5.3 Crop production under semi-arid conditions, as determined by nitrogen and moisture availability

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5.3.1 Introduction

The sequence of models on plant growth and production presented in this book is such that at each subsequent step more potentially limiting factors are taken into account. This requires extension of the models, to include simulation of the status of the relevant factors, both in the vegetation and in the soil in which it is growing. This requirement very soon leads to the construction of models that become unwieldy by their very size. It is therefore almost a prerequisite that concurrent with the addition of one more limiting factor, the remainder of the model description is simplified (cf. Subsection 1.2.3). That in itself need not be a serious disadvantage, since introduction of the additional factor is sensible only if it is expected to have an appreciable effect on the final result and the other factors consequently become relatively less important. The model presented here is, to my judgement at the limit of what can be handled reasonably. It has basically the same structure as the one in which only water as a limiting factor was considered (Section 4.1 and 4.2). State variables pertaining to the nitrogen (N) balance in soil and plants have been added. Most attention will be paid here to these state variables and the associated processes.

The model is outlined in Subsection 5.3.2 and its principle is repeated in an example (Subsection 5.3.3). A discussion of the performance of the model is presented in the Subsections 5.3.4 and 5.3.5.

5.3.2 The simulation model PAPRAN

A detailed description of the simulation model PAPRAN, whose main elements are illustrated in the simplified relational diagram of Figure 71, is presented elsewhere (Seligman & van Keulen, 1981). Conceptually the model is a soilwater balance model, where plant growth is closely related to the amount of water transpired by the canopy and its N status. The description of N uptake and redistribution in the plant tissue is based on a relatively simple set of demand and supply functions (Seligman et al., 1975); N transformations in the soil are represented by immobilization and mineralization processes, the rates of which are dependent on environmental conditions and on the C/N ratio of the organic material present.

Nitrogen in the soil Nitrogen transformations in the soil have long been recognized as important processes in connection with the supply of the element to the plants. The com-

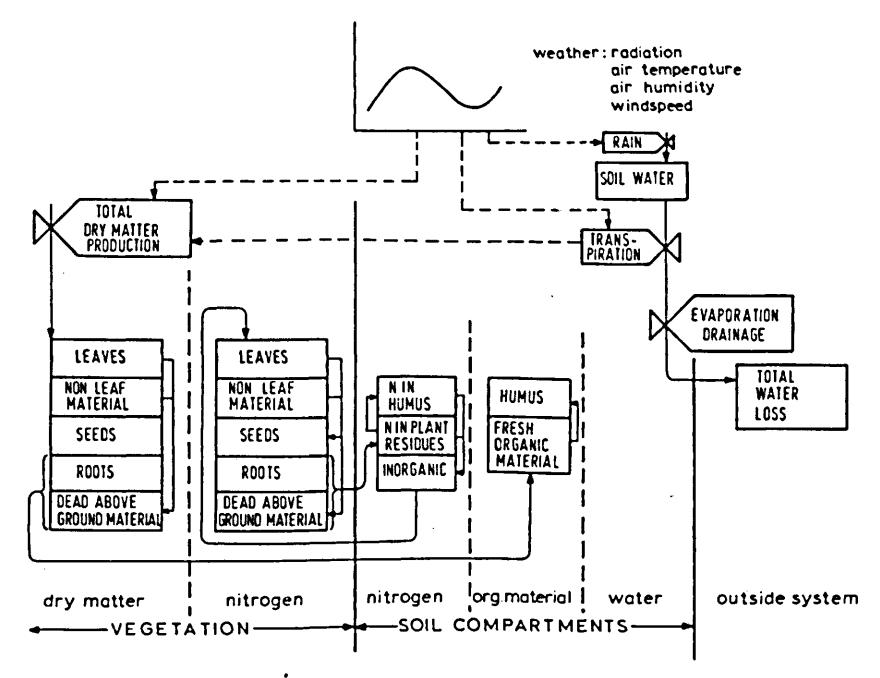


Figure 71. Schematized relational diagram of the simulation model PAPRAN.

plexity of the subject is well reflected in the voluminous literature available, as well as in detailed models of the soil N system that have been developed (Beek & Frissel, 1973; Hagin & Amberger, 1974; van Veen, 1977). Especially van Veen has emphasized that a useful method to treat the complexity is to divide the overall model into submodels that deal with the major processes separately but still influence each other through the relevant state variables. Van Veen's model (Section 5.2) focuses on microbiological processes, and the microbial biomass and its N content are treated as separate state variables. However, because of methodological problems, it is almost impossible to determine the relevant microbial values, and it is also very difficult to determine components of the soil organic matter for field situations. That situation seriously restricts the applicability of these concepts since both initialization and validation must then be based on indirect measurements so that unverifiable detail has been added to the model. Nevertheless, these concepts are theoretically sound, since most of the N transformations in the soil are governed by microbiological activities, so that their application awaits the development of more accurate experimental techniques (Subsection 5.2.3). The soil N section included in the present model is compatible with the degree of detail and the time resolution of the other parts of the model. In this concept, the total N store in the soil is separated into three states only; inorganic N (including NH_4^+ , NO_3^- and NO_2^-), N in 'fresh' organic material (including N in plant debris, roots of last year's crop and also N incorporated in the microbial biomass) and N in the 'stable' organic material, which has at least once undergone microbial transformation. This approach necessitates lumping of some of the processes and their associated parameter values:

- immobilization, i.e. the transformation of inorganic N into organic compounds through microbial action, indicates total immobilization of any form of inorganic N by microbial growth. This generalization seems permitted since the microbial population in the soil active in decomposition of organic material is highly diverse and can easily adapt to the available source of inorganic N.

- mineralization from organic N to NH_4^+ and the (possible) transformation into NO_3^- are not distinguished in the model. This simplification is justified by the fact that in the well-aerated soils in semi-arid conditions the rates of nitrification are not normally limited by lack of suitable oxidizing micro-organisms nor by environmental conditions affecting oxidation. The rate-limiting process is generally the decomposition rate of the organic material, so that usually NH_4^+ or NO_2^- do not accumulate in the soil. (Exceptions are however possible as indicated by experimental results obtained in the Sahelian region, where NH_4^+ accumulation was observed, especially after hot-dry periods. This phenomenon could be the result of partial soil sterilization, when soil surface temperatures rise above 50 °C, thus leading to a depletion of the population of nitrifying organisms. Such situations cannot be treated with the present version of the model.)

- incorporation of the microbial biomass in the fresh organic material presents two problems:

1 how to deal with the lag associated with the initial build-up of the microbial population and its subsequent adaptation to various substrates?

2 how to handle the influence of the dying microbial biomass on the composition of the fresh organic material?

The first problem is on the whole not too serious with models of the present type, which simulate crop growth on a seasonal basis. The time coefficient for adaptation of the microbial populations has a value on the order of days, hence initial population size itself will not be the limiting factor for decomposition on a seasonal basis. Major controlling factors are then the available carbon (C) and N as substrates and environmental conditions, particularly temperature and moisture conditions. In the present model the rate of decomposition of the fresh organic matter is reduced when its C/N ratio exceeds 25. The inorganic N present is included in the calculation of the current C/N ratio. The second point is part of a more general problem, since the overall rate of decomposition depends on the composition of the fresh organic material. This is accounted for in the model by changing the rate constants for decomposition sequentially as more of the originally present material had decomposed. The switch for the various rate constants can be adjusted to allow for different compositions of the added material. Continuous or discrete additions of dead microbial biomass to the fresh organic material could be treated in the general framework of the model, but they have not been incorporated. This simplification is probably the main reason why the so-called 'flush' of mineralization frequently observed after hot and dry periods, and presumably the result of rapid decomposition of dead microbial biomass, is not reproduced by the current version of the model.

The actual calculation procedure in the model PAPRAN is best explained on the basis of the relational diagram presented in Figure 72. The rate of decomposition of the fresh organic material is based on first-order kinetics (Subsection 5.2.2), the relative rate (RDX) being determined by the component currently decomposing. Since RDX represents the specific decomposition rate under optimum conditions for growth of the micro-organisms, the actual rate of decomposition is also influenced by soil temperature (TS), the moisture status of the soil (WCON) and the overall C/N ratio (CNR) in the profile. The N contained in the material being decomposed is mineralized and added to the pool of inorganic N in the soil. The concurrent build-up of microbial tissue requires nitrogen (NREQ), which is immobilized. The rate of immobilization is directly proportional to the decomposition rate of the organic material, it being assumed that a fixed proportion of the C (EFFBS, the biosynthesis efficiency) is used for

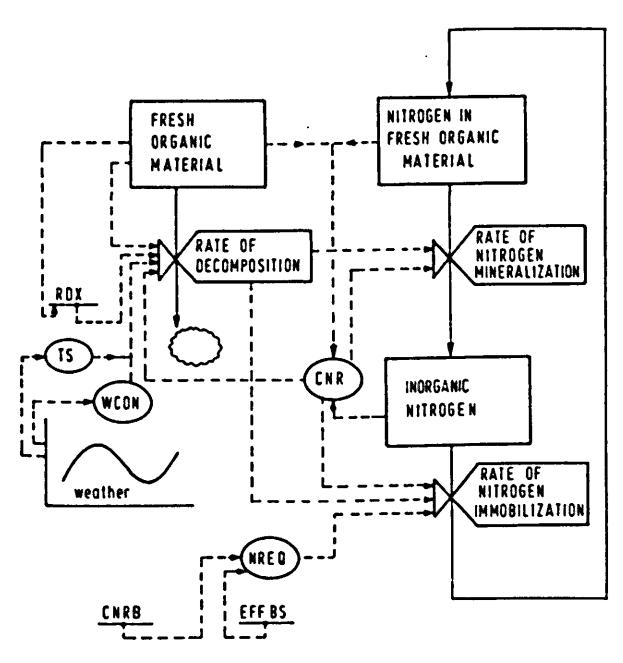


Figure 72. Schematized relational diagram of the PAPRAN module for decomposition of fresh organic material in the soil.

the formation of microbial tissue, the remainder being lost in respiration. The rate of N accretion is furthermore dependent on the C/N ratio of the microbial biomass (CNRB). Whether the result of both processes is net mineralization or net immobilization depends on the intensities of both processes.

Volatilization of ammonia takes place from the top soil layer only, and is treated in a rather rudimentary way in the model. In reality the rate of N loss through volatilization is dependent on the NH_4^+ concentration, on pH and temperature and on environmental conditions governing the rate of exchange with the atmosphere. Since the time coefficients of the chemical and physical processes involved are much smaller than the resolution of the model, volatilization is approximated by an imitating procedure, assuming a constant relative rate of disappearance of NH_4^+ from the top soil compartment.

Adsorption of NH_4^+ to the exchange complex of the soil is not considered, because the NH_4^+ involved is in general a small and fairly constant fraction of the total amount of inorganic N and changes have only a small effect on the seasonal N dynamics. Fixation of NH_4^+ into the clay mineral lattice is neglected as well, as it is not of significance in most soils of interest in the arid region.

Denitrification is disregarded in the present model, because anaerobic conditions are unlikely to occur in the arid zone. The possibility that local anaerobic pockets may develop as a result of oxygen depletion under intensive biological activity or localized water logging is recognized, but since the extent of these phenomena is not clear and as they are extremely complex for a simulation approach, they have not been treated as yet.

Transport of inorganic N over compartment boundaries takes place with movement of soil water (Subsection 5.2.2), that is with infiltration only (Subsection 4.2.3). To account for combined effects of mass flow and diffusion, the concentration of N in the water transported is calculated by 'mixing' the N present in a compartment and that moving over its upper boundary with the water in that compartment and all water transported through it.

Soil organic matter

In each soil layer, two organic components are distinguished, the 'fresh' organic material consisting of roots and other plant residues of the previous year and 'stable' organic material or soil humus.

The rate of decomposition of the fresh organic material is based on firstorder kinetics, modified by the influence of moisture, temperature and the C/N ratio of the available substrate. The rate constants applied in the model are: 0.8 d^{-1} for proteins and sugars, 0.05 d^{-1} for cellulose and hemi-cellulose and 0.0095 d^{-1} for lignin. The rate constants change in a stepwise manner, the moments at which the rate constant changes being controlled by the composition of the material added. The stable organic material, which has a constant C/N ratio of 10, decomposes at a much slower rate, a rate constant of $8 \cdot 10^{-5} d^{-1}$ being assumed. Again this rate may be modified by temperature and moisture conditions, in the same

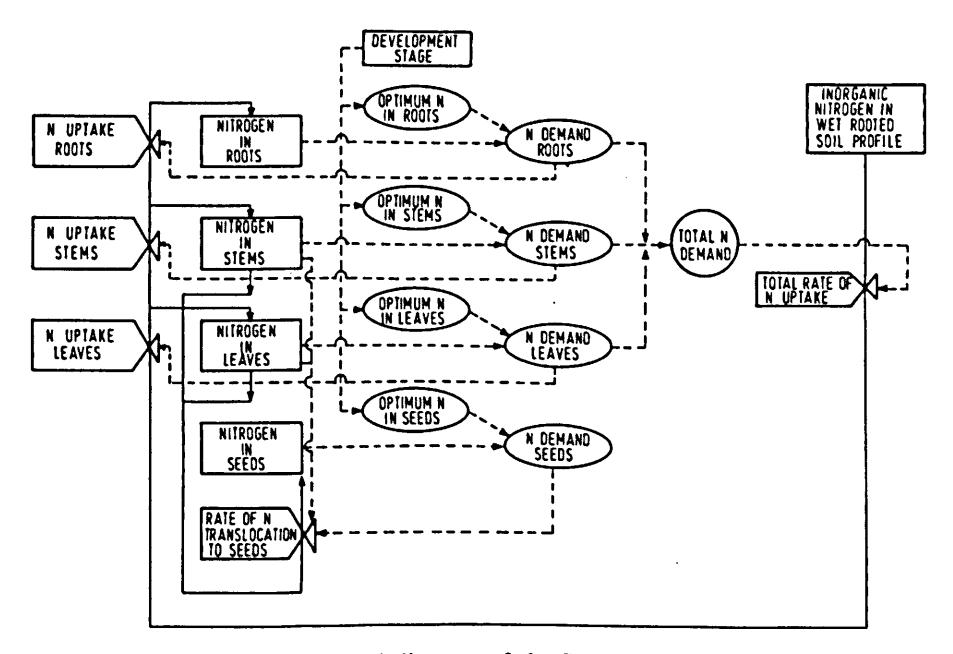


Figure 73. Schematized relational diagram of the PAPRAN module for the nitrogen balance in a natural vegetation.

way as the fresh organic material.

There may also be accretion of stable organic material due to the residual stable compounds originating from the fresh organic material. In the model this is linked to the C/N ratio of the decomposing material. When the C/N ratio is below 25 inorganic N is released, 20% of which is incorporated in the stable fraction. Application of the constant C/N ratio of 10 then also gives the accumulation of C in the humus fraction.

Nitrogen in the vegetation

A simplified relational diagram of this part of the model is given in Figure 73. It is assumed that N is taken up by the plant as NO_3^- and that the root system of the vegetation is dense and active over the full rooted depth. Nitrate is then highly available to the plant either by mass flow with the transpiration stream or by diffusion of the anions along a concentration gradient, created by low NO_3^- concentrations near the root surface (van Keulen et al., 1975), as long as the soil is wet enough. Thus the demand for N can be satisfied within a relatively short time, a time coefficient of 2 days being assumed in the model. The demand for N is created by the difference between the current N content of the plant and a maximum N content. The latter value is different for the various organs of the plant and decreases as the phenological development of the plant proceeds (Figure 74a, cf. Figure 67, Section 5.1). The present version of the model assumes

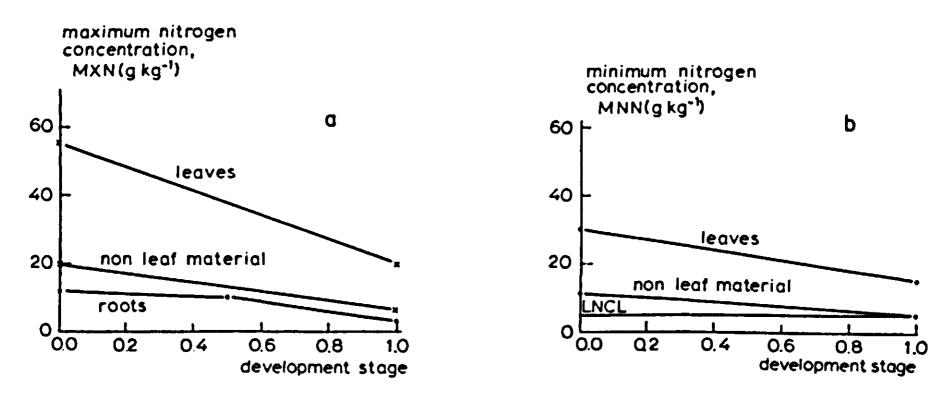


Figure 74. The maximum (a) and minimum (b) nitrogen concentration for various organs of natural grassland vegetation as a function of phenological age (development stage, here defined as being 1.00 at maturity). LNCL is the nitrogen irreversibly incorporated in the leaf tissue.

that under limited supply of N, the actual amount taken up is partitioned among the various vegetative organs (roots, stems and leaves) in proportion to their relative demands (sink-size determined).

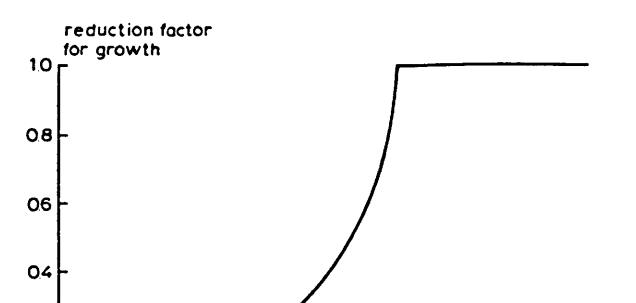
The N demand of the seeds is met by translocation from the above-ground vegetative parts. It is withdrawn from leaves and non-leaf material in proportion to the amounts in each of the compartments. As the tissue becomes depleted (below MNN), translocation to the developing seeds is retarded, eventually the demand may not be met and consequently seeds with a lower N concentration are the result. Below an absolute minimum level of non-degradable nitrogenous compounds (LNCL, Figure 74b) redistribution ceases. The definition of the absolute minimum level in PAPRAN corresponds with the minimum concentration of Figure 67, Section 5.1. In reality, part of the N in the seeds may be supplied directly from uptake by the roots. However, with an integration interval of one day the demand will be transferred to the vegetative tissue within a relatively short time and when sufficient N is available in the rooting zone, it will be supplied. When the stock of inorganic N in the soil is exhausted, the vegetative tissue will be depleted of nitrogen, which will lead to impaired functioning of the leaves and accelerated senescence (self-destruction, Subsection 5.1.4. Compare also Subsection 3.4.7 for modelling aspects). Dying of vegetative tissue also leads to withdrawal of N from the plant. The concentration of the element in the dying tissue depends on the cause of death: if the tissue dies of water shortage or senescence, the dead tissue N concentration equals that of the live tissue; if death occurs from N shortage, the concentration is equal to the unextractable residual concentration, thus imitating the transfer of N from older to younger tissues.

Growth of the vegetation

The total daily dry matter production, unrestricted by N shortage, is calculated in the same way as in the model described earlier (Section 4.1). The influence of the N status of the vegetation is taken into account through a reduced growth rate, when the concentration of N in the leaf tissue (ANCL) drops below a threshold value (MNN, Figure 75), which in itself is a function of the phenological stage of the plants (Figure 74b). The reduction function given is based on a qualitative description of the influence of N shortage on growth, since suitable experimental data to define the instantaneous effect of N level on dry matter production are absent.

The N level of the vegetation also affects the distribution of the dry matter formed. Nitrogen deficiency in the above-ground tissue favours growth of the roots at the expense of the shoot. This description is based on the functional balance principle (Subsection 3.3.6): N shortage hampers growth of the shoot much stronger than that it reduces the rate of CO_2 assimilation, which leads to accumulation of primary photosynthates and hence to a greater availability of carbohydrates to the root system. The actual values of the partitioning function are the results of 'guestimates', as once more experimental data, especially from field situations are extremely scarce. The distribution of dry matter between leaves and non-leaf tissue is also influenced by the N status of the vegetation: when N is limiting growth, a larger fraction is incorporated in non-leaf tissue.

It is obvious from what is presented in this subsection and in Section 5.1 that quantitative descriptions of the influence of N deficiency on processes related to plant growth and production are lacking. That in itself is a surprising conclusion, more than 125 years after the pioneering work of Von Liebig. The finding



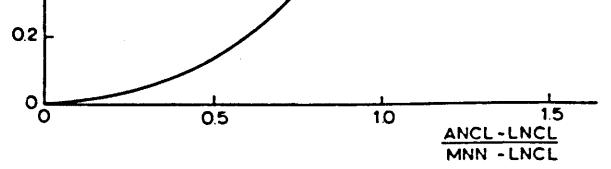


Figure 75. The reduction factor for dry matter accumulation as a function of a normalized nitrogen concentration, computed as: (ANCL-LNCL)/(MNN-LNCL). For abbreviations: see text.

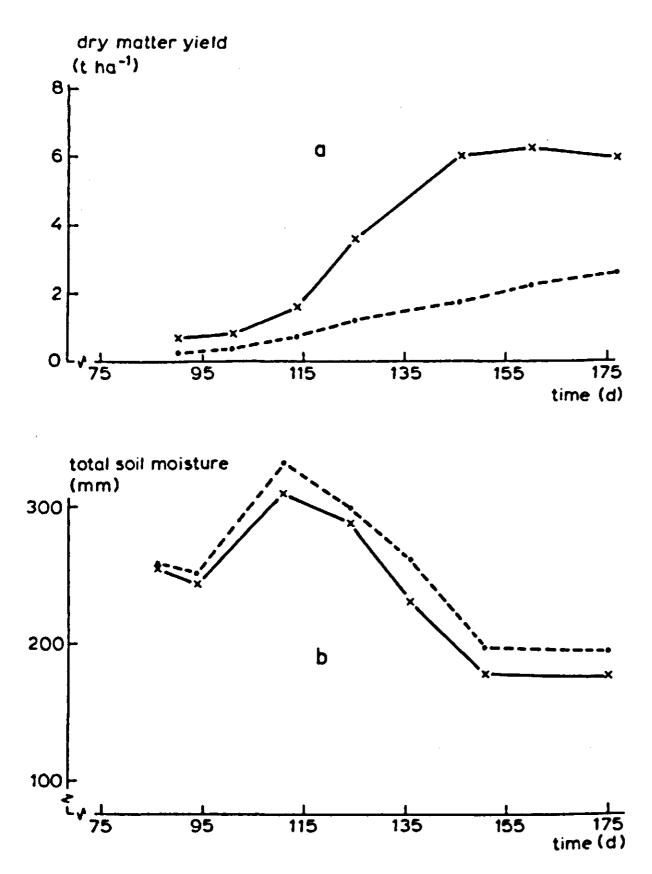


Figure 76. The measured growth curve of a natural vegetation with (x) and without (\cdot) nitrogen fertilizer in Migda, Israel, in 1972/1973 (a), and the time course of total soil moisture in the 0-180 cm layer for both situations (b).

of this gap in knowledge may serve as an argument in favour of systems analysis and model building as useful tools in agricultural research.

Nitrogen nutrition and water use

A basic problem that needs attention is the influence of N deficiency in the

vegetation on transpiration. The constancy of the transpiration coefficient, discussed earlier (Section 4.1) was restricted by de Wit (1958) to situations where the 'nutrient status is not too low', whereas Viets (1962) concluded that 'all evidence indicates that water-use efficiency, . . . can be greatly increased if fertilizers increase yield'. The latter conclusion seems to be confirmed by experimental results obtained in the northern Negev desert of Israel (Figure 76), where the soil with the fertilized vegetation, growing substantially faster than the non fertilized soil, loses water at practically the same rate.

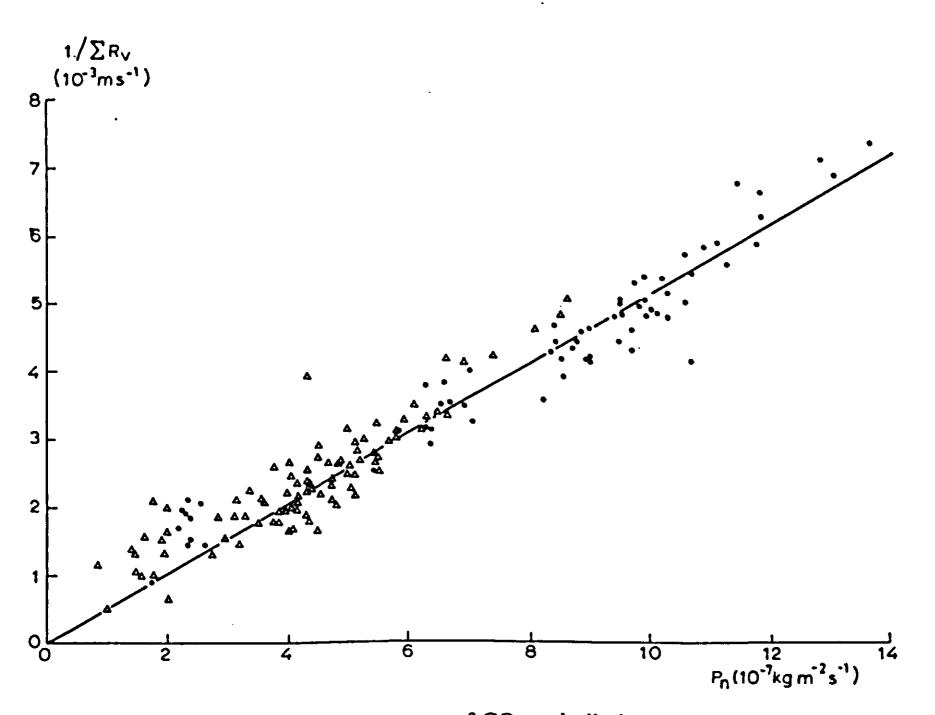


Figure 77. The relation between net rate of CO₂ assimilation (P_n) and total conductance for water vapour $(1./\Sigma R_v)$ for maize plants grown with ample (•) and limited (Δ) N supply.

When examining the basic processes of CO_2 assimilation and transpiration, however, the conclusion of a lower water-use efficiency under N deficiency is not so obvious. In Figure 77 the relation between the net rate of CO_2 assimilation (P_n) and total conductance for water vapour exchange $(1./\Sigma R_v)$ (Goudriaan & van Laar, 1978) is given for maize under optimal and suboptimal N supply. The data were obtained under controlled conditions on attached individual leaves of plants grown in the greenhouse. In maize, plants with suboptimal N supply exhibit a markedly lower maximum rate of net CO_2 assimilation compared to the plants amply supplied with N, but there is a proportional decrease in conductance for water vapour, hence a virtually constant assimilation/tran-

spiration ratio. A more or less similar behaviour is shown by Hordeum leporinum plants, a grass species from the natural vegetation in Israel (Lof, 1976): a drop in N concentration in the dry matter from about 43 to 23 g kg⁻¹ is coupled with a decrease in net CO₂ assimilation of about 25%, however again with a proportional decrease in conductance. The behaviour of *Phalaris minor*, another natural grassland species, tends to be slightly different, in that a somewhat more favourable assimilation/transpiration ratio exists for the plants well supplied with N, especially at higher light intensities at which most of the production takes place in the field (Figure 78). These data would thus suggest that,

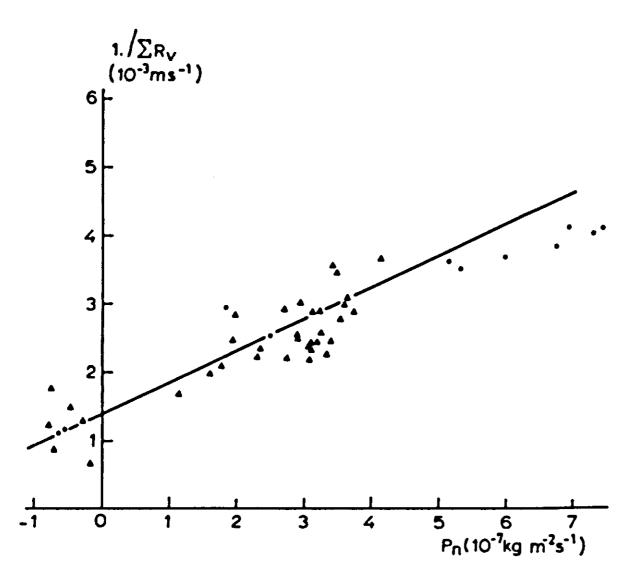


Figure 78. The relation between net rate of CO_2 assimilation (P_n) and total conductance for water vapour $(1./\Sigma R_v)$ for *Phalaris minor* for nitrogen depleted plants (\blacktriangle) and controls (•).

maybe with the exception of Phalaris, no differences in water-use efficiency or at least in transpiration efficiency are to be expected for different nutritional conditions. Overall water-use efficiency may be affected, however, since vegetation low in N exhibits a slower rate of accumulation of dry matter, which combined with a different distribution pattern of the material may lead to prolonged periods in which soil cover is incomplete. During such periods appreciable losses of moisture may occur through direct soil surface evaporation (Subsection 4.2.3). That may result in a much more unfavourable ratio between non-productive and productive water consumption. A more thorough investigation of the processes of assimilation, transpiration and growth under N deficient conditions is necessary, however.

Application in the simplified crop growth model SUCROS 5.3.3

These considerations may be illustrated with the simplified model developed in Sections 3.1 and 4.1. The data specified relate to a cereal crop, in particular. The amount of N in the various plant organs is established in integrals:

- ANLV = INTGRL(ANLVI, NUPL NUPSO * ANLV/(ANLV + ANST))ANST = INTGRL(ANSTI, NUPST - NUPSO * ANST/(ANLV + ANST))
- ANRT = INTGRL(ANRTI, NUPRT)
- ANSO = INTGRL(ANSOI, NUPSO)

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INCON ANLVI = 1.125, ANRTI = 0.28, ANSTI = 0., ANSOI = 0.

referring to the N in leaf (ANLV), stem (ANST), root (ANRT) and storage organs (ANSO) expressed in kg ha⁻¹, respectively. The rate variables for the vegetative organs are calculated from the total N uptake from the soil (TNUPSL, kg ha⁻¹ d⁻¹):

```
NUPL = TNUPSL*NDEML/(NDEML + NDEMST + NDEMRT)
NUPST = TNUPSL*NDEMST/(NDEML + NDEMST + NDEMRT)
NUPRT = TNUPSL*NDEMRT/(NDEML + NDEMST + NDEMRT)
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The demand for N of the vegetative organs (kg ha⁻¹ d⁻¹) at any particular moment is:

NDEML = (WLV*XNCL-ANLV)/TC NDEMST = (WST*XNCST-ANST)/TC NDEMRT = (WRT*XNCRT-ANRT)/TC

TC, the time coefficient (Subsection 2.1.7) for fulfillment of the demand, is set at 2 days.

The maximum levels of N in the vegetative organs (kg kg⁻¹) are defined in dependence on the development stage of the vegetation (cf. Figure 74), in a schematized way:

XNCL = AFGEN(XNCLT, DVS)FUNCTION XNCLT = 0., .045, .7, .0275, 2., .02 XNCST = 0.5 * XNCL XNCRT = 0.5 * XNCST

The total uptake of N is equal to the minimum of the demand of the vegetation or the maximum supply by the soil:

```
TNUPSL = AMIN1(NDEML + NDEMST + NDEMRT, ANSL/DELT)
```

The soil N stock, considered for simplicity as one state variable, is represented by an integral:

```
ANSL = INTGRL(ANSLI, - TNUPSL)
INCON ANSLI = 50.
```

The expression 'ANSL/DELT' in the rate equation thus indicates uptake of all

available N in one time step.

The initial amount may represent the amount of N available from the unfertilized soil. Alternatively, simulating fertilization in its simplest form, ANSLI may be computed in an INITIAL section of the program by:

ANSLI = ANSLU + FERT*REC

in which ANSLU is the N available from the unfertilized soil, FERT the amount of fertilizer applied, and REC the recovery fraction.

PARAM REC = 0.7

will often be a good first estimate.

Somewhat more detail could also be added by incorporating a net rate of mineralization, but that leads to speculative formulations in this example, geared to the response of the crop to N availability.

The storage organ is treated in a somewhat different way:

```
NUPSO = NDEMSO * FNDEF
NDEMSO = (WSO * XNCS - ANSO)/TC
PARAM XNCS = 0.025 \qquad (species specific)
FNDEF = 1. - SQRT (1. - AUX * AUX)
AUX = (LIMIT(LNCL, MNCL, ANCL) - LNCL)/(MNCL - LNCL)
ANCL = ANLV/WLV
PARAM LNCL = 0.005, TC = 2.
MNCL = 0.5 * XNCL
```

The latter two variables represent the minimum N concentration for unrestricted growth (MNCL) and the irreversibly incorporated N (LNCL) in the leaf tissue. All concentrations of N in dry matter in this example are given in kg kg⁻¹.

The influence of the N concentration on the rate of production is defined by the auxiliary variable AUX as well:

AGTWN = GTW * AUX

or:

AGTWN = AGTW * AUX

when the soil-water balance (Subsection 4.1.3) is also considered. Two alternative formulations can then be proposed for the influence on transpiration (Subsection 5.3.2, N nutrition and water use):

TRANSA = TRANS * AUX

or:

TRANSA = TRANS

In this schematized way, the major influences of availability of N on growth may be simulated.

Exercise 64

Combine the submodel of the amount of N in the various plant organs and its influence on growth of the crop with the summary model SUCROS and study the results. Replace GTW in Lines 107 and 108 (Table 9, Section 3.1) by AGTWN and add AGTWN = GTW*AUX. Simulate, for instance, situations with little and with ample N in the soil initially (PARAM ANSLU = 10., 25.,

50., and 100., respectively) and with various fertilization rates (PARAM FERT = (0., 50., 200.)).

5.3.4 Performance of the model PAPRAN

The performance of the model PAPRAN was studied by analyzing its behaviour under the conditions prevailing in the semi-arid region of the northern Negev desert of Israel, a winter rainfall area (average precipitation 250 mm per year) with a natural vegetation consisting of a mixture of annual plants species, typical of an abandoned cropland vegetation. For more details reference is made to van Keulen (1975). From this area dry matter yields in situations with and without application of nitrogenous fertilizer are available for a number of years.

Due to a lack of field observations, initial conditions were assumed to be identical for all growing seasons. At the onset of the growing season, an amount of 3000 kg ha⁻¹ of fresh organic material was assumed to be present in the upper 60 cm of the profile. The average N content of this material is set at 10 g

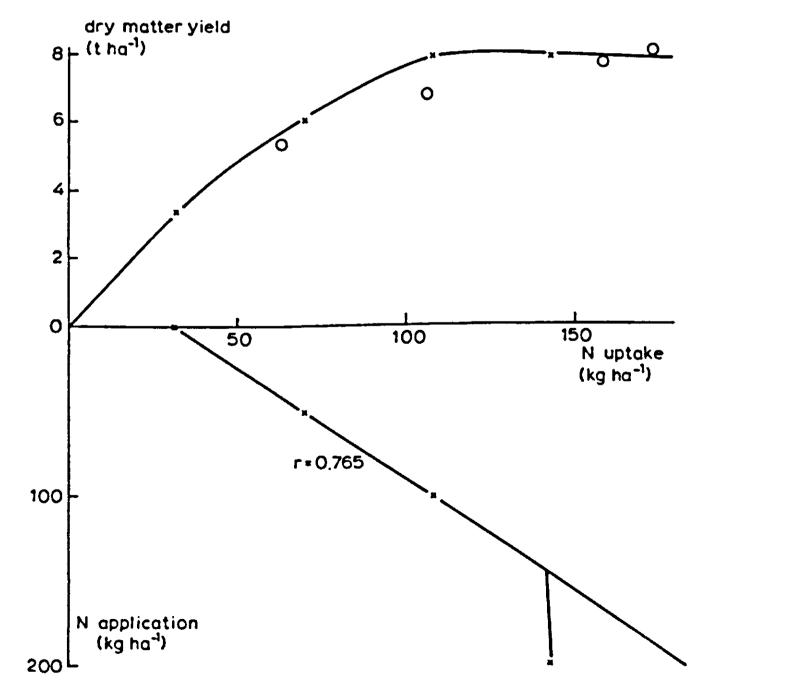


Figure 79. Simulated (x) and measured (o) results of experiments on natural vegetation in the northern Negev in the 1971-1972 growing season. The simulated recovery fraction (r) of fertilizer is indicated. kg^{-1} (dry matter). When fertilizer was applied in the model, this was assumed to be present at the start of the simulation, in ammoniacal form, evenly distributed in the upper 10 cm of the soil.

Some typical results are presented in Figures 79 and 80, in the form of results of fertilizer trials with experimental data for comparison. This gross output, when inspected in the way introduced in Subsection 5.1.2 with Figure 65 does not show a consistent picture:

- In 1971/1972 the various experimental treatments resulted in the uptake of varying amounts of nitrogen. A 'zero treatment' could not be analyzed in that season since all the experimental fields were disked for uniformity, incorporating into the soil substantial quantities of sheep droppings accumulated from preceding seasons. The simulated yield-uptake curve is situated within the accuracy limits of the measured data points. At the highest application rate, the model predicts a levelling off of the application uptake curve, resulting from 'nitrogen saturation' of the vegetation throughout the growing season. The predicted maximum uptake is in reasonable agreement with the measured value, which was determined at an even higher application rate.

- For 1972/1973 the experimentally determined points of the yield-uptake

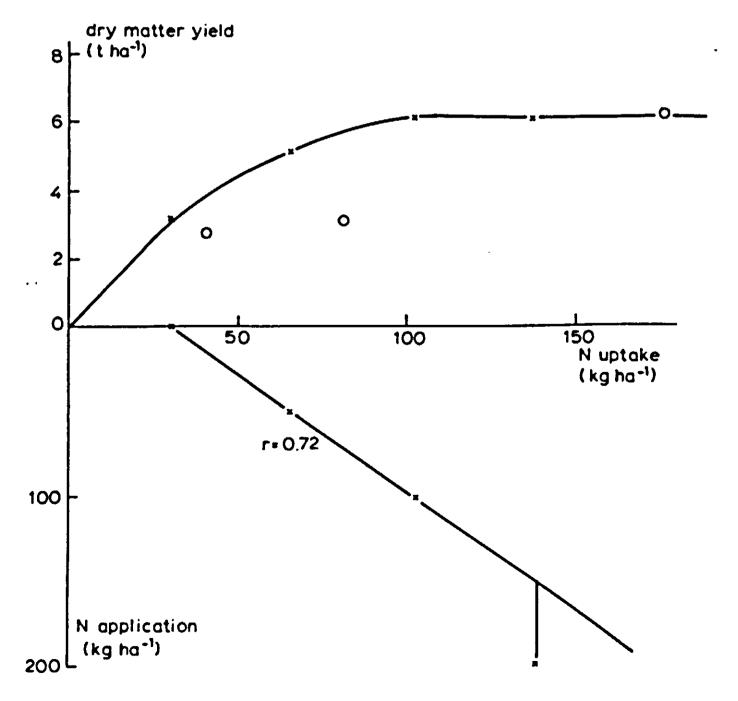


Figure 80. Simulated (x) and measured (o) results of experiments on natural vegetation in the northern Negev in the 1972-1973 growing season. The simulated recovery fraction (r) of fertilizer is indicated. curve deviate considerably from the simulated curve. Part of the explanation could be the relatively high proportion of legumes in the vegetation that season, having inherently a higher N content, even under limiting conditions (Subsection 5.1.3). The measured maximum uptake of the vegetation is about 25% higher than that predicted by the model, which suggests that the maximum concentrations applied in the model may be somewhat low, since total uptake was again dictated by the ability of the vegetation to absorb the element.

5.3.5 Discussion

The gross output of the model as presented in the previous section is probably not the most interesting part of the analysis, since these results were achieved for situations very close to those for which the model was developed (and hence calibrated). At this stage, the behaviour of some particular elements of the model may be more worthwhile looking at.

The fresh organic material, for instance, assumed to be present at the onset of the growing season decomposes almost completely, 5-15% being left at the end of the growing period, depending mainly on moisture conditions. Concurrent with this decomposition there is a slow, but gradual net release of inorganic N from organic material of this quality. When the N concentration of the initially added material is lower, the model predicts net immobilization first, only later followed by net mineralization. The major question in this connection is whether it is possible at all to describe quantitatively the dynamics of the N transformations in the soil and their consequences for the availability of this element to the vegetation, without explicitly simulating the microbial population in the soil. A satisfactory answer to this question is hampered by the inaccuracy of the experimental techniques available for the determination of the various components of the total N store in the soil and by the inherent heterogeneity of the system under field conditions. When the answer to this question is negative. there is a long way to go before the behaviour of such systems can be accurately described in a quantitative way, considering the state of knowledge at the microbiological side (Subsection 5.2.3).

With respect to the effects of N deficiency on the various processes related to plant growth and production, it has already been said that in many cases they had to be estimated based on incomplete and often qualitative information, and more research seems certainly warranted in that field. In conclusion, it may be stated that PAPRAN provides a useful framework for a systematic investigation of the relative importance of the various processes that play a role in determining crop growth under semi-arid conditions.