light intensity at height *h* for one of the species, the assimilation rate of species *i* at that specific canopy height can be calculated with Equation 10. This procedure is followed for sunlit and shaded leaves separately. Based on photosynthesis characteristics of single leaves, the photosynthesis profile of each species in the mixed canopy is obtained. Integration over the height of the canopy and over the day gives the daily CO_2 assimilation rate for each species.

Profiles of absorbed radiation, CO_2 assimilation and the cumulative CO_2 assimilation of a mixture with two species with the same characteristics and the same leaf area index (LAI=2) but a different height are illustrated in *Figure 13.6*.

As in the monoculture model, the amount of assimilates, produced per day is converted to glucose production by multiplying by 30/44 (molecular weights of CH_2O/CO_2). After subtraction of respiration requirements for maintenance of the species, the net daily growth rate in kilograms dry matter per hectare per day is obtained using a conversion factor. The dry matter produced is partitioned among the various plant organs, using partitioning coefficients that are introduced as a function of the phenological development stage of the species. Phenological development rate is tracked in the model as a function of ambient daily average temperature. When the canopy is not yet closed, leaf area increment is calculated from daily average temperature (Kropff and Spitters, 1992). When the canopy closes, the increase in leaf area is obtained from the increase in leaf weight using the specific leaf area (SLA, m^2 leaf kg^{-1} leaf). Integration of daily growth rates of the organs and leaf area results in the time course of LAI and dry weight in the growing season. Plant height development follows an S-shaped pattern throughout the growing season. Height is obtained by integration of the height growth rate.

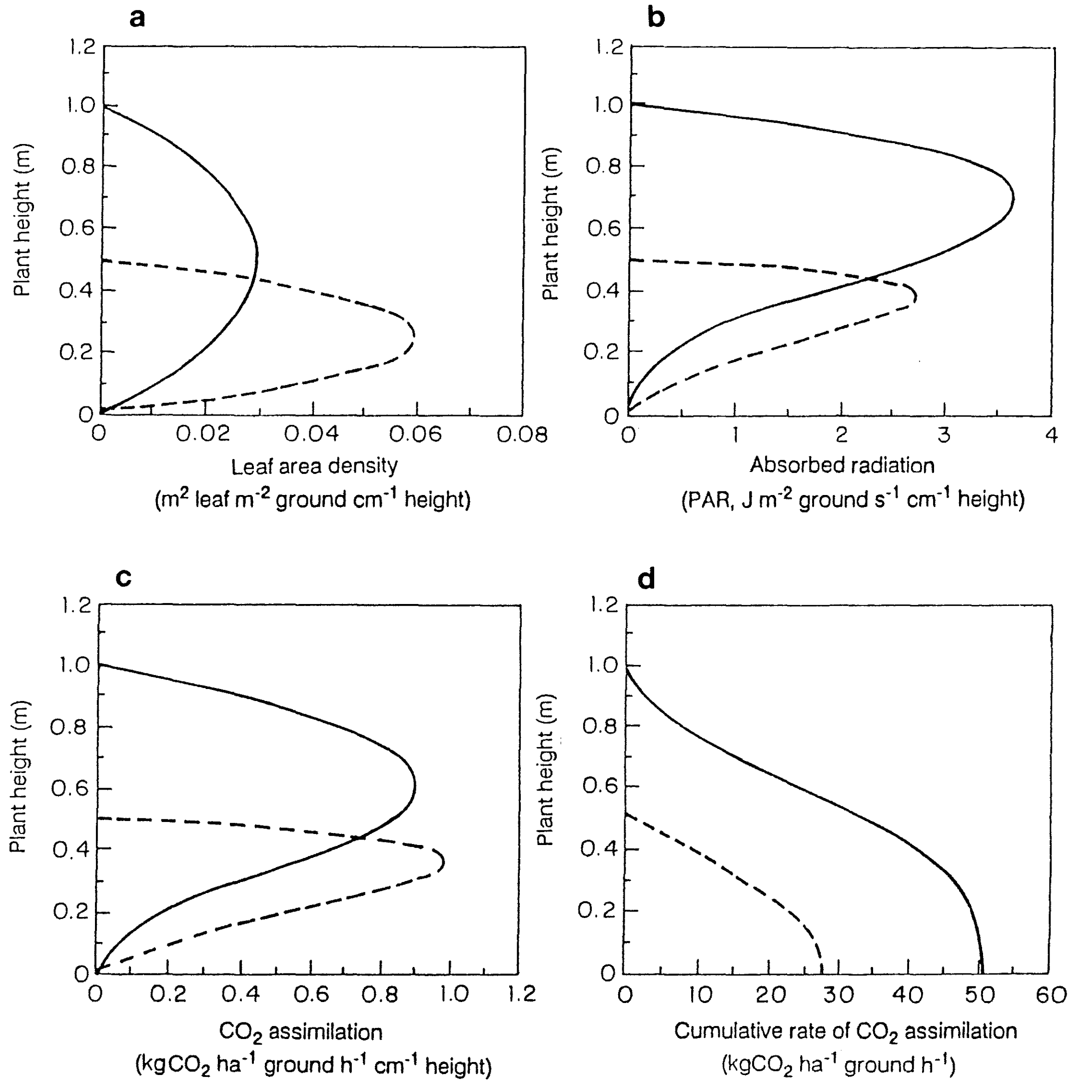

Figure 13.6 Simulation of competition for light using a parabolic leaf area distribution. (**a**) Leaf area distribution over height for two identical species with both LAI=2 and plant height of 1 m (solid line) and 0.5 m (broken line). (**b**) Profile of absorbed visible radiation (PAR) for both species in mixture with 300 J m^{-2} s^{-1} diffuse radiation as input. (**c**) CO_2 assimilation profile in the canopy for both species (kgCO_2 ha^{-1} h^{-1} cm^{-1} height). (**d**) The cumulative CO_2 assimilation rate counted from the top of the canopy (kgCO_2 ha^{-1} ground h^{-1})

In competitive situations however, height growth can be strongly reduced by shortage of assimilates as a result of shading. In crop–weed competition studies this is the case for late emerging weeds. In the model, an empirical function was introduced that limits the Specific Stem Length (SSL, m of height kg^{-1} stem) to a maximum value which depends on plant height. This function is based on the response observed in *Chenopodium album* L. growing in a wide range of competition situations (*Figure 13.7*), showing *C. album* to have high phenotypic plasticity with respect to height growth.

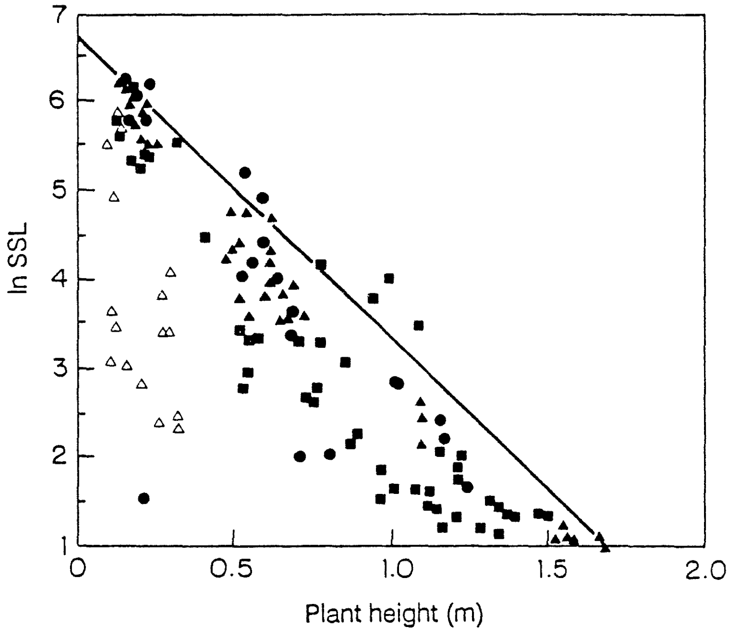

Figure 13.7 The relation between the Specific Stem Length (SSL) and plant height for *Chenopodium album* L., measured in different experiments in monoculture and competition situations. Symbols indicate different growth stages (Δ: 500 < temperature sum (*ts*) < 500; ■ : 600 < *ts* < 800; ● : 100 < *ts* < 1300; ▲ : 1300 < *ts* < 1500). The line indicates the maximum SSL possible in relationship to height

Plants growing in a mixture in a water-limited production situation compete for water and generally also for light during periods when water is not limiting growth. The importance of competition for water is determined by the length, severeness and timing of the drought period(s). Competition mechanisms for water differ principally from competition for light. Competition for light is a process of direct competition for resource capture, with instantaneous consequences for the growth rate of the plants. The amount of absorbed radiation generally limits the photosynthesis of closed leaf canopies in potential production situations. Light absorption by neighbouring plants reduces the rate of CO_2 assimilation and growth of the plant. When plants compete for water, the competition effect is not instantaneous, but delayed. Water requirements differ between the species because they are determined by the amount of absorbed radiation, temperature, vapour pressure deficit and species characteristics. The amount of available soil moisture will be reduced during the growing season if rainfall and other processes that increase soil moisture content, cannot meet the water losses by evapotranspiration and drainage. Therefore, plant transpiration in a period when water is not limiting growth, can affect the growing situation later in the season. Especially when the growth cycles of species in a mixture differ, it may happen that an early maturing species does not suffer from water stress itself, but will increase the water stress effects for the later maturing species if water stress occurs later in the growing season. For example, in one of the experiments with maize and *Echinochloa crus-galli* L., severe drought occurred during stem elongation of the maize. The competing *Echinochloa* plants had almost completed their life cycle by then, and were hardly affected by the drought. Water competition effects on maize, however, were very strong, as the mixtures transpired more water than the monoculture maize which had an open canopy for a long period, but in which a crust on the soil prevented evaporation (Kropff, Weaver and Smits, 1992).

Because both light and water competition are important in water-limited production situations, competition effects have to be studied in an integrated way. That can be done by incorporating modules that simulate processes related to the water balance in the canopy and the soil in the competition model for potential production. The processes that have to be simulated explicitly are evaporation and transpiration. The transpiration requirements of the species are calculated based on their share in absorbed radiation, and actual transpiration is simulated by using a reduction function that is a fraction of soil moisture content.

In many production situations, the supply of macronutrients (N, P, K) limits the growth of the crop or vegetation for at least part of the growing season. A mechanistic understanding of the soil and plant processes related to availability, uptake and use of these nutrients is difficult to obtain. Mechanistic simulation models have been developed for nitrogen effects, but their predictive capability is still limited (van Keulen and Seligman, 1987). Relatively simple approaches are, however, available (cf. Janssen *et al.*, 1990) and may be used to obtain more insight into processes related to competition for nutrients between plants.

In production situations where mobile soil elements like water and nitrates are not limiting growth, root length density has hardly any effect on the total uptake of these elements by the crop (van Keulen and Seligman, 1987). Therefore, the total uptake by mixed vegetation can be calculated in a similar way to the procedure described for the monoculture situation.

However, when the nutrient supply from the soil cannot meet demand, uptake by a species in mixed vegetation will be related to its share in the total effective root length. Below-ground competition for soil elements is modelled in analogy with competition for light. The fraction of nutrient ions that is taken up by a species is related to its share in the total root system. It is important to note that the relative, rather than the absolute, effective root length of a species determines its competitive ability. This approach could also be used for the water competition model. A species with an extensive root system, relative to its demand, is able to meet its demand at a lower soil nitrogen supply. At limited soil supplies, the soil nitrogen which is not used by such a species is distributed over the other species. For further details we refer to Kropff and Spitters (1992).

PERFORMANCE OF THE ECOPHYSIOLOGICAL MODEL FOR INTERPLANT COMPETITION

Most parts of the ecophysiological model have been evaluated and tested for monoculture crops (Penning de Vries and van Laar, 1982; Rabbinge, Ward and van Laar, 1989). The ecophysiological competition model was tested firstly with data from competition experiments with maize (*Zea mays* L.), yellow mustard (*Sinapis arvensis* L.) and barnyard grass (*Echinochloa crus-galli* L.) (Kropff *et al.*, 1984; Spitters and Aerts, 1983; Kropff, Weaver and Smits 1992). In these studies, the difference in the effect of barnyard grass on maize production between field experiments in two successive years was only partly explained by the model due to severe drought stress in one experiment that influenced competitive interactions. The analysis by Kropff, Weaver and Smits (1992) showed that the simulation of leaf area development and maize height deviated strongly from observed values in the dry year. When measured leaf area and height data were input in the simulation model, dry matter production and yield loss were simulated accurately (Kropff, Weaver and Smits, 1992). Irreversible effects of drought stress – such as strongly reduced stem elongation and death of leaves or the whole plant – were not included in the model. Quantitative information of extreme stress effects on physiological processes is lacking. In a subsequent study, the ecophysiological model was parameterized for sugar beet and the weed lambsquarters (*Chenopodium album* L.) and used to analyse data from five field experiments (Kropff, 1988). The experiments were conducted at the same site in Wageningen for three years. Weed densities ranged from 5.5 to 22 plants/m^2 and the period between crop and weed emergence ranged from 0 to 30 days. Yield loss in sugar beet ranged from –6 to 96%. Measured inputs in the model included daily weather variables measured at a nearby station (maximum and minimum temperature, total global radiation, rainfall, humidity and windspeed), weed density and dates of crop and weed emergence. Data on species characteristics were derived from the literature, unpublished results of experiments and three field experiments with sugar beet and lambsquarters (Kropff *et al.*, 1992). Soil parameters such as soil moisture content at permanent wilting point, field capacity and rootable depth were experimentally determined. To assess the explanatory power of the ecophysiological model, the same set of species-specific parameter values was used in the simulation of all five experiments. Since the simulation model explained 98% of the variation between experiments, the model was used to analyse the contribution of the different factors to differences in yield loss between experiments. Analysis (by changing the values of variables step by step) showed that variation between the experiments was mainly due to differences in the period between crop and weed emergence. Additional validation of the ecophysiological model was performed using data from critical period experiments with the same species (Weaver, Kropff and Groeneveld, 1992).

This model was evaluated subsequently (Kropff, Weaver and Smits 1992) using data with tomato (*Lycopersicon esculentum* L.) – redroot pigweed (*Amaranthus retroflexus* L.) and tomato – eastern black nightshade (*Solanum ptycanthum* L.) (Weaver, Smits and Tan, 1987) in Canada. Yield loss – weed density responses, effects of transplanting *versus* direct seeding and effects of weed-free or weed-infested periods (critical period experiments) were simulated accurately.

Sensitivity analysis showed that morphological species characteristics (height growth development and leaf area development) are the most significant plant factors determining competitive relationships in favorable growing conditions (Kropff *et al.*, 1992). Physiological characteristics such as photosynthetic rates or respiration characteristics are less important.

The ecophysiological model described, was developed on basis of general crop growth models, and competition was introduced by distributing the resources light, water and nutrients over the species in a mechanistic way. In principle, the physiological processes that determine plant growth are the same, irrespective of whether a species is grown in monoculture or in competition with other species. However, in competition situations, where one is interested in the biomass per individual or per species, and not in the total biomass per unit of area, the attributes determining resource interception become more important because they regulate the distribution of the limiting resources between the competing plants. For a monoculture crop in the linear growth phase, light capture hardly increases with LAI above 4, and plant height does not affect light capture at all. In a mixture, however, small differences in plant height or leaf area development may cause dramatic changes in the competitive relationships, although total biomass production may be more or less the same. The attributes that determine the capacity of a species to capture resources, such as starting position, plant height, leaf area dynamics and root morphology, therefore, need special attention in a competition model.

PRACTICAL APPLICATION

Although complex models for interplant competition in weedy crops will not be a practical tool in weed management because of the detailed input requirements, the models can be used to derive and pre-test simple approaches that may be promising for practical application. The ecophysiological model was used to analyse the possibility of predicting yield loss early in the season, based on observations of the relative leaf area index of the weeds (Kropff, 1988). A very close relationship was predicted between relative leaf area index of the weeds and yield loss for a wide range of weed densities and periods between crop and weed emergence. Based on these results, an alternative regression model for early prediction of crop losses by weed competition was introduced by Kropff and Spitters (1991). Their model was directly derived from the well-tested hyperbolic yield density model (Equation 6). This model relates yield loss to relative weed leaf area index (L_w expressed as weed leaf area index /crop+weed leaf area index) shortly after crop emergence, using the 'relative damage coefficient' q as the single model parameter:

$$Y_L = q\, L_w \,/\, (1 + (q - 1)\, L_w) \qquad (11)$$

It was demonstrated that this model also accounts for the effect of the period between crop and weed emergence besides weed density (Kropff and Spitters, 1991). *Figure 13.8* shows the fit of the model to data from field experiments in which the effect of *C. album* on sugar beet was studied for different periods of weed emergence and densities (Kropff, 1988). A strong advantage of the approach is that separate flushes of the weeds do not have to be handled separately, since they are included in the total value of relative leaf area of weeds, if the weeds emerge before the time of observation.

An extended version of Equation 11, developed in analogy with Equation 7, also accounts for a limited maximum yield loss caused by weeds (m):

$$Y_L = q\, L_w \,/\, (1 + (q\,/m - 1)\, L_w) \qquad (12)$$

Equation 12 gave a more accurate description of competition effects for several situations (Kropff *et al.*, unpublished results). In conclusion, the relative leaf cover–yield loss regression model accounts for the effect of weed densities, different flushes of weeds and the period between crop and weed emergence. However, it should be noted that the effect of other factors, such as transplanting shock or severe water stress, is not accounted for in such simple regression models (Kropff and Spitters, 1991)

To implement the approach in practical decision making, a methodology has to be developed that enables simple determination of the relative leaf area in the

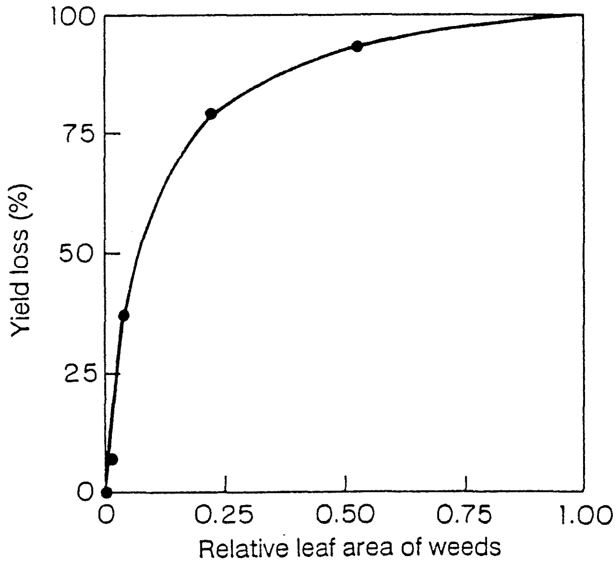

Figure 13.8 Yield loss in sugar beet related to relative leaf area of the weed *Chenopodium album* L. determined 30 days after sugar beet emergence. (After: Kropff and Spitters, 1991)

field, e.g. by estimating relative leaf cover. Preliminary studies showed that in early stages of the crop, the leaf area index is closely related to leaf cover. The potential use of the relative leaf cover model in practical weed management will be increased when weeds of different species with similar competition characteristics can be grouped. Then, the model could be parameterized per species group. Applicability will also be improved by identifying the time window for decision making with respect to specific problem weeds, because of the time dependence of the relative damage coefficient (Kropff and Spitters, 1991).

THE COMPLEMENTARITY OF ECOPHYSIOLOGICAL AND DESCRIPTIVE APPROACHES TO QUANTIFY INTERPLANT COMPETITION

The descriptive or phenomenological approaches and ecophysiological approaches to quantify interplant competition are complementary. The ecophysiological model is very comprehensive, directed towards understanding of the basic principles governing interplant competition. It is, therefore, intended as a research tool. Such a model facilitates the study of plant attributes determining the competitive ability of plants, the improvement of the efficiency of intercropping systems, the evaluation of newly developed weed control strategies and the development of improved descriptive approaches. The simple approaches, however, are more tailored for use as practical tools for on-farm decision making in weed management. They are easy to parameterize and require simple observations.

References

Ampong-Nyarko, K. and De Datta, S.K. (1989) Ecophysiological studies in relation to weed management strategies in rice. In *Proceedings of the Asian-Pacific Weed Science Society*, Twelfth Conference, Seoul, pp 31–45

Berendse, F. (1985) Een simulatiemodel voor de stikstofkringloop en de concurrentie tussen plantesoorten in vochtige heidevegetaties. *The Utrecht Plant Ecology News*, Report No. 1, Utrecht University, the Netherlands

Caldwell, R. and Hansen, J. (1990) Simulation of intercropping with IBSNAT models. *Agrotechnology Transfer*, **12**, 1–4

Connolly, J. (1986) On difficulties with replacement-series methodology in mixture experiments. *Journal of Applied Ecology*, **23**, 125–137

Cousens, R. (1985) An empirical model relating crop yield to weed and crop density and a statistical comparison with other models. *Journal of Agricultural Science*, **105**, 513–521

Cousens, R., Brain, P., O'Donovan, J.T. and O'Sullivan, A. (1987) The use of biologically realistic equations to describe the effects of weed density and relative time of emergence on crop yield. *Weed Science*, **35**, 720–725

Darwinkel, A. (1978) Patterns of tillering and grain production of winter wheat at a wide range of plant densities. *Netherlands Journal of Agricultural Science*, **26**, 383–398

Firbank, L.G. and Watkinson, A.R. (1987) On the analysis of competition at the level of the individual plant. *Oecologia (Berlin)*, **71**, 308–317

Firbank, L.G. and Watkinson, A.R. (1990) On the effects of competition: from monocultures to mixtures. In *Perspectives on Plant Competition* pp 165–192 Edited by J.B. Grace and D. Tilman. New York: Academic Press

Goudriaan, J. (1982) Some techniques in dynamic simulation. In *Simulation of Plant Growth and Crop Production*, pp 66–84 Edited by F.W.T. Penning de Vries and H.H. van Laar. Simulation Monographs, Wageningen: Pudoc

Grace, J.B. and Tilman, D. (Eds) (1990) *Perspectives on Plant Competition*. San Diego: Academic Press 484 pp

Graf, B., Gutierrez, A.P., Rakotobe, O., Zahner, P. and Delucchi, V. (1990) A simulation model for the dynamics of rice growth and development. Part II. The competition with weeds for nitrogen and light. *Agricultural Systems*, **32**, 367–392

Håkansson, S. (1983) Competition and production in short-lived crop–weed stands. *Sveriges Landbruks University, Uppsala, Sweden. Report* No.127, 85 pp

Harper, J.L. (1977) *The Population Biology of Plants*. London: Academic Press, 892 pp

Hodges, T. and Evans, D.W. (1990) Light interception model for estimating the effects of row spacing on plant competition in maize. *J. Prod. Agric.* **2**, 190–195

Janssen, B.H., Guiking, F.C.T., van der Eijk, D., Smaling, E.M.A., Wolf, J. and van Reuler, H. (1990) A system for quantifying evaluation of the fertility of tropical soils (QUEFTS). *Geoderma*, **46**, 299–318

Jones, C.A. and Kiniry, J.R. (1986) *CERES-Maize: a simulation model of maize growth and development*. College Station, Texas: Texas A and M University Press

Jones, J.W., Boote, K.J., Hoogenboom, G., Jagtap, S.S. and Wilkerson, C.G. (1989) SOYGRO V5.42, soybean crop growth simulation model: user's guide.

Florida Agricultural Experiment Station Journal No. 8304. Gainsville, Florida: Agricultural Engineering and Agronomy Department, University of Florida

Keulen, H. van and Seligman, N.G. (1987) *Simulation of Water Use, Nitrogen and Growth of a Spring Wheat Crop*. Simulation Monographs, Wageningen: Pudoc, 310 pp

Kira, T., Ogawa, H. and Sakazaki, N. (1953) Intraspecific competition among higher plants. I. Competition-yield-density interrelationships in regularly dispersed populations. *Journal of Institute for Polytechnics, Osaka City University*, Series **D 4**, 1–16

Kropff, M.J. (1988) Modelling the effects of weeds on crop production. *Weed Research*, **28**, 465–471

Kropff, M.J., Cassman, K.G. and van Laar, H.H. (1993) Quantitative understanding of the irrigated rice ecosystem for achieving high yield potential in (hybrid) rice. In *Proceedings of the International Rice Research Conference*, 21–25 April, 1992. International Rice Research Institute, Los Banos, Philippines (in press)

Kropff, M.J. and Spitters, C.J.T. (1991) A simple model of crop loss by weed competition from early observations on relative leaf area of the weeds. *Weed Research*, **31**, 97–105

Kropff, M.J. and Spitters, C.J.T. (1992) An eco-physiological model for interspecific competition, applied to the influence of *Chenopodium album* L. on sugar beet. I. Model description and parameterization. *Weed Research*, **32**, 437–450

Kropff, M.J., Spitters, C.J.T., Schnieders, B.J., Joenje, W. and de Groot, W. (1992) An eco-physiological model for interspecific competition, applied to the influence of *Chenopodium album* L. on sugar beet. II. Model evaluation. *Weed Research*, **32**, 451–463

Kropff, M.J., Vossen, F.J.H., Spitters, C.J.T. and de Groot, W. (1984) Competition between a maize crop and a natural population of *Echinochloa crus-galli* (L.). *Netherlands Journal of Agricultural Science*, **32**, 324–327

Kropff, M.J., Weaver, S.E. and Smits, M.A. (1992). On the use of eco-physiological models for crop–weed competition. 1. Relations between weed density, relative time of weed emergence, relative leaf area and yield loss. *Weed Science*, **40**, 296–301

Pacala, S.W. and Silander, Jr J.A. (1987) Neighborhood interference among velvet leaf, *Abutilon theophrasti*, and pigweed, *Amaranthus retroflexus*. *OIKOS*, **48**, 217–224

Pearcy, R.W., Tumosa, N. and Williams, K. (1981) Relationships between growth, photosynthesis and competitive interactions for a C_3 and C_4 plant. *Oecologia (Berlin)*, **48**, 371–376

Penning de Vries, F.W.T. and van Laar, H.H. (1982) Simulation of growth processes and the model BACROS. In *Simulation of plant growth and crop production* pp 114–135 Edited by F.W.T. Penning de Vries and H.H. van Laar Simulation Monographs, Wageningen: Pudoc

Rabbinge, R., Ward, S.A. and van Laar, H.H. (Eds) (1989) *Simulation and Systems Management in Crop Protection*. Simulation Monographs 32, Wageningen: Pudoc 420 pp

Radosevich, S.R. and Holt, J.S. (1984) *Weed Ecology: Implications for Vegetation Management*. New York: John Wiley, 265 pp

Rimmington, G.M. (1984) A model of the effect of interspecies competition for light on dry-matter production. *Australian Journal of Plant Physiology*, **11**, 277–286

Ryel, R.J., Barnes, P.W., Beyschlag, W., Caldwell, M.M. and Flint, S.D. (1990) Plant competition for light analyzed with a multispecies canopy model. I. Model development and influence of enhanced UV-B conditions on photosynthesis in mixed wheat and wild oat canopies. *Oecologia*, **82**, 304–310

Shinozaki, K. and Kira, T. (1956). Intraspecific competition among higher plants. VII. Logistic theory of the C-D effect. *Journal of Institute for Polytechnics, Osaka City University*, Series **D 7**, 35–72

Silander, Jr J.A. and Pacala, S.W. (1985) Neighborhood predictors of plant performance. *Oecologia (Berlin)*, **66**, 256–263

Spitters, C.J.T. (1983a) An alternative approach to the analysis of mixed cropping experiments. I. Estimation of competition effects. *Netherlands Journal of Agricultural Science*, **31**, 1–11

Spitters, C.J.T.(1983b) An alternative approach to the analysis of mixed cropping experiments. II Harvestable yield. *Netherlands Journal of Agricultural Science*, **31**, 143–155

Spitters, C.J.T. and Aerts, R. (1983) Simulation of competition for light and water in crop–weed associations. *Aspects of Applied Biology*, **4**, 467–484

Spitters, C.J.T., van Keulen, H. and van Kraalingen, D.W.G. (1989) A simple and universal crop growth simulator: SUCROS87. In *Simulation and Systems Management in Crop Protection*, pp 147–181 Edited by R. Rabbinge, S.A. Ward and H.H. van Laar. Simulation Monographs, Wageningen: Pudoc

Spitters, C.J.T., Kropff, M.J. and de Groot, W. (1989) Competition between maize and *Echinochloa crus-galli* analysed by a hyperbolic regression model. *Annals of Applied Biology*, **115**, 541–551

Suehiro, K. and Ogawa, H. (1980) Competition between two annual herbs *Atriplex gmelini* C.A. Mey and *Chenopodium album* L. in mixed cultures irrigated with seawater of various concentrations. *Oecologia*, **45**, 167–177

Taylor, D.R. and Aarssen, L.W. (1989) On the density dependence of replacement-series competition experiments. *Journal of Ecology*, **77**, 975–988

Tilman, D. (1988) Plant strategies and the dynamics and structure of plant communities. *Monographs in Population Biology* No.20. Princetown, New Jersey: Princeton University Press, 360 pp

Trenbath, B.R. (1976) Plant interactions in mixed crop communities. In *Multiple Cropping*. pp 129–169 Edited by M. Stelly. American Society of Agronomy Special Publication No. 27

Vandermeer, J. (1989) *The Ecology of Intercropping*. Cambridge: Cambridge University Press, 237 pp

Watkinson, A.R. (1980) Density-dependence in single-species populations of plants. *Journal of Theoretical Biology*, **83**, 345–357

Weaver, S.E., Smits, N. and Tan, C.S. (1987) Estimating yield losses of tomato (*Lycopersicon esculentum*) caused by nightshade (*Solanum* spp) interference. *Weed Science*, **35**, 163–168

Weaver, S.E., Kropff, M.J. and Groeneveld, R.M.W. (1992) Use of eco-physiological models for crop–weed interference: The critical period of weed interference. *Weed Science*, **40**, 302–307

Wilkerson, G.G., Jones, J.W., Coble, H.D. and Gunsolus, J.L. (1990) SOYWEED: A simulation model of soybean and common cocklebur growth and competition. *Agronomy Journal*, **82**, 1003–1010

Willey, R.W. (1979a) Intercropping – its importance and its research needs. Part I. Competition and crop yield advantages. *Field Crop Abstracts*, **32**, 1–10

Willey, R.W. (1979b) Intercropping – its importance and its research needs. Part I. Agronomic relationships. *Field Crop Abstracts*, **32**, 73–85

Wit, C.T. de, van Laar, H.H. and van Keulen, H. (1979) Physiological potential of crop production. In *Plant breeding perspectives*, pp 47–82 Edited by J. Sneep and A.J.T. Hendriksen. Wageningen: Pudoc

Wit C.T. de (1960). *On Competition*. Agricultural Research Reports 66.8, Wageningen: Pudoc 82 pp

Wit, C.T. de, Goudriaan, J., van Laar, H.H., Penning de Vries, F.W.T., Rabbinge, R., van Keulen, H., Sibma, L. and de Jonge, C. (1978) *Simulation of Assimilation, Respiration and Transpiration of Crops*. Simulation Monographs, Wageningen: Pudoc 141 pp

Wright, A.J. (1981) The analysis of yield-density relationships in binary mixtures using inverse polynomals. *Journal of Agricultural Science (Cambridge)*, **96**, 561–567

Yoda, K., Kira, T., Ogawa, H., Hozumi, K. (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University*, **14**, 107–129

Yoshida S. (1981) *Fundamentals of Rice Crop Science*. Los Banos, Philippines: International Rice Research Institute, 269 pp