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Influence of environmental factors on herbicide performance and crop and weed biology

Simulation of competition for light and water in crop-weed associations

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Summary A deterministic model, named WEED-CROP, is introduced to simulate the competition between a crop and weeds for light and water. The potential daily assimilation of a species is calculated from its light interception combined with its assimilation-light response curve of single leaves. The potential rate is reduced in dependence on the available soil moisture. From this actual rate of assimilation the daily dry matter increment is derived. To account for differences among the species in the spatial position of their leaves and roots, the canopy as well as the root zone are divided into a number of horizontal strata. The model showed a close fit of the results of two field experiments, one with maize and yellow mustard and the other with maize and barnyard grass. A sensitivity analysis of the parameters revealed the prime importance of plant height and starting position (number of seedlings per m^2, initial seedling size, earliness of emergence) for competitive ability. The effect of starting position reflects the importance of seed population dynamics and germination strategy, which are translated into dry matter in course of the growth. C_4 characteristics gave, in general, a competitive advantage over C_3 characteristics.

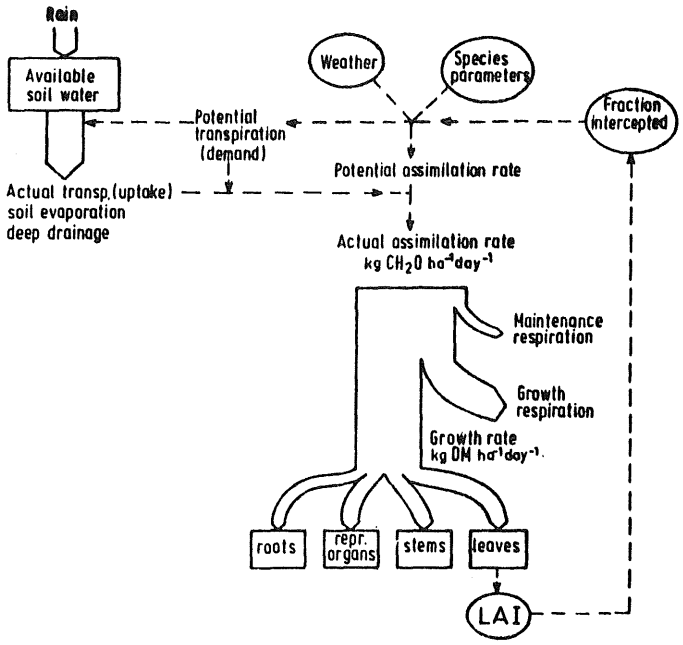
On the other hand, the greater water use efficiency of C_4 species favoured their yield in monoculture more than their yield in a mixed vegetation. Modelling of stomatal regulation appeared to be of crucial importance in modelling water consumption.

INTRODUCTION

Research on weed control is dominated by empirical studies where different measures or applications are compared on their effect upon crop yield. The weed itself is considered to be a black box. More effective weed management requires a better understanding of weed growth and its interaction with crop growth. This interaction can probably be understood from the same ecophysiological processes which are so well studied for the various crop species. That forms our starting point for the procedure followed in this paper. The knowledge about the growth of crops in relation to the availability of light and water is summarized in a dynamic simulation model. Replacing the species characteristics of the crop by those of the weed provides also a model for the growth of each weed species. Subsequently, the simultaneous growth of crop and weed is modelled on the basis of partitioning of the limiting resources, light and water, over the species.

After giving a short outline of the model, its structure is discussed in more detail. The model was tested with the results of two field experiments. To identify the characters that determine the competitive ability of a species, a sensitivity analysis was made by changing in turn the value of the main parameters in the model.

Fig. 1 Simplified scheme for the simulation of crop production in absence of weeds.



GENERAL STRUCTURE

In the WEED-CROP model, two levels of production are distinguished. In the potential level growth is only limited by actual weather, especially by the amount of incoming light. The crop is well supplied with water and nutrients, and free from pests and diseases. In the second level growth is limited also by soil moisture (Fig. 1).

At the potential level, the daily gross assimilation is calculated from the absorbed amount of light and the photosynthesis-light response curve of single leaves. After subtracting respiration the growth rate is obtained. This daily dry matter increment is allocated to the different plant organs. This part is mainly based on the simple and general crop growth model SUCROS (van Keulen, Penning de Vries & Drees, 1982).

In modelling the limitation of soil moisture, first the transpiration demand of the canopy is computed from the weather data. This potential transpiration is reduced with a factor depending on the available amount of soil moisture, which is tracked by a water balance. Because of stomatal closure, the potential rate of assimilation is reduced with the same factor as applied for the potential transpiration. These processes are simulated mainly according to the model ARID CROP (van Keulen, 1975; van Keulen, Seligman & Benjamin, 1981).

The interference between the species in a mixed vegetation is simulated on the basis of their shares in the absorbed amounts of light and water. The partitioning of these resources over the different species is affected by the spatial positions of their leaves and roots. Both the canopy and the root zone are therefore divided into a number of horizontal layers. For each day,

the relevant quantities and rates are calculated per layer, and summated over all layers to give the potential assimilation and transpiration. The actual rates and the daily growth rate of each species are derived similarly to those in monoculture.

Input for the model are daily weather data, hydraulic properties of the soil and some species characteristics. The major output is the time course of the biomass of each species. The program is written in CSMP, the Continuous System Modelling Program (IBM, 1975). Time step is one day.

The following sections, describing the model, are discussed in an ascending order of comprehensiveness. That holds also for the discussion within the sections, making it easier to derive simplified versions from the WEED-CROP model.

GROWTH OF THE CROP ALONE UNDER POTENTIAL CONDITIONS

We start with describing the growth of a crop under potential conditions and in absence of weeds. In that situation, available light, and to a lesser extent also temperature, determine growth. This section provides the frame of the model, which is represented schematically in the right-hand side of Fig. 1.

Available light. The incoming photosynthetic active radiation (400-700 nm) can be estimated roughly from the latitude of the site, the calendar day and the average degree of cloudiness (Goudriaan & van Laar, 1978b). It is however more accurate to use the daily values as measured at a nearby meteorological station. By dividing these values by the effective daylength, the average light intensity during the day is obtained.

This is sufficient to calculate the assimilation rate for situations where all of the incoming light is diffuse, i.e. under an overcast sky. To account for the bimodal distribution of light intensity under a clear sky, a differentiation into diffuse and direct light is made. The fraction of the day that the sky is overcast and the fraction that it is clear are estimated by relating the observed radiation to the expected values for a clear and a standard overcast sky (Goudriaan, 1977, p. 85).

Fraction absorbed. The incoming light is partly reflected and partly absorbed by the canopy and, for the remaining part, falling on bare soil. The light transmission through the canopy decreases exponentially with the amount of leaf area. So the fraction of the incoming light intensity which is absorbed by the canopy is given by

$$F_{abs} = (1 - 0.08)\ (1 - e^{-k.LAI}) \qquad (1)$$

with 0.08 the reflection coefficient of the canopy, k the extinction coefficient, LAI the leaf area index in m^2 leaves / m^2 area.

Gross assimilation. The instantaneous rate of assimilation of single leaves responds to light intensity according to an asymptotic exponential relation, characterized by the initial slope and the maximum level. Both parameters are species dependent (Goudriaan, 1982). The maximum level responds also to temperature, which reaction decreases with the age of the crop (de Wit et al., 1978, p.38,77,78).

The daily total crop assimilation may be calculated with the simplified procedure of Goudriaan & van Laar (1978) on the basis of the average light intensity during the day, the photosynthesis-light response curve of individual leaves, and the total leaf area of the crop. Here, however, a more comprehensive approach is applied where the canopy is divided into a number of horizontal leaf layers, and the crop assimilation calculated as the sum of the assimilation rates of the different layers. This approach was necessary to model the competition for light, so that it will be discussed in the next section.

The absorbed CO_2 is converted into carbohydrates (CH_2O). By multiplying the CO_2 assimilation rate with 30/44, the ratio of the molecular weights of CH_2O and CO_2.

Maintenance respiration. The respiration required for maintenance of a certain plant organ is roughly proportional to its dry weight. Following Penning de Vries & van Laar (1982), the daily maintenance respiration is set at

$$R_{maint} = 0.03\ W_{leaf} + 0.015\ W_{stem} + 0.01\ W_{roots} + 0.01\ W_{repr}$$

with the W's referring to the dry weights of the leaf blades, stems and petioles or leaf sheaths, roots and reproductive organs, respectively. The coefficients are given in g CH_2O/gDM/day. They are given at a reference temperature of 25°C. With each change of 10°C, they change with a factor two.

Conversion efficiency and growth rate. The efficiency with which the carbohydrates are converted into structural dry matter depends only on the chemical composition of the formed dry matter. Van Keulen, Penning de Vries & Drees (1982) and Penning de Vries & van Laar (1982) give typical values for the different plant organs. On the average, 1 g carbohydrates give 0.7 g structural dry matter with the remaining 0.3 g, the growth respiration, lost as CO_2 and H_2O.

The growth rate of the crop can now be summarized to be

$$GR = CVF\ (\frac{30}{44}\ A - R_{maint}) \qquad (2)$$

with CVF the conversion efficiency being about 0.7, A the daily assimilation rate and in the order of roughly 500 kg CO_2/ha/day for a closed crop surface under potential conditions, and R_{maint} the maintenance respiration being about 1.5% per day times the standing biomass.

Partitioning of dry matter. The dry matter increment is allocated daily to the different plant organs according to empirically determined distribution factors. First, a partitioning is made over roots and shoots. Then, the dry matter allocated to the shoot is distributed over the shoot organs. The distribution factors change with the stage of plant development. Examples may be found in Penning de Vries & van Laar (1982).

Leaf area expansion. The leaf area determines the fraction of the incoming light that is absorbed by the canopy (eqn 1). The area of the leaves is obtained by multiplying the simulated leaf dry weight with the specific leaf area (SLA), the leaf area per unit leaf weight. SLA changes with the developmental stage according to an empirical relation.

Development. Dry matter distribution as well as SLA depend on the developmental stage of the crop. The following scale is used for crop development: 0 at emergence, 1 at beginning of anthesis, and 2 at maturity. The rate of development becomes about constant when it is plotted against time in °C days, rather than against the chronological time in days. With that, each developmental stage is characterized by its own temperature sum required to reach it. Photoperiodicity is not considered explicitly

GROWTH OF CROP AND WEEDS IN COMPETITION UNDER POTENTIAL CONDITIONS

In this section, the distribution of the incoming light over the species in the vegetation, and the computation of daily assimilation per species is described. The calculation of the growth rates from the assimilation rates and the distribution of dry weight increment over the plant organs proceed analogously to that described for the growth of the crop alone.

Species with 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 light absorbed by the total canopy that corresponds with its share in the total leaf area. Thus, the amount of light absorbed by a species is obtained by multiplying the absorption of the total canopy (eqn 1) with the share of

that species in the total LAI. The daily assimilation of the species is calculated thereafter along the lines presented in the preceding section.

Species differing in plant height. However, most species differ in plant height; the taller species gaining a greater part of the incoming light than its share of the total LAI. Allowance is made for these differences in the position of the leaf area by stratifying the canopy into a number of horizontal layers. For each time step of one day, the following procedure is applied. The distribution of leaf area with height is characterized for each species by a parabola. The surface underneath the parabola is defined by the LAI of the species, and the upper limit by the plant height. Both LAI and plant height change with time. The canopy is divided into a number of height layers. For each day, the canopy is scanned layer after layer, from the top downwards. From the parabolic leaf area density functions, the LAI of each species and the total LAI are determined for each layer. The amount of light absorbed by that layer is given by the difference between the light intensity at the top and that at the bottom of the layer (eqn 1). Division by the total leaf area in the layer gives the mean illumination intensity in that layer. From the assimilation-light response curve of the species, its assimilation rate per unit leaf area is computed. Multiplication by its leaf area in the layer gives its assimilation rate in that layer. Summation over the different layers yields the daily assimilation of each species in the mixture.

To account for the bimodal distribution of the light intensity under a clear sky, distinction is made between the sunlit leaf area, which receives direct as well as diffuse light, and the shaded leaf area, which receives only diffuse light (Goudriaan, 1977, p. 83-84). For the assimilation-light response not the asymptotic exponential is used, but a rectangular hyperbola. This more gradually proceeding curve is applied because a daily average of the light intensity is considered instead of the time course of the light intensity during the day.

A summary equation to account for the height differences. The detailed approach followed above to account for the differences in plant height can be avoided in a summary model, by setting the assimilation rates of the two species proportional to the light intensities at half of their heights. A simple expression for these light intensities is derived from equation 1 under the assumption of a rectangular rather than a parabolic leaf area density function. This gives for the light intensities I, and with that for the assimilation rates A of the species 1 and 2 the ratio:

$$A_1 : A_2 = I_1 : I_2 = LAI_1 : LAI_2 . e^{-k(LAI_{\frac{1}{2}H_2} - LAI_{\frac{1}{2}H_1})} \qquad (3)$$

where the total LAI above half of its height H_1 is for species 1:

$$LAI_{\frac{1}{2}H_1} = \tfrac{1}{2} LAI_1 + \frac{H_2 - \frac{1}{2}H_1}{H_2} LAI_2 \qquad \text{with} \quad \frac{H_2 - \frac{1}{2}H_1}{H_2} \geq 0$$

The total LAI above $\frac{1}{2}H_2$ is found in a similar way. Combining equation 3 with $A_1 + A_2 = A_{tot}$ gives an expression for the assimilation rate of each species as fraction of the total stand assimilation A_{tot}. A first calibration on the comprehensive model showed that for the extinction coefficient a value of about 0.9 times the actual value should be used.

Limitations. The model does not account for (i) heterogeneity in the distribution of the leaf area over the ground area, and for (ii) adaptation to shading. It is assumed that the leaf area is equally distributed over the ground area. Especially during the early growth stages in the field, the leaves tend to be clumped together within the plants as units, so that the model overestimates slightly the light absorption. In a mixed vegetation, leaves of a species are surrounded more frequently by leaves of the same species than by leaves of other species so that the competitive ability of the taller species tends to be overestimated in the model. This is especially true for tall row sown crops, like maize, in competition with short weeds.

Adaptation to shading is not accounted for. The major adaptations are the production of thinner leaves (higher SLA), often an enhanced stem elongation, and probably a lower maintenance respiration due to the reduced photosynthetic capacity.

GROWTH OF THE CROP ALONE, WHEN LIMITED BY WATER

Under water shortage the stomata are closed to restrict the water loss of the plant. With the reduction of the transport of water vapour going out of the leaf, also the CO_2 transport into the leaf decreases. The reduction of CO_2 assimilation due to the closing stomata is more or less proportional to that of the transpiration for a wide range of environmental conditions. In formula:

$$\frac{A_{act}}{A_{pot}} = \frac{T_{act}}{T_{pot}} \quad \text{or} \quad A_{act} = \frac{T_{act}}{T_{pot}} A_{pot} \qquad (4)$$

where the subscripts of the assimilation A and the transpiration T refer to their potential values at an adequate water supply and to their actual values under water stress.

Thus, the assimilation rate A_{act} under water limitation is obtained by reducing the potential assimilation A_{pot}, calculated in the preceding sections, with the reduction factor T_{act}/T_{pot}. We will now discuss the calculation of the potential transpiration and its reduction in dependence on the available soil moisture.

Potential transpiration. The evaporation demand of the air is calculated according to the method proposed by Penman (van Keulen, 1975, p.51,77,120). Input are the daily averages of incoming short wave radiation, air temperature, vapour pressure of the air, and windspeed. The potential transpiration of a canopy differs from this evaporative demand for a free water surface, especially due to the deviating resistances for the diffusion of water vapour. These are the stomatal resistance, the boundary layer resistance around the leaves (van Keulen, 1975, p.122) and the turbulence resistance above the canopy (Goudriaan et al., 1984). By means of the stomatal resistance, allowance is made for the differences among the species in their stomatal control (Goudriaan, 1977, p. 76-77; de Wit et al., 1978, p.43-45, 87-92; Goudriaan, 1982). The potential transpiration may be calculated according to van Keulen (1975, p.120-123,132) with the turbulence resistance above the canopy according to Goudriaan et al. (1984). Here, however, the more comprehensive approach is followed where the potential transpiration is calculated for each leaf layer within a stratified canopy (see next section).

Available soil moisture. Available to the plants is that amount of the soil moisture that is within the root zone and above wilting point. The available water is tracked with a water balance in which two levels are distinguished: (i) in and out the system defined by the rooted zone and (ii) the spatial distribution within the system. The second level is not strictly necessary to simulate the growth of a crop alone, but is required to account for differences in rooting pattern between crop and weeds. Therefore it is discussed in the next section.

The infiltrated water, here rainfall, composes the input of the system. No account is made for capillary rise from soil layers below the root zone, which flow was negligible in the experiments on sandy soils without a water table. Water moves out of the system by soil evaporation, water uptake by the plants, and by deep drainage to layers below the root zone.

Potential soil evaporation is calculated with the Penman equation, taking into account the resistance of the boundary layer and the turbulence resistance above the soil surface (van Keulen, 1975, p.77). The actual soil evaporation is obtained by reducing this potential value with a factor owing to soil cover by the canopy (Stroosnijder, 1982) and with another factor

owing to the desiccation of the top 2 cm of the soil (van Keulen, 1975, p.89). Deep drainage is given by the rate of flow of infiltrated water out of the system. Crop water uptake is supposed to equal the actual transpiration of the crop.

Actual transpiration. When the crop is well-supplied with water, the transpiration equals its potential value. That value is determined by weather, stomatal control and degree of soil cover. Under water shortage, the potential value is reduced with two empirical factors (van Keulen, 1975, p.133) depending only on soil moisture content. They are supposed to be unaffected by the transpiration demand and the species, which is probably an over-simplification (Doorenbos & Kassam, 1979, p.28).

A low soil temperature hampers water uptake, which leads to an additional reduction of the transpiration when the plants suffer from water stress. This process is modelled according to a procedure proposed by van Keulen (pers. commun.), which replaces an incorrect procedure published earlier (van Keulen, 1975, p.134). In the two maize experiments considered here, soil temperature appeared of no influence for water uptake: during mid summer when there was water shortage the temperature was high enough, whereas during spring when the temperature could be limiting there was enough water available.

Growth rate. The ratio T_{act}/T_{pot} provides the factor with which the potential rate of assimilation has to be reduced to account for the stomatal closure under water stress (eqn 4). In the present version of the model, the growth rate rather than the assimilation rate is reduced with this factor. In addition to the increased stomatal resistance, water stress depresses the assimilation rate also by deterioration of the photosynthetic apparatus. The resulting decrease of the assimilation-light response is modelled according to van Keulen, Seligman & Benjamin (1981).

The simulation of dry matter allocation and leaf area expansion proceeds as described for crop growth under potential conditions. Only the distribution of the dry weight increment over shoots and roots is allowed to be affected by water stress (cf. van Keulen, Seligman & Benjamin, 1981).

GROWTH OF CROP AND WEEDS IN COMPETITION, WHEN LIMITED BY WATER

In a summary model, the simulated total growth of the vegetation could be partitioned over the species according to their share in the total leaf area, but then no account would be made for differences among the species in their spatial position with respect to the limiting factor. For that reason, both the canopy and the root zone are stratified in the WEED-CROP model. The demand side and the supply side for water uptake are discussed successively.

Potential transpiration. The computation of the potential transpiration proceeds analogously to that of the potential assimilation. The canopy is divided into a number of horizontal layers. For each layer the average values during daytime (stomata are closed at night) are determined for absorbed short wave radiation, outgoing long wave radiation, vapour pressure deficit, and wind speed. The simulation of these gradients is based on Goudriaan (1977), de Wit et al. (1978), and Goudriaan et al. (1984). Again a differentiation is made between sunlit and shaded leaf area. The potential transpiration is calculated as described in the preceding section, but here for each canopy layer separately. Adding the values layer by layer provides the total potential transpiration per species per day. This represents the demand for water.

Actual transpiration. The soil is also partitioned into a number of strata so that differences among the species in rooting pattern may be accounted for, and the spatial distribution of available moisture within the system can be characterized. The available amount of soil moisture is tracked per soil layer by simulating the daily inflow and outflow for the layers.
(1) The infiltration rate of rain forms the inflow into the top layer. The excess above field capacity is the influx into the second layer, and so on.

The excess of water from the bottom layer is drained below the root zone. (ii) The evaporated soil moisture (preceding section) is not only withdrawn from the top layer, but all layers contribute to the evaporation loss but in an exponentially descending order. That mimicks the upward flow replacing the soil moisture evaporated from the top layer by soil moisture from deeper layers. (iii) The transpiration demand of a species is equally distributed over its rooted depth. That gives its potential water demand for each soil layer. That demand is only satisfied with an adequate water supply in all layers. When the available soil moisture in a layer is below a certain value, the water uptake of the species in that layer is reduced with a factor depending on the available moisture. The total water uptake of a species, and with that its actual transpiration, is obtained by adding its uptake layer by layer.

This compartmentalized water balance is taken from the model ARID CROP (van Keulen, 1975, p.89-91,127-128,132-133). Applied to a mixture of species the distribution of the transpired soil moisture among the species is largely according to their demands. Differences in rooting pattern are involved only as far as they concern differences in rooted depth.

This approach neglects that (i) at a given water supply, stomata tend to be closed more strongly when the transpiration demand is larger. This is the case for a tall crop compared to the shorter weeds growing under its shade, and for a water spending C_3 herb compared to a water saving C_4 grass. The approach also neglects that (ii) a species with a greater root density withdraws more water than its sparser rooting neighbour. (iii) At low light intensity, as received by shaded plants, CO_2 assimilation will be limited more by the carboxylation resistance than by the stomatal resistance, i.e. light instead of water being the limiting factor. Equation 4 is then no longer valid. This aspect may be accounted for by reducing the maximum level of the assimilation-light response curve with the reduction factor T_{act}/T_{pot}, instead of reducing the assimilation rate A_{pot} with this factor. In conclusion, the model has to be seen as a first approach in modelling competition for water. Future improvements should be focussed on the above mentioned points.

COMPARISON OF MODEL PERFORMANCE WITH RESULTS OF FIELD EXPERIMENTS

The model is mainly built out of elements of crop growth models developed in Wageningen, and most of these elements were more or less validated with field experiments (e.g. van Keulen, 1975; de Wit et al., 1978). The main new aspect introduced by the WEED-CROP model is that it accounts for the differential growth of species within a mixed vegetation. Its performance will now be confronted to the results of field experiments.

Experimental design. Two field experiments with maize in mixture were carried out in Wageningen in the years 1981 and 1982. Dry weight progression of the species was determined by frequent harvesting.

In the first experiment (1981), maize cv. Brutus and yellow mustard (Sinapis arvensis L.) were grown in monoculture at 30x30 cm^2/plant and about 9x17.5 cm^2/plant, respectively. In a mixture of both, each species was spaced as in the monoculture. Leaf production and height progression of mustard were of such a degree that at calendar day 155 the mustard was thinned to about 12x17.5 cm^2/plant in the mixture and about 18x17.5 cm^2/plant in the monoculture. This appeared to be insufficient to keep the maize growing so that at day 175 all mustard plants were removed from the mixture. The soil was a loamy sand with field capacity at 28.3 vol% and wilting point at 8.9 vol%, and with maximum rooting depth only 0.50 m. Maize emerged at day 134 and mustard at day 131.

In the second experiment (1982), maize cv. LG11 was grown at 10x75 cm^2/plant. Some plots were kept weed-free, whereas in other plots the naturally emerging weed population was thinned to a stand of 300 plants/m^2 of barnyard grass (Echinochloa crus-galli (L.) P.B.). The main flush of emergen-

ce of barnyard grass was at day 140, while maize emerged at day 135. Field capacity of the sandy soil was at 20.2 vol% and wilting point at 5.6 vol%. Maximum rooting depth was supposed to be 1.20 m.

Input. The main input variables were: daily weather data, field capacity and wilting point of the soil, day of emergence, maximum rooting depth, initial slope and maximum level of the photosynthesis-light response curve of single leaves, stomatal reaction to internal CO_2 concentration, pattern of dry matter partitioning over the plant organs, specific leaf area, plant height, rate of development in relation to temperature, relative rate of litter fall and rate of senescence. Most species characteristics were derived from the literature or from other experiments in order to pursue an independent testing of the model. This was, however, not always possible, especially with respect to yellow mustard.

The light intensity at the top of the maize plants in mixture with yellow mustard was at day 175 only 5% of that above the whole vegetation. To account for the reduction in photosynthetic capacity due to prolonged shading, the maximum level of the photosynthesis-light response curve of maize was reduced to 13% of its optimal value (cf. van Laar & Penning de Vries, 1972, p. 21,23). After removal of the mustard, this maximum level was recovered with a relative rate equal to the relative growth rate (cf. van Keulen, Seligman & Benjamin, 1981).

Initialization and leaf area expansion. Two approaches are applied for the leaf area development. (1) Firstly, the progression of LAI as measured in the experiment is fed into the model. This provides a test for the simulation of transpiration, assimilation and the resulting dry weight increment at given leaf areas, i.e. given the size of the assimilating and transpiring surfaces. The initialization of the model is then of no effect. (2) In general, however, one wants to simulate growth without doing the experiments beforehand. In the second approach LAI is therefore generated in the model by multiplying the simulated weight of green leaves with the specific leaf area. Simulation of total stand growth remains then rather insensitive to initialization. But that is not true anymore for the growth rates of the individual species in the mixed vegetation. Initialization has a very large influence on these, which can be understood from the large effect of starting position on competitive ability (next section). To avoid problems conferred with the simulation of seedling growth, the model is initialized with the leaf area per plant as measured after seedling stage.

Fig. 2 Simulated time course of above-ground dry weight of maize and yellow mustard in monoculture and in mixture. Crosses and circles represent data points.

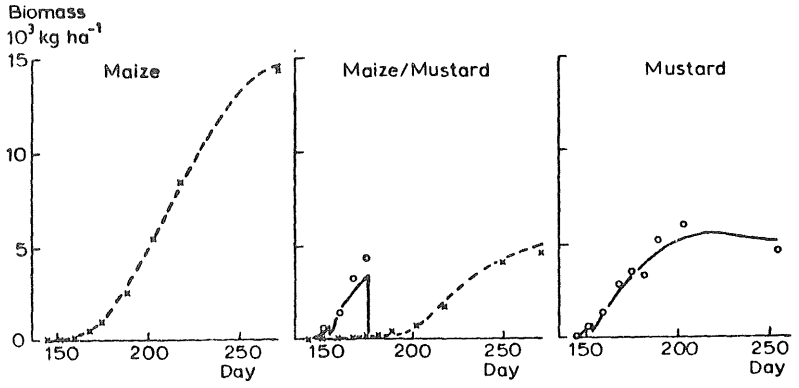
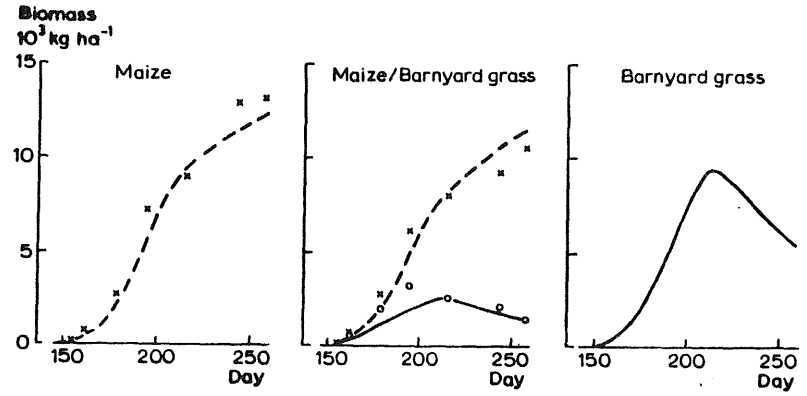


Fig. 3 Simulated time course of above-ground dry weight of maize and barnyard grass in monoculture and in mixture. Crosses and circles represent data points. Maize was grown at 0.10 x 0.75 m^2/plant and barnyard grass at 300 plants/m^2.



Results. The simulation results are presented in Figs 2 and 3, together with the experimental data. The progression in the dry weights is fitting well, except that of barnyard grass in the mixture. The presented curves are based on the measured LAI's, but the simulation results where LAI is predicted in the model were hardly inferior. The growth reduction due to water shortage was substantially, especially in the second experiment. This is illustrated by the difference between the actual maize yield of 13 tons/ha (Fig. 3) and the simulated yield of 19 tons/ha if there had been no water stress.

The lower fit of the growth of barnyard grass in mixture exposes some weak points of the model. (i) The assumption that the leaf area of any species is distributed homogenously over the ground area was clearly not true

Fig. 4 Simulated time course of the amount of moisture in the root zone (top 50 cm of the soil) in monocultures of maize and yellow mustard. The observed amounts (x,o) were determined gravimetrically. The dotted curve represents the simulated time course if mustard had the same stomatal regulation to the internal CO_2 concentration as maize.

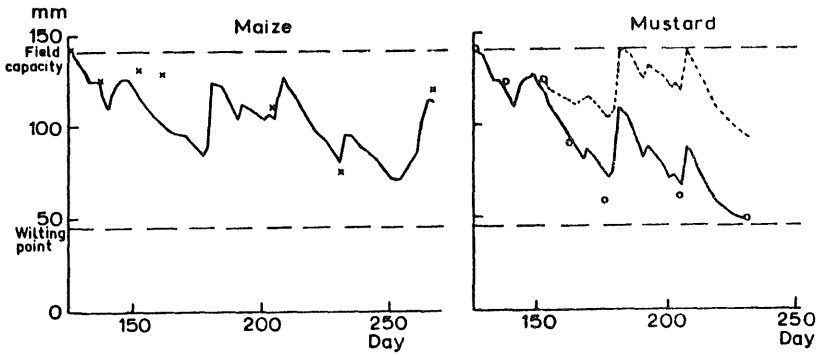


Table 1 Characters determining the competitive ability (dry-matter production) of a species in a mixed vegetation and its monopolization of light and water. The characters mentioned are largely accounted for in the WEED-CROP model.

o Starting position
  - number of plants per m^2
  - weight per seedling
    - weight per seed
    - earliness of emergence

o Length of (vegetative) growing period

o Absorption capacity per unit of absorbing organs:

  - light: canopy architecture → extinction coefficient
  - water:
    - transpiration demand
      - canopy architecture → extinction coefficients
      - stomatal behaviour
    - uptake capacity: root activity

o Spatial position of absorbing organs with respect to absorption of the limiting resource:

  - light: plant height
  - water:
    - transpiration demand: plant height
    - uptake capacity: rooting pattern, rooting depth

o Carbohydrates produced per unit absorbed of the limiting resource:

  - light: maximum level and slope of photosynthesis-light response curve
  - water: water use efficiency

o Dry weight increment per unit assimilated carbohydrates:

  - coefficients of maintenance respiration
  - conversion efficiency: chemical composition of dry matter

o Amount of absorbing organs formed per unit dry weight increment:

  - light: leaf area ratio = leaf weight ratio x specific leaf area
  - water:
    - transpiration demand: leaf area ratio
    - uptake capacity: root length ratio = root weight ratio x specific root length

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      - stomatal behaviour
    - uptake capacity: root activity
- o Spatial position of absorbing organs with respect to absorption of the limiting resource:
  - light: plant height
  - water:
    - transpiration demand: plant height
    - uptake capacity: rooting pattern, rooting depth
- o Carbohydrates produced per unit absorbed of the limiting resource:
  - light: maximum level and slope of photosynthesis-light response curve
  - water: water use efficiency
- o Dry weight increment per unit assimilated carbohydrates:
  - coefficients of maintenance respiration
  - conversion efficiency: chemical composition of dry matter
- o Amount of absorbing organs formed per unit dry weight increment:
  - light: leaf area ratio = leaf weight ratio x specific leaf area
  - water:
    - transpiration demand: leaf area ratio
    - uptake capacity: root length ratio = root weight ratio x specific root length

for the stand of 1982 where maize was sown in rows 75 cm apart. That underestimates the growth of barnyard grass, which short-statured species took advantage of the greater light penetration between the maize rows. (ii) In the present version of the model, the available soil water is allotted to the species mainly proportionally to their demands. This underestimates the growth of the shorter species because of reasons discussed in the final paragraph of the preceding section. In a simulation run with the total water uptake of the species redistributed among them according to their share in the total root mass, the peak biomass of barnyard grass was 2.8 tons/ha and the final yield of maize 10.4 tons/ha, i.e. a closer fit than the original results presented in Fig. 3.

Soil moisture content was measured only in the first experiment. Its time course is fitted well by the model (Fig. 4). The water consumption of maize is remarkably smaller than that of yellow mustard, which is brought about by their difference in stomatal control. Maize is a C_4 species, and regulates its stomatal opening to keep the CO_2 concentration in the substomatal cavity constant at 120 vpm (Goudriaan & van Laar, 1978a). Yellow mustard is a C_3 species and, given its extremely low water use efficiency compared with other species in a pot experiment (G. Dekkers, unpubl.), it is probably a species without a reaction of its stomata to the internal CO_2 concentration. The model results of Fig. 4 support this assumption. The model run where for mustard the regulatory mechanism of maize was supposed (dotted curve in Fig. 4) emphasizes the large effect of stomatal behaviour on water consumption. Crop yield losses due to weeds will, therefore, be strongly affected by the particular mechanism of stomatal control of the weed species. Water-saving C_4 weeds, like barnyard grass, will reduce crop yield less than water spending species like mustard.

WHAT DETERMINES THE COMPETITIVE ABILITY OF A SPECIES?

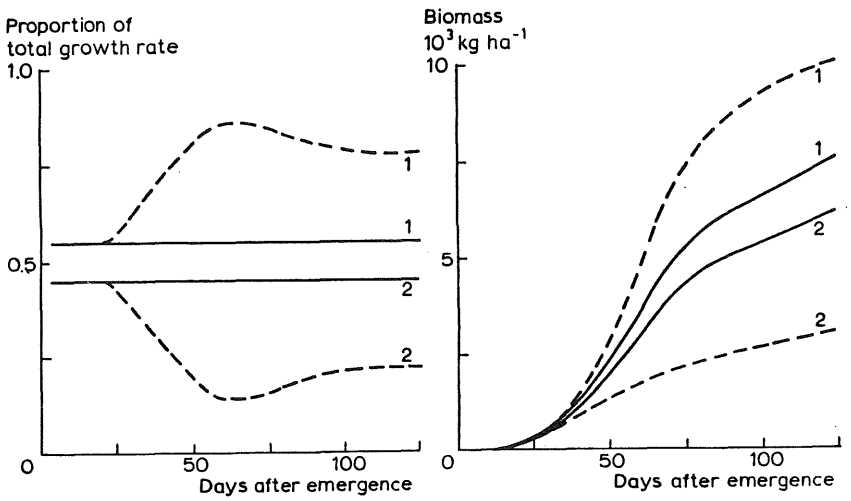
The influence of individual characters is studied with the model by starting with two species which are fully identical. Then, every time only one parameter is changed for one of the species. The reference species is one having the characteristics of maize. In fact, we create any time two isogenic maize cultivars. The location is the field in the second experiment with the weather data of that year. So a sensitivity analysis is executed for a number of parameter values, but not for the weather.

Table 1 summarizes the characters that determine the competitive ability of a species and which are accounted for in the model. Some of these will be discussed in relation to the results of the sensitivity analysis. Competitive ability is defined here as dry-matter production in mixture.

Starting position. A species that starts with a two times greater leaf area than its neighbour intercepts twice as much light as that neighbour. The next day their LAI's will still relate as 2 : 1, provided that both have the same efficiency of photosynthesis and the same pattern of investment of new dry weight into leaf area. At the time of canopy closure, the first species has gained a twofold share of the total leaf area. At equal plant heights, that species intercepts twice as much light leading to a twofold growth rate. The absolute differences between the species swell up in time (Fig. 5b, solid curves), illustrating the effects of competition. However, the relative differences remain the same. Thus, a two times greater starting position results into a two times larger final biomass in the mixture. This emphasizes the extreme importance of the starting position in competition (Spitters, 1984). It reflects the materialization of germination strategy and soil seed population dynamics into dry weight production. This is the translation of numbers into dry matter.

A favourable starting position is achieved with a large number of seedlings per m^2 as well as with big seedlings. A large seedling size at a certain time is obtained from large seed reserves as well as by an early emergence. These three aspects are mutually substitutable as the initial

Fig. 5 Time course of (a) proportion of total stand growth rate and (b) above-ground dry weight of two isogenic maize cultivars in mixture. Cultivar 1 is present in the mixture with 15.4 plants/m^2 and cv 2 with 12.6 plants/m^2. Cultivar 2 has either the same height as cv 1 (solid curves) or 70% of the height of cv 2 (broken curves). Simulation based on weather and soil data of the 1982 experiment.



biomass per unit area at a certain early time t is given by:

$$y_t = N \cdot w_t = N \cdot w_o \cdot e^{rt} \qquad (5)$$

where N the number of plants per m^2, w_o the weight per plant at emergence being roughly equal to half of the weight per seed, r the relative growth rate during the exponential stage being in the order of 0.15 per day.

This suggests that crop yield losses have much more relation with the difference in starting position between crop and weed than with the number of weed plants alone. A comparison of the 1982 experiment with a similar experiment carried out in 1983 supports this view. In the 1982 experiment, besides plots with 300 plants per m^2, also plots with 100 barnyard grass plants per m^2 were grown. Maize yield was reduced there with only 8%. In the 1983 experiment, however, the same number of barnyard grass plants depressed the yield of maize with 88%. In the first experiment, maize emerged 5 days earlier than the weed but in 1983 1½ day later. The effect of the retarded start of maize in the second year was reinforced because it was not able to overtop the weed. That shows that a difference in emergence is usually more effective than predicted with equation 5 because it interferes with a difference in plant height. The early drought occurring in 1983 was probably a second cause responsible for the large difference between both experiments.

The extreme variable yield reduction caused by the 100 plants of barnyard grass shows that action thresholds for weed control are necessarily set at low weed numbers in order to prevent the serious yield reductions in exceptional years and sites. For most situations, however, it means an overkill which draws on the financial profits. More efficient action criteria are therefore highly desirable. The model suggests that the initial ratio between the leaf area of the weeds and that of the crop provides a better criterion than thresholds with fixed weed numbers.

Plant height. In Fig. 5 (solid curves), the relative differences in biomass between the species remained constant in time, because the light absorption of each species was proportional to its share of the total canopy. At different plant height, however, the taller species intercepts with the same leaf area more light than the shorter one. With the additional growth it increases steadily its share in the canopy as long as new leaves are produced (broken curves in Fig. 5a). The occupied positions change in favour of the taller species, the one showing priority for the factor light.

Evidently, the greater the difference in plant height the stronger the effects are. Height appears to be of greater advantage under potential conditions when light, instead of water, limits growth. That is because under these more productive conditions, total LAI is greater and with that the intensity of the light received by the short species is smaller. Fertilization and irrigation improve thus the competitive ability of a tall crop against shorter weeds. The reverse will be true for short crops, like onions.

When there is water shortage, the assimilation of any species in the mixture is reduced in the model with the same factor. This reduction factor depends only on the soil moisture content. With an equal LAI, the effect of plant height becomes then the same under stressed and non-stressed conditions. This will overestimate the effect of plant height in stressed field conditions. The short species will suffer less from water shortage because: the evaporative demand is lower at the bottom of the canopy, its share in the total root mass will often be less inferior than its share in total light absorption, and its assimilation may be limited more by light than by water (see final paragraph of the section on water competition).

Absorption capacity formed per unit growth. An alteration of the occupied positions does not only occur when there are differences in plant height (broken curves in Fig. 5a), but also when one species makes more absorptive capacity from its biomass. For example, a 20% greater specific

Table 2 The simulated effect of C_4 characteristics on biomass production in monoculture and in a ½ : ½ mixture with an isogenic C_3 species. This C_3 reference has maize characteristics except for the typical C_4 traits. Presented are % changes compared to the yield of the C_3 reference (6.2 tons/ha in the stressed and 10.8 tons/ha in the non-stressed monoculture, and half of these values in mixture). In each line only one C_4 characteristic is assigned to the C_3 reference, but in the last line all C_4 characteristics are assigned together. 'C_4 mono' refers to the effect of the C_4 traits in monoculture and 'C_4 mix' to the effect in mixture with the C_3 species of which the associated yield change is denoted by 'C_3 mix'. Simulation based on weather and soil data of the 1982 experiment.

Modification \ % yield change	Water-stressed			Non-stressed		
	C_4mono	C_4mix	C_3mix	C_4mono	C_4mix	C_3mix
Maximum photosynthesis 60 instead of 30 kg CO_2/ha/h	+ 66	+168	-61	+62	+171	-66
Light efficiency of photosynthesis 14 instead of 11 x 10^{-9} kg CO_2/Joule	+ 23	+ 54	-26	+27	+ 63	-27
Constant internal CO_2 conc. 120 instead of 210 vpm	+ 26	+ 17	+17	0	0	0
Temperature dependence of maximum photosynthesis	- 28	- 55	+35	-27	- 53	+37
Temperature dependence of rate of vertical root extension	- 7	- 18	+12	0	0	0
All C_4 characteristics	+122	+203	-37	+82	+199	-64

leaf area (thinner leaves) gave rise to a 3.4 times greater final biomass of the species in the mixture in the sensitivity analysis. Rearrangement of competitive positions are mainly brought about by differences in phasic development of the leaf area to plant weight ratio, which differences occur especially in vegetations of perennial species.

C_3 versus C_4 characteristics. Maize and barnyard grass are C_4 species, while mustard is a C_3 species. Both types are differentiated not only in assimilation characteristics, but also in stomatal regulation, nitrogen demand and temperature requirement. Table 2 presents the effect of each of the differences separately.

We will discuss first the performance in monoculture. The C_4 photosynthesis gives a greater light use efficiency (initial slope as well as maximum level) and with that a larger biomass production. In combination with the water saving stomatal reaction, it gives also a greater water use efficiency, leading to a higher yield when moisture is in short supply. In the model runs, the C_4 species produced 11.0 grams of dry matter per litre transpired water, whereas the C_3 species had a water use efficiency of 6.3 g/litre. This C_3 species is of the saver type as it keeps its internal CO_2 concentration at a constant level. A C_3 species without a regulation of its stomata to the internal CO_2 concentration, like mustard, spends about twice as much water. Here, its water use efficiency was 3.7 g/litre. That demonstrates the big advantage of a high water use efficiency in attaining a high yield in monoculture, especially when the plants have to draw on a limited stock of soil moisture.

In the situation where the species had to compete with each other, the effects were even more pronounced. Competition acts as a magnifying-glass for growth differences (Spitters, 1984). A greater light use efficiency gives a larger growth rate which leads to the production of additional leaf area. In a mixed vegetation that leads to additional light absorption at the cost of the neighbours so that the competitive position of the species is improved (cf. broken curves in Fig. 5). This is opposite to a closed monocrop, where the additional leaf area is of no advantage because all the incoming light is already monopolized by the species. Contrary to its greater light use efficiency, the water saving stomatal behaviour of the C_4 species is of no advantage in a mixed vegetation. The water saved by the C_4 plants is then consumed by their water spending neighbours.

The conclusion that C_4 species are more competitive than C_3 species may, however, not be drawn. The advantage of C_4 species presented in Table 2 may be cancelled due to lower air temperatures or by a later emergence due to a higher temperature requirement for germination. In general, considerable caution is needed in conclusions that a certain character provides a competitive advantage. A modification of a character seldom stands alone. For example, the different C_4 characteristics are all closely linked physiologically. An attribute which, shows an advantage at first sight, often has also its ecological penalties. For example, the production of thinner leaves contributes to a steady improvement of the share in the total leaf area of the vegetation, but it may mean also a reduced maximum level of the assimilation rate per cm^2 leaf area.

After all, the competitive ability of a seed reproducing annual species is dominated by its seed flow dynamics and its germination strategy. These are 'directed towards pushing the seedlings in the right time at the right place'. So they determine the starting position of the species, which is translated during the growing season into biomass. Differences in growth characteristics, like the C_3-C_4 contrast, are not more than amendments to the starting relations. Thus, the competitive ability of a species is not a fixed character, but something that depends strongly on its starting position relative to that of its neighbours. With that it varies greatly with environmental conditions of weather and soil.

CONCLUDING REMARKS

In modelling the effects of weeds, we may discriminate between two approaches: (i) an approach with biomass as main state variable and directed towards the short term effects within a growing season, and (ii) an approach with the numbers of propagules of the weed species as main state variable, which takes into account the long term effects over growing seasons. The first approach is in the field of ecophysiology and the second in that of population dynamics. The two approaches require different types of competition models, which will be discussed now.

The dynamics of biomass. Weeds reduce crop yield because, among other things, they capture the resources which were otherwise used by the crop. This competition process may be simulated by a dynamic and explanatory model. The WEED-CROP model is such a model where the time courses of the dry weights of crop and weeds are simulated on the basis of the underlying ecophysiological processes. Such a comprehensive model is above all things a way of integrating our knowledge about these processes. Their size, complexity and required number of input variables make comprehensive models less suited for forecasting purposes. Moreover, it is clearly not so, that the more extensive the model the better the fit it gives.

Simple, semi-empirical models are more appropriate for forecasting. The following procedure might be a starting point to allow for the aspects of competition within a weed control advisory system. Each time step, total stand growth is allocated to crop and weeds according to their shares of the total leaf area (Spitters, 1984). Equation 3 provides a correction factor for the height differences, but is has to be noted that this equation overestimates the effect of the height differences at a low production level. Initialization can be based on the weed infestation as observed in the field early in the season. With this approach primarily the percentage of yield reduction is forecasted in dependence of time and degree of weed removal. A cost-benefit analysis requires absolute yields. These are probably best achieved by multiplying the predicted percentage of yield reduction with the farmers' expectation of final yield.

The dynamics of numbers. Weed control has to anticipate for the possible effects in succeeding years. The standing weeds are the source that replenish the soil population of seeds (and rhizomes, etc.), from which future weed infestations have to be recruited. Forecasting the long term changes in weed populations is of prime importance for integrated weed management where certain measures are directed towards minimizing the soil seed population, and when crop rotation is involved. Long term forecasting draws upon models in which the dynamics of the numbers are simulated. It should, however, be possible to simulate seed flow dynamics also in terms of changes in total biomass and with that passing the level of the individual.

The population dynamic models ask for highly condensed competition subroutines. Instead of simulating the time course of competition during the growing season, an empirical measure of the outcome of competition will often be more appropriate. The method published in an earlier paper (Spitters, 1983) may be useful for that purpose. There the competitive ability of species 1, relative to species 2, was characterized by the number of plants of species 1 that has an equal effect on the yields as one plant of species 2. This number, measuring the relative competitive ability of 1 to 2, would be independent of the numbers of plants of each of the species and of the presence of other species provided that there is no serious self-thinning. It certainly depends on the time of emergence of species 1 relative to that of species 2 (eqn 5). With this measure of competitive ability, the final biomass in mixture can be calculated for each species separately from the numbers of plants of the different species and the presumed production level. The seed production of the different species is then obtained from their number of seeds produced per gram biomass.

Conclusion. The prime aim of the comprehensive WEED-CROP model introduced here is to summarize and to integrate the ecophysiological processes governing the competition between crop and weeds. The model may help also to derive and to calibrate more simple models which may be more appropriate for instruction and forecasting.

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