

17. Simulation of plant production in arid regions: a hierarchical approach

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Introduction

The increasing interest in the agricultural production potential of the world, reflected among other things by the enormous efforts put into the IBP programmes in recent years, has diverted much research into the development of tools suitable for the calculation of potential productivity. This has coincided with growing accessibility to high speed computers which enable relatively easy handling of rather complicated systems, resulting in the development of a variety of computer models of crop, growth, plant production and agricultural potential (e.g. Seligman, 1976). In many cases, these models are physiologically based and deal with situations where growth conditions, particularly water and nutrient availability are optimal, so that the productivity is mainly determined by climatological conditions. It appears that this approach has not been widely applied under more marginal conditions, for example in arid regions with low and erratic rainfall, where extensive grazing is the dominant way of exploitation. It seems, however, that the application of systems analysis followed by model building is also a most promising way to indicate means of improving the situation under these conditions either by changing the existing system or by hinting at better ways of exploiting the present system. In order to arrive at such recommendations the entire field of primary production, grazing, animal production and grazing management must be taken into account. The basis for such a systems approach is a thorough understanding of the principles that govern primary production. Therefore, a joint Dutch-Israeli research project was initiated in 1970 to assess, as a first step, how herbage production in arid regions is dependent on weather, soil conditions and type of plant cover (Van Keulen & De Wit, 1975).

One of the results of this project is described in this paper: a simulation model,* which deals with the calculation of plant production in situations where water is the main limiting factor. Obviously, it should be possible for these conditions to simplify the model with respect to the detail of physiological

* All models described in this chapter are written in CSMP (Continuous System Modelling Program) developed by IBM for its 360 and 370 series of machines. These or similar languages (according to the CSSL definition) are now also available for other machines.

processes, which may be of importance for the understanding of plant behaviour but have relatively little influence on production. However, before simplifications can be applied information should be available on the relative importance of the various processes. Otherwise, simplification leads to restricted applicability of the model for predictive and extrapolation purposes. A possible way to achieve that aim is the hierarchical approach, that is, a method where at each level of interest, models are developed, linking an explanatory level to an explainable level (De Wit, 1970). The results of such a model may then, after thorough validation, be incorporated into lower resolution models by means of functions or analytical expressions. An example of this approach is the work by Penning de Vries (1974), who calculated respiratory losses on the basis of biochemical transformations necessary to produce and maintain plant tissue from primary photosynthetic products. The results of that model are entered in models for crop growth in the form of 'production value' parameters (that is weight efficiency) for the main plant constituents (De Wit *et al.*, 1978). Another example is a model for the calculation of daily gross photosynthesis from the radiation climate, the geometrical and optical properties of the leaves, and the photosynthesis-light response curve of individual leaves (De Wit, 1965), the results being used in a tabulated form in models for plant production (Van Keulen, 1976a). The basic principle behind this approach is that it is in general undesirable to incorporate several explanatory and explainable levels in the same model because this renders it complicated and unwieldy.

In the model described in this chapter the transpiration coefficient, that is the ratio between dry matter production and transpiration, is used as the parameter to link it to a detailed model of canopy photosynthesis, respiration and transpiration (De Wit *et al.*, 1978). In the first section of this chapter attention is paid, therefore, to measurement of the transpiration coefficient and to its calculation by means of the detailed model, of which a brief description is also given. In the last section the application of the crop growth model to arid conditions is described.

Experimentation and simulation of the transpiration coefficient

The relation between dry matter production and water use by plants has been the subject of experimental work ever since the classical experiments by Briggs & Shantz (1913). In the framework of the joint research project on 'Actual and potential herbage production in semi-arid regions', such experiments were carried out at the Avdat Desert Research Station of the Hebrew University, in the central Negev desert of Israel. Plants from both the natural vegetation and cultivated species were investigated. The aim of the experiments was to study possible differences in water use efficiency between different species under varying climatological conditions.

Material and methods

The plants were grown in plastic buckets filled with local loess, which had been mixed with sufficient fertilizer to ensure optimum nutrient conditions. The surface was covered with 5 cm of coarse gravel to prevent direct soil evaporation and to avoid the deleterious effects of repeated watering on the surface layer of the soil which is susceptible to crust formation. The plants were watered regularly to avoid water stress, the exact timing being determined by the transpirational losses. Approximately once a week, all buckets were weighed and water was added to the original weight, corrected for the amount of biomass present. The plants were harvested after various growing periods, preferably in the vegetative stage. However, this was not possible with some of the species from the natural vegetation, which flowered very soon after sprouting. The aerial parts were dried for some days at 70 °C and the dry weight determined. The roots were washed free of soil over a narrow sieve, dried at 70 °C and, after careful removal of adhering sand and stones, weighed.

Meteorological data were collected concurrently in a standard weather station of the Israeli Meteorological Service, located near the experimental site.

Results and discussion

In Tables 17.1(a) and 17.1(b) the results of two series of the experiments are given, for the seasons 1971/72 and 1972/73, respectively. They include both cultivated species, for which local varieties were used, and species from the natural vegetation. The transpiration coefficients (TRC) were obtained by dividing the total amount of water transpired by the total dry matter harvested.

In the first series (Table 17.1a), the values for the cultivated species and the species from the natural vegetation are all within 20% of the average, except for oats (*Avena sativa*). Most of the differences between the other species can be attributed to differences in the growth pattern of the various plants, which resulted in a different distribution of the production in time. The weather conditions varied considerably during the experimental period: high radiation, high temperatures and low humidity in autumn and low radiation, low temperatures and high humidity in winter. Hence, the efficiency of water use varies in the different periods, as it is correlated with the evaporative demand of the atmosphere (De Wit, 1958).

There is no reason to attribute the very low value for *Avena sativa* measured in winter 1971/72, which is reminiscent of the values measured for C₄-species (De Wit, 1958), to experimental errors. A possible explanation is, that in this case the stomatal conductivity of the plants was governed by net assimilation

Table 17.1(a). Measured transpiration coefficients in Avdat from 8 October 1971 to 25 January 1972

Species	No. of pots	Dry shoot wt per pot (g)	Dry root wt per pot (g)	Total dry wt per pot (g)	Transpiration coefficient
<i>Avena sativa</i>	8	175	79	254	79
<i>Hordeum sativum</i>	8	98	71	169	104
<i>Triticum sativum</i>	6	110	47	157	129
<i>Reboudia pinnata</i>	6	35	7	42	146
<i>Medicago hispida</i>	10	47	17	64	157
<i>Hordeum murinum</i>	10	47	31	78	129
<i>Avena sterilis</i>	10	75	65	140	124

Table 17.1(b). Measured transpiration coefficients in Avdat in 1972/73

Species	Growing period	No. of pots	Dry shoot wt per pot (g)	Dry root wt per pot (g)	Total dry wt per pot (g)	Transpiration coefficient
<i>Avena sativa</i>	4 Oct. 72–26 Jan. 73	2	341	73	414	221
<i>Hordeum sativum</i>	5 Oct. 72–23 Feb. 73	3	373	136	509	224
<i>Triticum sativum</i>	17 Nov. 72–16 Feb. 73	3	161	51	212	131
<i>Reboudia pinnata</i>	10 Dec. 72–16 Feb. 73	3	37	4	41	168
<i>Medicago hispida</i>	18 Oct. 72–2 Mar. 73	3	72	11	83	192
<i>Hordeum murinum</i>	27 Oct. 72–16 Feb. 73	2	220	68	288	178
<i>Avena sterilis</i>	1 Nov. 72–26 Jan. 73	3	96	45	141	129
<i>Phalaris minor</i>	1 Nov. 72–16 Feb. 73	2	178	105	283	162

in such a way, that the internal CO₂-concentration is maintained at a constant value. Such behaviour, which allows plants to combine a high growth rate with a relatively low transpiration rate, and is therefore of special importance for production in (semi-)arid regions, has been reported before (De Wit *et al.*, 1978; Goudriaan & Van Laar, 1978). It is not clear, however, how widespread this phenomenon is, nor is it understood, whether varietal or environmental factors are responsible for its occurrence. Further research on the subject is of prime importance.

In the second series (Table 17.1b) the differences between cultivated and natural species are within 10% of the average. It is somewhat more difficult to compare these values, as the growing periods do not match exactly, due to a slightly different experimental set-up. These experiments (see also Van Keulen, 1975) indicate that, under normal circumstances, no basic difference in water use efficiency exists between the present-day cereals and their wild relatives.

Simulation of the transpiration coefficient

The simulation model

To test whether it is possible to calculate the transpiration coefficients, a number of experimental periods were simulated with the basic crop growth simulator (BACROS), developed at the Department of Theoretical Production Ecology, Wageningen. A detailed report on the model and its validation has been published (De Wit *et al.*, 1978). It is sufficient here to give a brief outline of the model.

The crop considered is in the vegetative phase and is well supplied with water and nutrients. Growth of the crop is defined as increase in dry weight of the structural plant material, that is, exclusive of the organic components that are classified as reserves. The model is based on physical, chemical and physiological processes so that it can be used without geographical limitation.

Micro-weather is calculated from daily weather data measured at screen height, the extinction of radiant energy from sun and sky within the crop being taken into account. The infrared radiation in the canopy is also computed. The distribution of radiation over the leaves is required in order to calculate assimilation and transpiration. This distribution is determined by the architecture of the crop, which has to be defined. The extinction of turbulence in the canopy is also considered, so that transfer of heat, vapour and carbon dioxide can be computed. The ratio of latent and sensible heat exchange regulates the micro-weather to a large extent, and this ratio is mainly determined by stomatal behaviour. Soil temperature is not simulated here, it is assumed that it follows the air temperature with a delay of 4 h and the associated decrease in amplitude. More detail on the simulation of micro-weather is given by Goudriaan (1977).

The assimilation of carbon dioxide by the canopy is calculated by adding the assimilation rates of the variously exposed leaves in successive leaf layers. The latter rates are dependent on light intensity, carbon dioxide concentration in the ambient air and the resistance for carbon dioxide diffusion from the atmosphere towards the active sites. This resistance is the sum of the resistance for turbulent transport in and above the canopy, the resistance of the laminar layer around the leaves, the stomatal resistance and the mesophyll resistance.

Respiration is the sum of maintenance and growth respiration. The latter is the result of the conversion of primary photosynthates into structural plant material and is therefore proportional to the growth rate. The intensity of growth respiration is affected by the chemical composition of the newly formed material. This intensity is independent of the temperature, but growth respiration is indirectly influenced by temperature through its effect on the growth rate. Usually, carbon dioxide evolution originating from transport processes is included in the growth respiration. The rate of maintenance

respiration depends on the turnover rates of proteins, the re-synthesis of other degraded compounds and the maintenance of ionic gradients. This respiration process is therefore dependent on the chemical composition of the plants and is, moreover, affected by temperature.

The growth rate of shoot and root is dependent on the amount of reserves present and the temperature. Under internal water stress, growth of above-ground organs is retarded by making a larger proportion of the reserves available for growth of roots. In this way a functional balance is maintained between shoot and root (Brouwer, 1963).

Up to now, no satisfactory solution has been found for the simulation of the growth of leaf surfaces in relation to the growth of shoot weight, so that these aspects are mimicked rather than simulated: their description is based on information obtained from field trials and not from knowledge of the underlying processes.

The water status of the crop is determined by the balance between transpiration and water uptake from the soil. The transpiration rate is found by adding the transpiration rates of the variously exposed leaves in successive leaf layers of the crop. The latter rates are found from the absorbed radiation, the resistance of the laminar layer, the humidity and temperature of the ambient air and the stomatal resistance. Contrary to the version published by De Wit *et al.* (1978) stomatal resistance in this case was governed either by light intensity or by the water status of the crop. The calculations also provide leaf temperatures, which are used in the photosynthesis section and averaged to give canopy temperature, applied in growth and respiration calculations. Water uptake is determined by the conductivity of the root system, the water status of the plant and that in the soil. The soil is assumed to be in optimum moisture conditions ('field capacity') so that transport in the soil can be neglected. The conductivity of the root system is determined by its weight, the degree of suberization of the roots and the soil temperature,

This model describes quite accurately the rates of photosynthesis, transpiration and respiration, when executed with time-steps in the order of minutes (enclosure experiments: Van Keulen & Louwarse, 1975; Van Keulen, Louwarse, Sibma & Alberda, 1975; De Wit *et al.*, 1978) and seasonal, above-ground dry matter production when the time-steps are 1 h (Goudriaan, 1973; Dayan & Dovrat, 1977; De Wit *et al.*, 1978).

Calculated and measured transpiration coefficients

The model described in the previous section had to be adapted to calculate transpiration coefficients of single plants, growing in containers. The leaf area index, which is normally entered as a forcing function loses most of its meaning in the pots as the radiation climate and the wind speed are distinctly different from that in a closed green crop surface. The simulation experiments

Table 17.2. Comparison between measured and simulated transpiration coefficients

Species	Growing period	Measured	Simulated	Ratio of simulated:measured
Oats (<i>Avena sativa</i>)	8 Oct. 71–22 Nov. 71	170	165	0.97
	8 Oct. 71–25 Jan. 72	79	149	1.86 ^a
	4 Oct. 72–17 Nov. 72	235	257	1.10
Wheat (<i>Triticum sativum</i>)	4 Oct. 72–5 Jan. 73	194	206	1.07
	8 Oct. 71–25 Jan. 72	129	147	1.14
	17 Oct. 72–27 Nov. 72	217	228	1.05
	17 Nov. 72–16 Feb. 73	131	218	1.67 ^a
Barley (<i>Hordeum sativum</i>)	5 Jan. 73–16 Mar. 73	166	202	1.22
	8 Oct. 71–22 Nov. 71	173	125	1.07
	8 Oct. 71–25 Jan. 72	104	149	1.44 ^a
	5 Oct. 72–17 Nov. 72	217	246	1.14
	5 Oct. 72–23 Feb. 73	224	209	0.94

^a Variation greater than 25%.

were therefore done with a constant leaf area index of two for the whole period. Physiological data used were those of Van Keulen & Louwse (1975) for wheat. For more details on the calculation procedure see Van Keulen (1975).

In Table 17.2 a comparison between measured and calculated transpiration coefficients is given. Only experiments with cultivated species are shown here, as the differences with the natural species are very small (Table 17.1). In general the measured and calculated values agree within 25%, except where indicated. The latter values could again be explained by the existence of stomatal regulation through internal carbon dioxide concentration. The deviations in the other cases do not seem to be systematic and several factors could have caused the observed discrepancies: the problems, mentioned already concerning the radiation climate, or the influence of respiration (especially maintenance respiration, which is proportional to the amount of biomass present, a value unknown during the growing period).

From the overall agreement it seems acceptable to use the calculated values of the transpiration coefficient when the production potential has to be calculated. In the crop growth model described in the next section, a procedure is incorporated to calculate the daily value of the transpiration coefficient from daily weather observations. This procedure is based on the results of BACROS (Van Keulen, 1975).

The simulation model 'Arid Crop'

A detailed description of the model, a complete listing and an evaluation of its behaviour are given by Van Keulen (1975).

Outline of the model

The model simulates the growth curve of a canopy and the water balance in the soil below it.

At the beginning of the growing season germination starts after initial wetting of the soil and continues until the temperature sum required for establishment is reached, provided that the upper soil layers do not dry out before then. In the latter case the seedlings die and a new wave of germination starts after re-wetting. After establishment, at which moment a constant initial biomass is assumed, the daily growth rate of the canopy is calculated from daily transpiration and the value of the transpiration coefficient.

Daily transpiration is a function of the evaporative demand of the atmosphere, determined by radiation and the combined effect of wind speed and humidity, the leaf area of the canopy and the interactive effect of the distribution of roots and moisture in the soil profile. For the latter relation an approach similar to that of Viehmeyer & Hendrickson (1955) is used, that is, soil water is almost freely available above 'wilting point' after which a sudden drop in availability occurs. When part of the root system is in dry soil layers, its reduced activity may be compensated by enhanced uptake from wetter layers. The transpiration coefficient is the ratio between potential growth rate, determined by the balance between gross photosynthesis and respiration and potential transpiration dependent on the same factors as the actual rate except for the soil component. The value of the transpiration coefficient is assumed to be independent of moisture conditions in the soil. This is an oversimplification (Lof, 1975) but the value of the transpiration coefficient has little effect on dry matter production because of the low transpiration rate under dry soil conditions.

The growth rate of leaf area is obtained from the increase in dry weight, assuming a temperature-dependent leaf area ratio. This simplification is mainly applied because many of the basic processes governing plant morphogenesis are insufficiently understood. The physiological age of the crop is defined in its development stage, being 0 at establishment and 1 at maturity. The rate of development is a linear function of temperature, the relation being constructed from field experience. When maturity is reached, the canopy ceases to grow, even when water is still available in the soil.

Root growth may refer to both vertical extension of the root system and to increase in dry weight. Due to lack of reliable data, there is no feedback of the one process to the other. For the vertical extension, it is assumed that a homogeneous root front moves downward with a rate dependent on soil temperature, till a dry layer is reached, after which growth ceases. The increase in dry weight is obtained from the growth rate of the crop by allocation of the new material between shoot and root: the ratio is dependent on the development stage, from 0.5 at the beginning of the season to 0.025 at the end.

To simulate the water balance in the soil, the potential rooting zone is divided into a number of homogeneous compartments (De Wit & Van Keulen, 1972) increasing in thickness from the top downwards. The total amount of water infiltrating into the soil, rain corrected for run-off or run-on, is distributed in such a way, that the compartments are consecutively filled to field capacity. Redistribution of soil moisture under the influence of potential gradients originating from uneven drying or wetting of the profile, is not taken into account as that has little influence on the availability of water for plant roots.

Direct evaporation from the soil surface, which may be a substantial source of moisture loss (especially with unfavourable rainfall distribution) is obtained from the potential rate, calculated according to Penman (1948), corrected for the dryness of the upper soil layer. The reduction factor, as a function of the moisture content, is again calculated with a detailed model: this is another example of the hierarchical approach (Van Keulen, 1975). Total evaporative losses are withdrawn from the various compartments, 'mimicking' redistribution by means of an extinction coefficient, depending on soil physical properties and moisture distribution, which is also obtained from the model just mentioned.

Water uptake by the roots depends on root distribution and moisture distribution in the soil, and is furthermore influenced by soil temperature, in its combined effect on root conductivity and viscosity of the water.

The temperature of the soil is calculated as a ten-day running average of the air temperature.

Time-steps of one day are employed, which is one-tenth of the minimum value of the time constant for the growth of vegetation (the maximum relative growth rate is $\pm 0.1 \text{ day}^{-1}$, cf. De Wit & Goudriaan, 1974), and the rectilinear integration method is used.

Results and discussion

Data to validate the model, were collected during three years of experimentation at the Tadmor Experimental Farm in the northern Negev desert of Israel. The site has a Mediterranean-type climate with an average annual rainfall of 250 mm, concentrated in winter (November–March). The vegetation under study is an abandoned cropland vegetation, consisting of herbaceous annuals (Tadmor, Eyal & Benjamin, 1974). Meteorological data were collected at a weather station of the Meteorological Service, located at about 8 km from the experimental site, except for rainfall, which was recorded at the site. Standing crop was determined approximately every fortnight, using a double sampling technique, based on visual estimates (Tadmor, Brieghet, Noy-Meir & Benjamin, 1975). Soil moisture was recorded every fortnight, and after heavy rains, by the neutron moderation technique complemented by gravimetric sampling of the upper 30 cm.

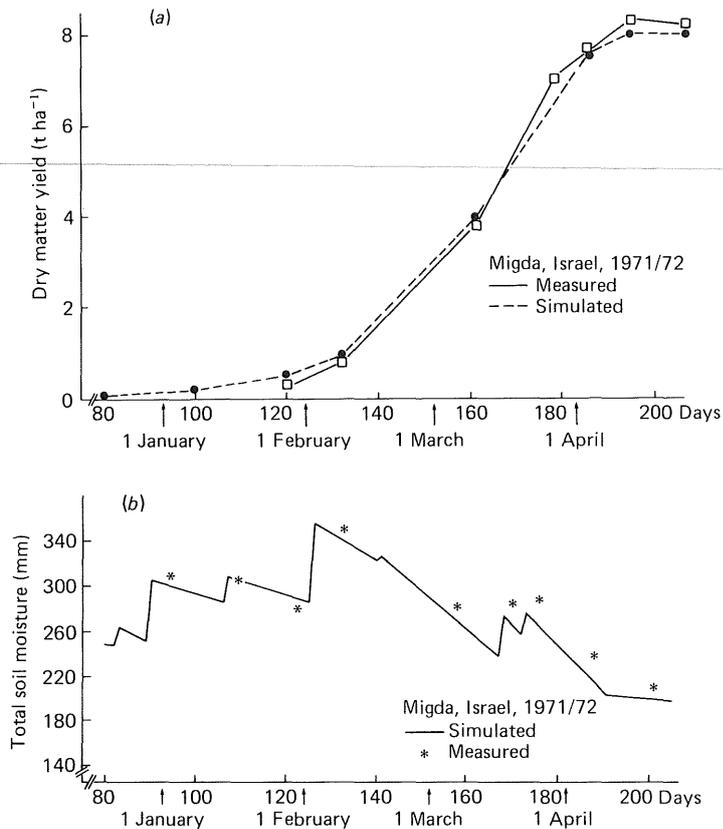


Fig. 17.1. Comparison between measured and simulated values in a site under natural vegetation in Migda, 1971/72. (a) Dry matter production. (b) Total soil moisture.

In Figs. 17.1 and 17.2 the measured and calculated values of above-ground dry matter production and total soil moisture content are given for the seasons 1971/72 and 1973/74. Comparison of the two figures shows some interesting features: it is striking, that the agreement for 1971/72 is much better than for 1973/74 (and likewise 1972/73, which is not shown here). The main reason for this difference must be that the 1971/72 data were continuously used to test the performance of the model during its development. This illustrates clearly the importance of using strictly independent data during model development and model validation, even in situations where a minimum of empirical relations is included (Van Keulen, 1976*b*). The deviations at the end of the 1973/74 season must be mainly attributed to the nitrogen situation in the field, as it is likely that at that time shortage did occur. Under natural conditions at the Migda site, nitrogen appears to be equally

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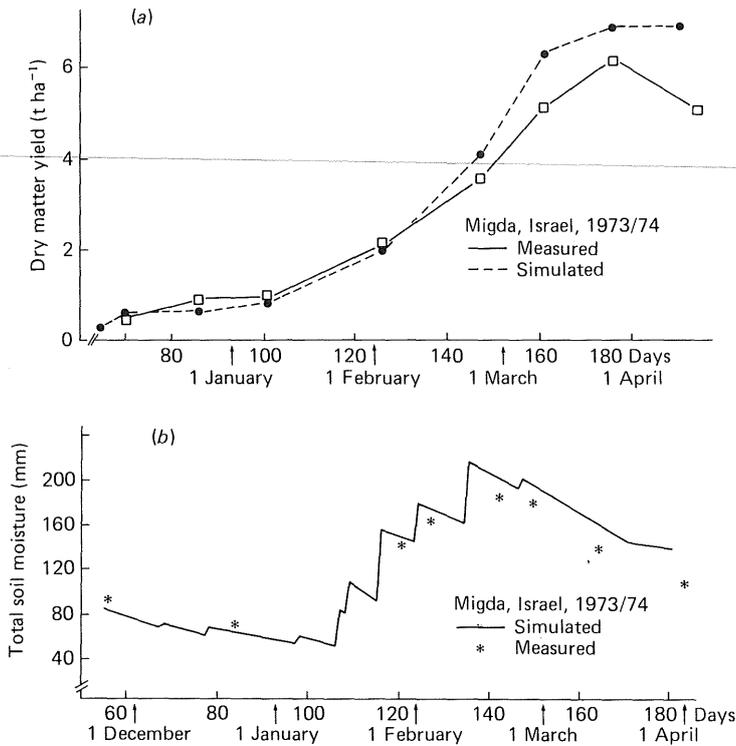


Fig. 17.2. Comparison between measured and simulated values in a site under natural vegetation in Migda, 1973/74. (a) Dry matter production. (b) Total soil moisture.

important as a growth limiting factor as water (Harpaz, 1975). Total soil moisture compares fairly well in both seasons, after taking into account that due to heterogeneity of the soil, the accuracy of measurement seldom exceeds 10% of the field mean.

Conclusions

Comparison of the results of the simulation model with the measurements, shows that the behaviour of herbaceous vegetation growing undisturbed under optimum nutrient conditions can be predicted reasonably accurately.

It is also clear, that several processes need further examination and better understanding (early development, morphogenesis) before the model may be used in connection with other models to predict the behaviour of a semi-arid ecosystem under its normal grazing management scheme. Formulation of this model, however, has increased our insight into the relevance of various factors that play a role in production under semi-arid conditions. It has served as

a basis for the formulation of a research project in the Sahelian zone (Penning de Vries & Van Heemst, 1975), a semi-arid area with summer rainfall, where it was shown that also under such conditions reliable estimates of potential productivity can be made. These experiences have also emphasized the fact that a better insight in the period of establishment of the canopy and in the vegetation dynamics must start from a better understanding of its behaviour in the reproductive stage of the previous season, that is seed production and survival.

The model is also used at the moment to provide a basis for the development of a management model for an intensified grazing system under arid conditions, as outlined in the Introduction. Our experience with but a small part of that system has shown that only thorough attempts, in which systems analyses and field experimentation are closely linked, may lead to trustworthy results. Such a procedure is in general time-consuming but quick results, however attractive at first sight, may turn out very costly in the long run.

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