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A SIMPLE SIMULATION MODEL FOR CROP-WEED COMPETITION

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Summary: A simple model is presented to simulate the time course
of competition between a crop and the associated weeds. First an
estimate is made of the growth rate of the total stand, adjusted
for the productivity level of the site and for incomplete soil
cover of the vegetation. With daily intervals, this total stand
growth rate is distributed over the species according to their
share in the total leaf area and accounting for differences in
plant height. Model performance was compared with the results of
two field experiments where maize was grown with and without
Echinochloa crus-galli.

INTRODUCTION

Weeds compete with the crop for growth requisites like light, water and
nutrients, which are available in a limited supply only. Better insight
in the competition process would be gained if the distribution of the
main growth limiting resources and the concomitant growth of the species
would be followed in course of time. In an earlier paper (Spitters &
Aerts, 1983), this was approached with a detailed simulation model for
competition for light and water in crop-weed associations. The share a
species acquires in the total leaf area of the vegetation appeared to be
the main determinant of its competitive ability. Not only its light ab-
sorption, but also its demand for water and nitrogen, and with that its
uptake and depletion of the stocks of these resources, appeared to be
related to leaf area.
    The aim of this paper is to present a simple, summary model in which
the competitive ability of a species is characterized in course of time
and in relation to its share in the total leaf area of the vegetation.
Two versions of the model, differing in their level of complexity, will
be discussed. The performance of the model will be evaluated using the
results of two field experiments with maize and *Echinochloa crus-galli*
(L.) P.B. (barnyard grass).

A SIMPLE MODEL FOR GROWTH OF SPECIES IN MIXTURE

First an expression is derived for the growth rate of the entire vegeta-
tion, whereafter the dry-matter increment is partitioned over the separate
species in relation to their share in the total leaf area and accounting
for differences in plant height.
    Potential total stand growth rate. The growth rate of a closed, green
vegetation well supplied with water and nutrients and free from pests and

diseases is in the order of 20 g DM/m^2/day (Sibma, 1968). In such potential situations, growth is mainly limited by the amount of light absorbed. Thus, a more accurate estimate of the growth rate is obtained on the basis of incoming light and the average efficiency E with which the species use the absorbed light for dry-matter production. This gives for the potential growth rate at time t

$$G_{pot,t} = (1-0.08) \cdot 0.5 \, R_t \cdot E \tag{1}$$

where 0.08 is the reflection coefficient of the vegetation and 0.5 denotes that about half of the total global radiation R is photosynthetically active. A 30-years' average may be used for the time course of the radiation in the growing season, but it is more accurate to use values measured actually at a nearby meteorological station. Either daily values or values per decade can be used.

The assimilation approach, discussed later on, gives for the light use efficiency E of C_3 species growing under optimal conditions a value of about 3 g DM/MJ absorbed visible radiation. for C_4 species, E becomes about 4½ g DM/MJ provided that temperatures are high enough. These values agree with those determined experimentally (e.g. Fischer, 1983).

Actual growth rates are lower than potential ones due to incomplete light interception, suboptimal temperatures and other constraints. These effects are quantified by means of reduction factors.

Fraction light absorption in relation to leaf area. Light intensity decreases exponentially with the amount of leaf area. Hence, the fraction absorbed is

$$f_{abs} = 1 - \exp(-k \cdot \Sigma L_t) \tag{2}$$

where k measures the rate of light extinction with total leaf area index (ΣL) summed over all the species. The extinction coefficient k is about 0.7. The leaf area index (L in m^2 green leaf area/m^2 soil area) of a species is obtained by multiplying its biomass Y with the appropriate leaf area ratio (LAR in m^2 leaf/g biomass):

$$L_t = LAR_t \cdot Y_t$$

LAR is introduced as function of the developmental stage (DVS) of the species. The following developmental scale is used: 0 at emergence, 1 at first anthesis, and 2 at maturity. The developmental rate (DVR) is expressed in scale units per °C day according to:

$$DVR = \frac{T - T_{base}}{S} \quad \text{and so} \quad DVS = \int DVR \cdot dt$$

where T the daily average temperature, T_{base} the base temperature beneath which development stops and S the temperature sum needed to reach a certain developmental stage. Both the periods DVS 0-1 and DVS 1-2 are characterized by their own temperature sum. Photoperiodicity and vernalisation requirement are not considered explicitly.

Temperature. Temperature exerts only a minor influence on the total growth of a closed vegetation. As reduction factor may be applied

$$f_{temp} = \frac{T}{T_{cr} - T_{base}} \quad \text{for } T < T_{cr}, \quad \text{and} \quad f_{temp} = 1 \quad \text{for } T \geqslant T_{cr}$$

where for temperate zone C_3 species the base temperature T_{base} and the critical temperature T_{cr} are at about a daily average temperature of 0°C and 10°C, respectively. For C_4 species these values are at about 9°C and 17°C, respectively.

On the other hand, temperature has a substantial effect on LAR, the leaf area per gram dry matter formed. For total stand growth this is only of relevance in the early stages before full light interception. For the growth of the individual species in competition, however, this effect is important during the entire period because growth in mixture is related to the share of the species in the total leaf area. Here, the temperature effect on LAR is neglected, which assumes that the values of LAR used are representative for the actual field situation.

Site index. In spite of the reduction factors for incomplete soil cover and low temperature, the simulated production will be higher than the measured one. This is brought about by shortages of water and nutrients and by occurrence of pests and diseases in the field. In this simple approach, the potential growth rate is therefore reduced with an empirical factor characterizing the productivity of the site. Especially in annuals under arable conditions, this site index (SI) will in general decrease during the growing season because limited stocks of soil moisture and nutrients are depleted or because an epidemic of a pest or disease is built up. As a simple approximation we assume that during the growing season SI decreases linearly with time from a value of one at emergence to a certain, lower value at crop harvest. This latter value is found by calibrating the simulated final production of the weed-free crop to the, measured or expected, actual level. A farmer's expectation of crop yield divided by average harvest index may be used. For north-west European conditions the actual yield level is roughly 60% of the potential one. This approach assumes that the time course of the growth limiting factors is about the same in all stands, i.e. it supposes that all stands have a similar biological density.

Actual total stand growth rate. The actual growth rate at time t can now be summarized to be

$$G_t = SI \cdot f_{temp} \cdot (1-\exp(-k \cdot \Sigma L_t)) \cdot G_{pot,t} \qquad (3)$$

Share of a species in total stand growth rate for species having the same plant height. If the species would show the same plant height in course of time, then each species would acquire that part of the total dry-matter increment that corresponds with its share in the total leaf area. Hence, the growth rate of species i at time t is then

$$G_{i,t} = \frac{L_{i,t}}{\Sigma L_t} \cdot G_t \qquad (4)$$

This proportionality is evident when light is the main growth limiting factor. Approximately, it holds also when water or nitrogen limits growth. As transpiring surface, leaf area determines plant's moisture demand and due to the relative high nitrogen content of the leaves also its nitrogen demand. Uptake of these growth factors is strongly regulated by the demand of the plants (Seligman & van Keulen, 1981; van Noordwijk, 1983), and with that closely related to their leaf area. Apart from that, the share of a species in the total leaf area will correspond closely to its share in the total root system, the uptake capacity, provided that

357

the species do not differ much in their dry-matter partitioning over the plant organs.

Species differing in extinction coefficient. Species with a larger extinction coefficient absorb a greater amount of light per unit leaf area. It can be shown that allowance is made for this difference by weighting the leaf area according to the extinction coefficients. Combination of equation (3) and (4) gives then

$$G_{i,t} = \frac{k_i \cdot L_{i,t}}{\Sigma \ (k.L_t)} \cdot SI \cdot f_{temp} \cdot (1-exp(-\Sigma(k.L_t))) \cdot G_{pot,t}$$

Differences in extinction coefficient are not discussed further, but they can easily be accounted for in the following equations by weighting the leaf areas of the species to their extinction coefficients.

Species differing in plant height. Most species differ in plant height; the taller species gaining a greater portion of the incoming light than its share in the total leaf area. We can account for these differences in position of the leaves by weighting the leaf areas to their average illumination intensities. These intensities are roughly proportional to the light intensities at half of the plant heights. Under the assumption that for each species leaf area is evenly distributed over plant height, i.e. that at any height its leaf area density is the same, the relative light intensity at half of the height of species i becomes

$$l_i = exp \ (-k.L_{\frac{1}{2}H_i}) \quad with \quad L_{\frac{1}{2}H_i} = \sum_{j=1}^{n} \left(\frac{H_j - \frac{1}{2}H_i}{H_j} \cdot L_j \right) \quad and \quad H_j - \frac{1}{2}H_i \geqslant 0$$

where $L_{\frac{1}{2}H_i}$ the total leaf area index of all n species above half of the plant height H_i of species i. For each species, the time course of plant height is given as function of the developmental stage DVS. For the growth rate of i, we find now

$$G_{i,t} = \frac{l_{i,t} \cdot L_{i,t}}{\Sigma(l_t \cdot L_t)} \cdot G_t$$

The equations show that the effects are fully explained by the relative differences in plant height. Hence, a reduction of plant heights in a low productive environment does not change the competitive relations, provided that plant height is reduced for each species with an equal percentage.

As at lower levels of productivity, soil factors become the more important contraints, one might consider the growth rate of species i being an average of equation (4) and (5) weighted to 1-SI and SI, respectively. This was not done here.

EXPANSIONS OF THE SIMPLE APPROACH

The most obvious way to elaborate the preceding model in a deterministic way is to consider the different resources light, water and nutrients

explicitly. In crop growth models this is usually done by first calculating the growth rate under potential conditions, i.e. with an adequate supply of water and nutrients but given the actual weather conditions. This rate is mainly determined by the amount of light energy absorbed in combination with the photosynthetic characteristics of the plants. Subsequently, the potential rate is reduced in dependence of the availability of water and nutrients (e.g. Seligman & van Keulen, 1981).

Here, an essentially similar approach will be applied for simulation of growth in competition. The potential growth rate will be calculated in a simple way for each species in the mixture from its light absorption, photosynthetic characteristics and leaf area. This potential rate is reduced to the actual level by the empirical site index.

Amount of light absorbed. In a mixture of species with the same plant height, each species absorbs an amount of light equal to its share in the total leaf area times the total light absorption of the vegetation. The amount of light absorbed by species i at day t is then found from equations (1), (2) and (4) to be

$$I_{i,t} = \frac{L_{i,t}}{\Sigma L_t} \cdot (1-0.08) \cdot 0.5 \; R_t \cdot (1-\exp(-k.\Sigma L_t))$$

Allowance is made for differences in plant height between the species by dividing the canopy in horizontal layers and calculating the light absorption per species from the distribution of its leaf area with height in combination with the exponential light extinction profile.

Suppose first a mixture of two species with their leaf areas evenly distributed over their plant heights. Hence, the leaf area density of a species is the same at all its heights. The canopy is stratified into two horizontal layers: an upper layer where the tall species 1 has a monopoly, and a lower layer which both species share together. The leaf area index of the species in the different layers is then obtained from their total leaf area index L and their plant heights H as

$$L_{1,u} = \frac{H_1 - H_2}{H_1} \cdot L_1 \quad \text{and} \quad L_{1,1} = \frac{H_2}{H_1} \cdot L_1$$

$$L_{2,u} = 0 \qquad \text{and} \qquad L_{2,1} = L_2$$

with the subcripts u and l referring to the upper and lower layer, respectively. The amount of light absorbed by a species in a certain layer is found by multiplying (a) its share in the total leaf area of that layer with (b) the light intensity above the vegetation (I_o) and (c) the fraction of I_o that enters the respective layer and (d) the fraction of this incoming light that is absorbed by this layer. The total amount I absorbed by the species is then obtained by summing its absorbed amounts over the height layers:

$$I_1 = I_{1,u} + I_{1,1} = I_o \cdot (1 - \exp(-k.L_{1,u})) +$$

$$\frac{L_{1,1}}{L_{1,1} + L_{2,1}} \cdot I_o \cdot \exp(-k.L_{1,u}) \cdot (1 - \exp(-k(L_{1,1} + L_{2,1})))$$

$$I_2 = I_{2,1} = \frac{L_{2,1}}{L_{1,1} + L_{2,1}} \cdot I_o \cdot \exp(-k.L_{1,u}).(1-\exp(-k(L_{1,1}+ L_{2,1})))$$

with $I_o = (1-0.08) \cdot 0.5\ R$

In the general situation of n species, the canopy is divided into n layers, bounded by the plant heights of the different species and counted from the top downwards. The leaf area index $L_{i,h}$ of a species i in a layer h with upper limit H_{h-1} and lower limit H_h is then

$$L_{i,h} = \frac{H_{h-1} - H_h}{H_i} \cdot L_i \quad \text{with} \quad H_{h-1} \leq H_i$$

and its light absorption in that layer h is

$$I_{i,h} = \frac{L_{i,h}}{\sum\limits_{j=1}^{n} L_{j,h}} \cdot I_o \cdot \exp(-k \cdot \sum\limits_{j=1}^{n} \sum\limits_{g=1}^{h-1} L_{j,g}) \cdot (1-\exp(-k \cdot \sum\limits_{j=1}^{n} L_{j,h}))$$

where $\Sigma\Sigma\ L_{j,g}$ denotes that the leaf area is summed over the height layers g = 1 to h-1 from the top downwards and over all species j = 1 to n. Summation over the height layers gives the total light absorption of species i at the respective time step.

The daily light absorption I is converted into an average hourly intensity I' by division by the daylength D:

$$I' = I/D \tag{6}$$

In order to exclude the twilight periods, only that part of the day is considered where solar heights exceed 8°. Goudriaan (1982) derived for this effective daylength (D in hours) the expression

$$D = 12 + 12 \cdot \frac{2}{\pi} \cdot \frac{\pi}{180} \cdot \arcsin \frac{\sin \lambda \cdot \sin \delta - \sin 8°}{\cos \lambda \cdot \cos \delta} \tag{7}$$

Where λ is the latitude having a posititve sign for the northern hemisphere, and δ is the declination of the sun being

$$\delta = -23.45 \cos(\frac{360}{365}(t + 10))$$

with t is the number of the day since 1 January.

Assimilation rate. The daily assimilation rate of a species in the mixture is calculated from its light absorption, photosynthesis characteristics and leaf area. Photosynthesis-light response is curvilinear. In using light intensities which are averaged over times within a day and over the different leaves within the canopy, a more gradual proceeding curve must be used than the asymptotic exponential that characterizes instantaneous photosynthesis-light response of single leaves Therefore, a rectangular hyperbola is chosen, characterized by the initial efficiency ε at low light and the maximum assimilation rate A_{max} at high light. The

360

initial efficiency ε is 11 and 14 x 10^{-6} g CO_2/J absorbed for C_3 and C_4 species, respectively. For the ruderal types of these groups A_{max} is about 4 and 7 g CO_2/m² leaf/ hour, respectively.

In using averaged light intensities, we consider the canopy of a species in the mixture as one layer with a maximum assimilation rate equal to its leaf area index times its A_{max}. This gives for the daily assimilation rate (A in g CO_2/m² soil/day) of a species in the mixture:

$$A = D \cdot \frac{\varepsilon \cdot I'}{\varepsilon \cdot I' + L \cdot A_{max}} \cdot L \cdot A_{max} \qquad (8)$$

with the daylength D from equation (7) and the average hourly intensity of absorbed light I' from equation (6). This equation gave assimilation rates which corresponded quite well with those of more detailed approaches (e.g. Spitters & Aerts, 1983), provided that on the canopy assimilation maximum $L.A_{max}$ of the whole vegetation an upper limit of 5 A_{max} is imposed. From the exponential light extinction profile, it can be seen that the light absorption by additional leaf area is negligible.

Growth rate. From each g CO_2 absorbed 30/44 g carbohydrates is formed, which quantity is found as the ratio of the molecular weights of CO_2 and CH_2O.

The carbohydrates are partly used to maintain the living biomass. Maintenance respiration of a plant organ is roughly proportional to its dry weight. Modified after Penning de Vries & van Laar (1982), the daily maintenance respiration is obtained as:

$$R_{maint} = 0.02 \, Y_{leaf} + 0.01 \, Y_{stem} + 0.007 \, Y_{root} + 0.007 \, Y_{repr.}$$

with the Y's referring to the dry weights of leaf blades, stems and petioles or leaf sheaths, roots and reproductive structures, respectively. As simplifying approximation may be used

$$R_{maint} = 0.015 \, Y \quad \text{for DVS} \leq 1 \quad \text{and} \quad R_{maint} = 0.01 \, Y \quad \text{for DVS} > 1$$

with Y the total plant dry weight. The coefficients are given in g CH_2O/ g DM/ day and refer to the long term average temperature at which the plants grow, e.g. 20°C in temperate climates. With each change of 10°C, these coefficients change with a factor two.

The remaining carbohydrates are converted into structural dry matter. The conversion efficiency CVF is about 0.7 g DM/g CH_2O and depends only on the chemical composition of the formed dry matter (Penning de Vries & van Laar, 1982).

Hence, for the daily growth rate we obtain

$$G = SI \cdot CVF \cdot (\frac{30}{44} A - R_{maint})$$

where A the daily assimilation rate (equation 8) and SI the site index, used as an empirical reduction factor to bring the growth rate down to the average actual level.

Leaf area expansion and partitioning of dry matter. In the simple model, leaf area was calculated by multiplying biomass with the leaf area ratio, being the green leaf area per unit biomass. A more dynamic approach

is reached when the dry-matter increment G is distributed each day over the different plant organs according to certain distribution coefficients. The daily growth rate of plant organ o is then

$$G_o = DC_o \cdot G_{total}$$

and the accumulated dry weight of the organ is found as integral of its growth rate. The distribution coefficients DC are given as function of the developmental stage DVS.

Leaf area at time t is obtained by multiplying the weight of the leaves at that time with the specific leaf area (SLA in m^2 leaf/g leaf). Also SLA is given as function of DVS. Senescence of the leaves is accounted for by a death rate expressed relative to the weight of green leaves. This relative death rate is in the order of 0.03 per day, starting at onset of anthesis.

COMPARISON OF MODEL PERFORMANCE WITH EXPERIMENTAL RESULTS

The model outcome was compared with the results of two field experiments.

Experimental design. Maize, cultivar LG11, was grown with and without a natural vegetation of *Echinochloa crus-galli* (L.) P.B. (barnyard grass) at a sandy soil in Wageningen in the years 1982 and 1983.

In the first experiment (1982), maize was grown at 12 x 75 cm^2/plant. Some plots were kept weed-free, whereas in other plots the naturally emerging weed population was thinned to stands of 100, 200 or 300 Echinochloa plants/m^2. The main flush of Echinochloa emergence was at day 140, whereas maize emerged at day 135. Experimental data were from G. Coster, W. de Groot and C.J.T. Spitters.

In the second experiment (1983), maize was spaced at 30 x 30 cm^2/plant. The naturally established densities of Echinochloa were maintained. For each of the periodic harvests, the mixture yields were interpolated to the average density of 100 Echinochloa plants/m^2 by means of a weighted multiple regression procedure outlined by Spitters (1983). In this multiple regression, the reciprocal values 1/W of the per-plant weights W of a species were regressed on the plant densities of the different species in the mixture. To account for the serious heterogeneity in the variances of 1/W a weighting factor equal to $(E(1/W))^2$ was used for the observations in the regression, with E denoting the expectation values. This weighting factor is based on constancy of the variation coefficient of 1/W, which holds when the variation coefficient of the biomass per unit area is constant. An iterative procedure was applied as with each iteration E(1/W) is estimated more accurately. Effective times of emergence were day 156 and 154 for maize and Echinochloa, respectively. Experimental data were from M.J. Kropff, F.J.H. Vossen, C.J.T. Spitters and W. de Groot.

Input. The most comprehensive version of the model was used. Input for this were species characteristics and daily weather data of total global radiation and average temperature. Required species characteristics were the photosynthesis characteristics   and A_{max}, temperature sums needed to reach anthesis and maturity, dry-matter distribution coefficients as function of developmental stage, specific leaf area as function of developmental stage, relative death rate of green leaves, relative rate of litter fall, and light extinction coefficients. Most characteristics were derived from the literature or from other experiments. For Echinochloa, however, this was not always possible so that information from the expe-

362

riment itself was used. In the weed plots of 1983, plant height of maize was reduced strongly because of severe water stress. Therefore, the heights observed in the field were used in the model, rather than a general relation between plant height and developmental stage. The site index was taken to decline linearly from a value of one at emergence to a value of 0.31 and 0.14 at the final harvest dates of 1982 and 1983, respectively, with the latter values estimated on the basis of the observed final biomass of the weed-free maize.

Initialization. As the outcome of the competition process is strongly affected by the initial status of the species with respect to each other in the mixture, a correct initialization is of prime importance in competition models (Spitters & Aerts, 1983). The leaf areas observed at the first harvest were used as initial values. In 1982, the initial leaf area index was 0.85 for 11 maize plants/m^2 and 1.16 for 300 Echinochloa plants/m^2 at day 162. In 1983, these values were 0.34 for 11 maize plants/m^2 and 0.69 for 100 Echinochloa plants/m^2 at day 178.

Results. The simulation results did fit quite well with the dry weights measured in 1982 (Fig. 1). In the model it is assumed that the leaf area of the species is distributed uniformly over the soil area. However, maize was sown in spaced rows, so that Echinochloa received more light than predicted with the model. This may explain why the early growth of Echinochloa was underestimated and, consequently, the later growth of maize in mixture slightly overestimated.

For 1983 the performance of the model was less (Fig. 2). The growth of maize in presence of Echinochloa was strongly overestimated, especially during the second half of its growing period. The main reason is that the maize plants in the weed plots suffered from water stress in a very extreme way. They did hardly show any growth after day 205 because of a severe deterioration of their photosynthetic apparatus, an effect which is not accounted for in the simple model. Moreover, their height growth was strongly reduced. Their maximum height in the mixture was about 75 cm
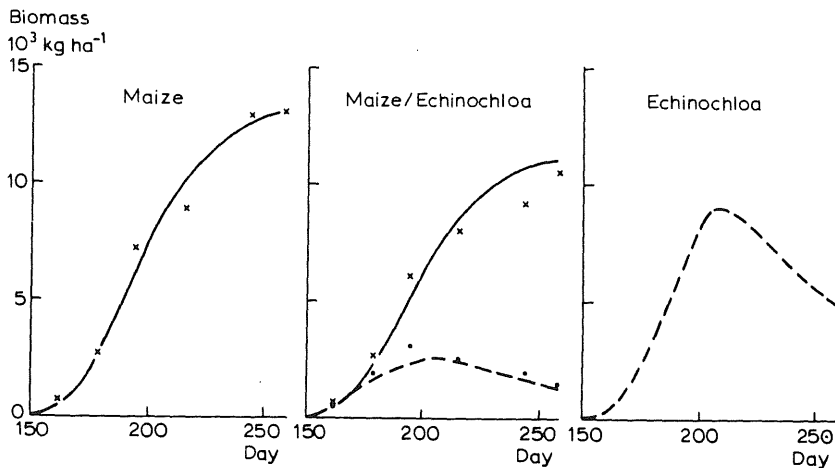

Fig. 1. Simulated time course of aboveground biomass of maize and Echinochloa in monoculture and mixture in 1982. Crosses and dots represent data points.
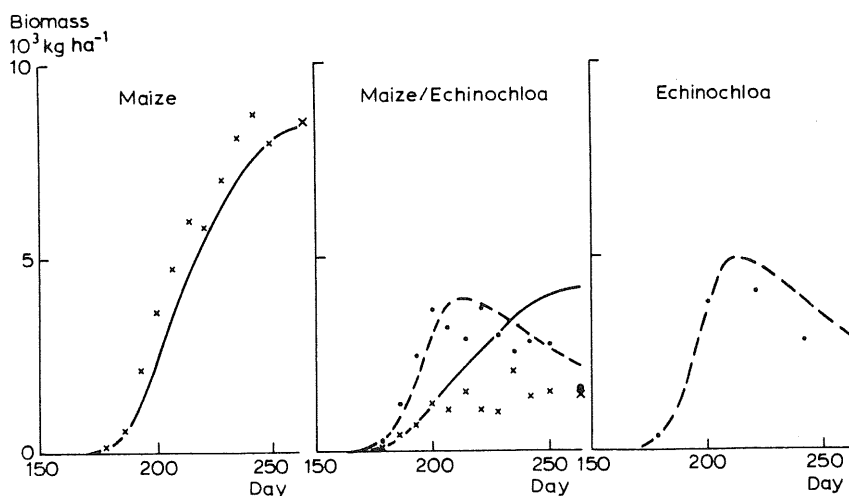
363

Fig. 2. Simulated time course of aboveground biomass of maize and Echino-
chloa in monoculture and mixture in 1983. Crosses and dots represent data
points.

and with that the maize plants were not able anymore to overtop Echino-
chloa, which with its 82 cm was hardly reduced in plant height.

DISCUSSION

Site index. As an empirical way to reduce the calculated potential growth
rate to the actual level, the site index SI is used as reduction factor.
    In the model, it was assumed that SI declines linearly in time from a
value of one at emergence to a lower value at the final harvest date of
the crop. This linear relation performed well as is shown by the good
agreement between simulated and measured growth course of the weed-free
maize (Fig. 1 and 2). with respect to the yields in mixture, the model
is, however, not very sensitive to the choice of the time course of SI.
Applying a constant SI over the growing season changed the simulated
final biomass of maize in mixture with only $-\frac{1}{2}\%$ and 0% and that of Echi-
nochloa in mixture with +10% and 0% in 1982 and 1983, respectively.
    Characters determining competitive ability in mixture. The presented
model is primarily an explanatory model. It supplies insight into the
underlying processes determining the competition between the species
constituting the vegetation. This facilitates conclusions about charac-
teristics that determine the competitive ability of a species in mixture.
This was worked out in detail by Spitters & Aerts (1983), where a similar
but more comprehensive model was used (erratum to their Table 2: top line
referring to maximum photosynthesis must be +66, +168, -61, +62, +171,
-66).
    Table 1 summarizes the effect of several attributes on the competitive
ability of a species. The values were generated by creating a mixture of
two identical maize cultivars in the 1982 situation with each time chan-
ging only one characteristic of the second cultivar. The effects of the
imposed differences were much greater in presence than in absence of

364

Table 1. Simulated effect of single characteristics on the ratio in bio-
mass production Y of two isogenic maize cultivars when grown alone in
monoculture or together in mixture. Cultivar 1 had the standard characte-
ristics of maize. For cultivar 2, in each line only the characteristic
mentioned was reduced to a value amounting 80% of that of cultivar 1.
Simulation based on the 1982 situation.

Modification	Biomass	$Y_{2,mono}/Y_{1,mono}$	$Y_{2,mix}/Y_{1,mix}$
Initial leaf area		0.97	0.80
Plant height		1.00	0.48
Specific leaf area (SLA)		0.64	0.17
Initial light use efficiency (ε)		0.69	0.30
Maximum leaf photosynthesis (A_{max})		0.86	0.50
Light extinction coefficient (k)		0.82	0.30

competition. In monoculture as well as in mixture, growth is related to
the absorbed amount of light energy. When a species grows alone in mono-
culture, its light absorption is related asymptotically to its leaf area
(equation 2). The same relation holds for the total light absorption of
the mixed vegetation. However, in the mixture, that part of the totally
absorbed amount of light that a species acquires is related linearly to
its leaf area, provided that the species have the same height and the
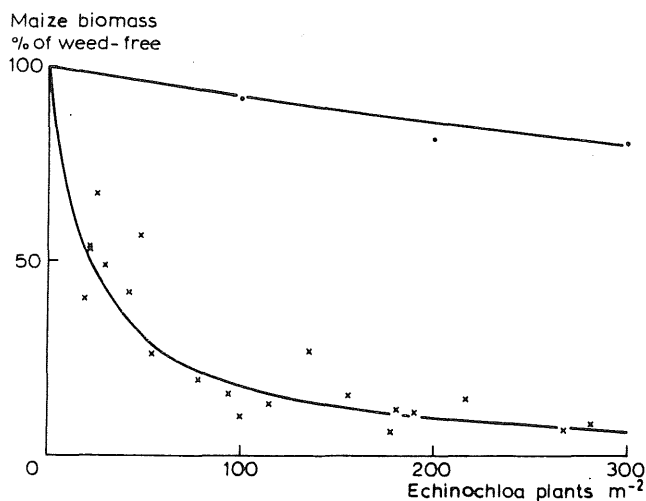same light extinction coefficient. Because of the principle of compound

Fig. 3. Final aboveground biomass of maize in 1982 (●) and 1983 (x), ex-
pressed as % of weed-free control, in dependence of initial density of
Echinochloa. Curves were based on a regression of the reciprocal per-
plant weights of maize on weed density, including yields of weed-free
maize plots (see text). This gave for the relative biomass yields
$Y_{mix}/Y_{mono} = b_o/(b_o + b_1 . N_{Ech})$ with the regression coefficients $b_o =$
0.0085 plant/g and $b_1 = 0.074$ cm²/plant in 1982, and $b_o = 0.0133$ plant/g
and $b_1 = 6.2$ cm²/plant in 1983.

interest, in mixture small differences in leaf area expansion are enlar-
ged in course of time.

Given the variation found in the field, plant height and initial
status appear as characteristics that affect competitive ability most.
The initial status is the product of the number of plants with which the
species is present in the mixture and the initial weight per plant. For
annuals, this initial weight at a given day is determined by time of
emergence and seed size. This points out that the plant density of the
weeds can explain only partly their competitive influence. This is empha-
sized by the large difference in yield reduction of maize between both
experiments conducted in two subsequent years at the same site (Fig. 3).
It was already discussed that the explanation for the large reduction of
maize yields due to the weeds in 1983 is complex. Nevertheless, we can
conclude that estimates of initial leaf area or soil cover of the weeds
will provide a more accurate, and in practice also more convenient,
measure of the degree of weed infestation than numbers of weed plants.

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UN MODEL SIMPLE DE SIMULATION DE LA COMPÉTITION CULTURE-MAUVAISE HERBE

Résumé: Un model simple est présenté pour simuler l'évolution (au cours
de la croissance) de la compétition entre une culture et les mauvaises
herbes associées. Une estimation a été faite d'abord de la vitesse de
croissance de la biomasse totale, ajustée pour le niveau de la produc-
tivité du site et pour le recouvrement incomplet du sol. Cette vitesse de
croissance de la biomasse totale a été distribuée journalièrement entre
les espèces selon leur contribution à la surface foliaire totale en
tenant compte des différences en hauteur des plantes. La performance du
model a été comparée avec les résultats de deux essais sur le terrain, où
du mais a été cultivé sans et avec Echinochloa crus-galli.