MODELLING DYNAMIC ASPECTS OF NITROGEN IN SOILS AND PLANTS

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INTRODUCTION

It is well over a century since the disagreements between Von Liebig and Gilbert/Lawes on the mineral nutrition of crop plants surfaced. Most of the questions that occupied these scientists at the time seem to have come to a state where reasonable agreement among scientists exists. However one can hardly avoid the conclusion that a hundred years of agricultural and plant physiological research have not advanced the understanding of the basic principles involved in plant nutrition sufficiently to permit the formulation of an unequivocally accepted quantitative description. True enough, the processes involved are complex and for a long time, even up to today may not have been amenable to direct measurements. It also appears however, that the interest in the nature of the processes has been only moderate, probably because a ceiling yield could be achieved anyway by increasing the amount of applied mineral fertilizer. Changing conditions and attitudes in recent years, which led on the one hand to a growing awareness of the (relatively) high costs of fertilizer manufacturing and on the other hand to a growing concern over the possible environmental effects of dumping high doses of plant nutrients on agricultural crops, have stimulated research aimed at a more efficient utilization of the nutrient resource. The basis of any improvement however, is a thorough understanding of the system, the way it operates and the constraints to which it is exposed.

In this presentation a model will be outlined in which an attempt is made to integrate the existing knowledge on nitrogen cycling in the soil-plant system. Because of the nature of the research project in which it was developed, it is especially

suitable for annual species, growing under conditions of limited
moisture supply. Certain modules could have a wider applicability,
but since in many cases descriptive rather than explanatory formu-
lations have been used, such an extrapolation may be dangerous at
the moment.

THE SIMULATION MODEL PAPRAN

The model has been developed in the framework of a research
project, concentrating on actual and potential production under
semi-arid conditions. It therefore concentrates on the effects
of moisture availability and of nitrogen supply on dry matter pro-
duction. The description given here refers to the version applied
to the natural pasture, an abandoned cropland vegetation, consist-
ing of annual grasses and herbs. Basically the same formulation
is being used for a parallel model, describing the production of
a wheat crop under these conditions. Since the validation studies
with that version are still in a preliminary stage it will not be
discussed here.

The main elements of the model are given in the schematized
relational diagram of Figure 1. The mixture of annual plants is
considered as a homogeneous stand with defined physiological prop-
erties. In the real situation the appearance of the canopy is
rather heterogeneous, especially at the onset of the growing
season. That heterogeneity is especially important when the vege-
tation is being exploited by grazing. The consequences of this
phenomenon for the performance of the model are being studied at
the moment. The model describes the growth of an annual crop from
the moisture balance and the nitrogen balance in the soil below it.

Plant Growth

Plant growth starts in the soil with germination of part of
the seed store. The process is initiated when the average moisture
content in the upper 10 cm of the soil is above field capacity and
proceeds until a temperature sum of 150 days by degrees C above
0 C has accumulated. When the soil dries out before that due to
evaporation, the germinating seeds are supposedly killed and a
new wave of germination starts only after additional precipita-
tion.

The initial amount of biomass present at establishment depends
on the seed stock in the soil in a given season and the conditions
during germination. The description used in the present version
does not allow for such a detailed treatment, hence the initial
value is estimated independently for each season.

After establishment, the gross rate of CO_2-assimilation is
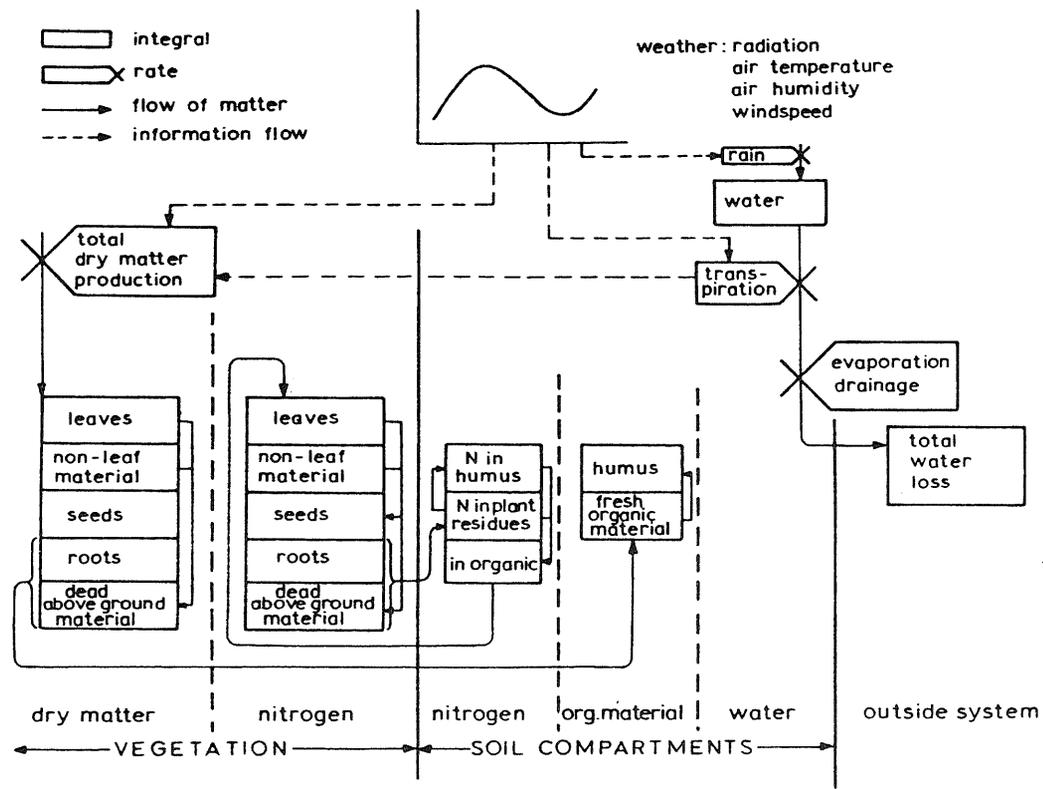obtained from the leaf area index and the radiation intensity for

Fig. 1.   Simplified relational diagram of the simulation model PAPRAN.

a given photosynthesis light response curve of the individual
leaves (Goudriaan and van Laar, 1978). The rate of maintenance
respiration, that is energy required to maintain the existing cell
structures (Penning de Vries, 1974) is calculated from the dry
weight present and the protein content of the structural material.
The potential rate of dry weight increase then follows from the
balance between gross assimilation and maintenance respiration,
by multiplying with a conversion efficiency, expressing growth
respiration, the energy lost in the conversion of primary photo-
synthates into structural plant material. That efficiency also
depends on the composition of the material being formed (Penning
de Vries, 1974).

The potential rate of transpiration of the vegetation is ob-
tained from the leaf area index and environmental conditions in-
fluencing the evaporative demand: level of irradiance, vapor
pressure and temperature of the ambient air and windspeed. The
values are integrated in a descriptive formula, using average
daily weather parameters (van Keulen, 1975).

The ratio of potential daily growth rate and potential trans-
piration rate, the water use efficiency, is a central parameter in
the model. This ratio is assumed to be constant, irrespective of
the moisture status of the canopy. Theoretical considerations
(van Keulen et al., 1980b) as well as experimental results (Lof,
1976) suggest that its value may change slightly when plants are
under water stress. The actual amounts of water transpired during
such periods are however so small that these differences hardly
affect the dry matter accumulation.

The actual rate of transpiration of the vegetation is calcu-
lated from the potential rate accounting for the influence of
moisture status in the soil and the distribution and activity of
the root system. In each soil compartment water is freely avail-
able until about 25 percent of available water is left, after
which uptake is reduced until cessation at wilting point.

The growth rate of the vegetation is obtained by multiplying
the water use efficiency by the actual rate of transpiration. Ni-
trogen deficiency in the tissue undoubtedly leads to reduced
growth rates. Its influence on water use is however far less
clear. A substantial amount of literature data suggest improved
water use efficiencies as a result of optimum nitrogen supply
(de Wit, 1958; Viets, 1962). This is confirmed by the experimental
results obtained in the northern Negev desert of Israel, where ap-
plication of nitrogenous fertilizer resulted in appreciable in-
creases in total dry matter production, without affecting the
moisture balance in the soil (van Keulen, 1975). In the present
version of the model transpiration is therefore unaffected by the

nitrogen status of the tissue. The point will be treated again in the discussion.

Allocation of Dry Matter. The total daily increment in dry matter is divided between leaves, non-leaf vegetative above-ground material (stems, leaf sheaths), roots and seeds. The allocation between the various organs is in first instance governed by the phenological state of the vegetation, represented by its development stage. First, a part of the available photosynthates is allocated to the roots. For this annual vegetation, the fraction varies between 0.5 at establishment and 0.025 toward maturity under optimum growth conditions. Insufficient moisture supply may modify this fraction, according to the functional balance principle: water stress favors root growth relative to that of above-ground material. A similar approach could be followed to account for the influence of nitrogen deficiency, but insufficient experimental data are available for a sound quantitative description.

A constant fraction of the material available for above-ground growth is diverted to the developing seeds after the flowering stage. The remainder is divided between leaves and non-leaf material, the actual proportions being governed by development stage (progressively less material is invested in new leaves with increasing age) and nitrogen status of the vegetation (nitrogen deficiency shifts growth in the direction of non-leaf material).

Death of the Vegetation. Vegetative plant parts may die as a result of stress, due to water or nitrogen shortage or due to senescence when the plants life cycle is completed.

The rate of dying of the material due to water shortage is governed by the balance between the rate of water loss by the vegetation and the rate of water uptake by the root system. Under severe moisture stress, the stomata are closed and water loss by the vegetation is restricted to cuticular transpiration. The rate of moisture loss through the cuticle is a function of the atmospheric demand, a constant conductivity being assumed. The rate of moisture uptake by the root system depends on the moisture status in the soil. Dying of the tissue is thus a function of both states of the system, whereas the buffering capacity of the vegetation is taken into account by applying a time constant of five days for dying. The death rate acts on both leaf and non-leaf material. The present description of tissue dying simulates actual situations during moisture stress reasonably well, but it has to be verified experimentally (van Keulen et al., 1980a).

Dying of the tissue due to nitrogen deficiency is a function of the nitrogen content of the vegetation. Dying starts when

the nitrogen concentration drops below the threshold value for unrestricted growth. The relative death rate increases gradually from there on, to reach a maximum value of 0.3 day^{-1} at the absolute minimum nitrogen concentration.

Dying of vegetative material due to senescence proceeds in reality from early stages of plant development. Leaves have a limited life span and the first ones may disappear relatively early. Since, however, in the present version of the model the leaves are not distinguished in age classes, senescence is disregarded before flowering. After that event senescence is accelerated as a result of translocation of especially plant nutrients to the developing seeds. At the end of the plant's life cycle, the relative death rate assumes a maximum value of 0.1 day^{-1}. This value causes almost complete drying of the standing vegetation in a fortnight, whigh is in good agreement with field observations.

Nitrogen in the Vegetation

Inorganic nitrogen present in the soil is taken up by the vegetation. No distinction is being made at present between NO_3^- and NH_4^+, since neither denitrification nor leaching play a role under the semi-arid conditions, and the vegetation may take up both forms of the element. It is assumed that the density and activity of the root system is sufficient to explore the total rooted volume. All the inorganic nitrogen in that volume is therefore available for uptake within a very short time, either by mass flow with the transpiration stream or by diffusion along developing concentration gradients resulting from low N-concentrations at the root surface (van Keulen et al., 1975).

The demand for nitrogen in the vegetation is created by the difference between the current concentration in the tissue and the maximum concentration possible. The latter value is a function of the development stage of the vegetation and varies between the different plant organs. For each of the components the value is high in the early stages and declines toward maturity.

When the supply of nitrogen is limited, that is when the total demand is not met by the actual uptake, the amount taken up by the vegetation is distributed between shoot and root in proportion to their relative demands. Neither experimental evidence (van Dobben, 1961) nor simulation results support the hypothesis that the closeness to the source gives the root system special advantage. Nitrogen transferred to the aerial plant parts is again distributed between leaves and non-leaf material in proportion to the relative deficiencies in the organs. The nitrogen demand created by the developing seeds after flowering is met by translocation from the vegetative tissue. All nitrogenous compounds accumulated in the seed are thus assumed to have passed through the vegetative tissue

first. This translocation process results in nitrogen depletion
of the vegetative tissue, when the supply from the soil does not
meet the seed requirements. In annual vegetations, both natural
pastures (Penning de Vries et al., 1980) and crop plants (Spiertz,
1978) it is often observed that accumulation of nitrogen ceases
after flowering. It is not clear, whether reduced root activity,
or e haustion of the soil nitrogen store, or spatial separation of
mois ure and nitrogen or a combination of these factors is respon-
sible for this phenomenon. When the vegetative tissue becomes
increasingly deficient in nitrogen, translocation to the seeds is
hampered, resulting in lower protein contents in the grain. A
lower limit for the nitrogen content has been introduced in the
model, forcing cessation of the carbohydrate flow to the seeds
when this limit is approached. This description is based on the
observation that under limited N-supply the protein content of
seeds is species-dependent only, irrespective of growing condi-
tions (van Keulen, 1977). Lack of understanding of the underlying
processes necessitated the adaptation of this descriptive formula-
tion.

     Death of vegetative tissue leads to loss of nitrogen from the
vegetation. The nitrogen concentration in the dying tissue depends
on the cause of death. Tissue dying from water shortage or sen-
escence disappears with a concentration equal to that of the live
material. Tissue, dying from nitrogen deficiency contains only the
irreversibly incorporated nitrogen, the remainder being translo-
cated to the remaining plant parts. This description mimics the
real-world situation where continuous breakdown and transfer of
nitrogenous compounds permits the growth of new tissue at the
expense of older ones.

Nitrogen in the Soil

     The complexity and importance of nitrogen transformations in
the soil is illustrated by the voluminous literature on the sub-
ject (Bartholomew and Clark, 1965; Tandon, 1974; van Veen, 1977).
Nevertheless our understanding of the processes that play a role
and their quantitative consequences is still very limited as is
demonstrated by the attempts to use the available information for
the development of detailed models of the soil nitrogen system
(Beek and Frissel, 1973; Hagin and Amberger, 1974; van Veen, 1977).
The approach followed by van Veen, which is microbiologically based
is theoretically sound, since the transformations in the soil are
governed by microbial activities. In practice however, the dis-
tinction of a separate pool of microbial biomass or proteins, is
difficult (if not impossible) because of the available experi-
mental techniques. Initialization of such a model for a specific
site, as well as validation of the results is therefore hardly
feasible. In the present approach nitrogen in the soil system
is divided into three states: inorganic nitrogen, nitrogen in

'fresh' organic material (including plant residues which have not
yet passed through the microbial pool and the microbial tissue
itself) and nitrogen in 'stable' organic material (soil humus,
which has at least once undergone a transformation through the
microbes).

Organic Matter Transformations. The rate of decomposition of
the two organic fractions in the soil is based on first-order kin-
etics: under optimum conditions a constant relative rate of de-
composition is assumed. The specific rate is different for various
compounds (Hagin and Amberger, 1974): it is of the order of 1
day^{-1} for easily decomposable proteins and sugars, $\pm$ 0.05 day^{-1}
for cellulose and hemi-cellulose and $\pm$ 0.01 day^{-1} for lignin. In
the model these different rates are introduced in a step-wise
manner, as the original amount of added fresh organic material
reduces. Different compositions of the added material can be
accounted for by changing the switch-values for the rate con-
stants. The rates of decomposition may be modified by environ-
mental conditions of soil moisture, temperature and C:N ratio of
the decomposing material. When the overall C:N ratio, including
the mineral nitrogen present is below 25, decomposition proceeds
at the potential rate (Parnas, 1975).

In this description it is implicitly assumed, that the acti-
vity of decomposing bacteria is never limiting the rate of decom-
position, while instantaneous adaptation to different substrates
is assumed.

The stable organic material, which is assumed to have a con-
stant C:N ratio of 10, decomposes at a much lower rate (Harpaz,
1975). Again soil moisture conditions and temperature may influ-
ence its rate. Accretion of stable organic material results from
stable compounds of the fresh organic material. It is assumed
that 'humus-formation' takes place when the overall C:N ratio of
the decomposing material is below 25. At that stage mineral ni-
trogen is released, of which 20% is assumed to be incorporated in
the stable fraction. The constant C:N ratio applied, also yields
the rate of humus accretion.

Soil Nitrogen Processes. .During decomposition of the fresh
organic material, mineral nitrogen is being released, when the
carbon of the substrate is used for build-up of microbial tissue
and supply of energy for the functioning of the microbial popula-
tion. The rate of release of mineral N is therefore a direct
function of the rate of decomposition of the substrate and its
nitrogen content. At the same time, however, the build-up of the
microbial biomass requires nitrogen for the build-up of proteins
and amino acids. The rate at which nitrogen is incorporated in
the tissue is again dictated by the rate of decomposition of the
substrate which provides energy and structural material. The

basic assumption is, that all carbon released during breakdown of
the organic compounds is used for build-up of microbial biomass,
with an average biosynthesis efficiency (Sörenson, 1975). The re-
quired protein content of the microbial tissue thus determines the
N-requirement during decomposition. The composition of the decom-
posing material then dictates whether mineral nitrogen is immobil-
ized in the tissue. Gross release of nitrogen is thus dependent
on the nitrogen content of the originally added fresh material.
Net release, i.e., the balance between gross release and immobili-
zation must in this description be considered as originating from
the microbial component of fresh organic material. The formula-
tion leads to realistic simulations of the switch from net immob-
ilization to net release at total C:N ratio's between 25-30.

The rate of change of nitrogen in the stable organic compound
is the balance between its rate of mineralization governed by the
decomposition rate and the rate of incorporation dictated by the
rate of release from the fresh organic material.

The amount of mineral nitrogen in each soil compartment
changes by release from or immobilization into the organic com-
ponents and by uptake by the plants. Furthermore transport be-
tween compartments is taken into account. The time interval of
one day employed in the model is much larger than the time con-
stant for solute transport (de Wit and van Keulen, 1972; de Wit
and Goudriaan, 1974). A mimicking procedure is therefore again
necessary. Transport is assumed to take place only with movement
of the water, that is during infiltration. The concentration of
mineral nitrogen transported over the lower boundary of a compart-
ment is obtained by 'mixing' the solutes present in the compart-
ment and those transported into it, with water in the layer and
all water flowing through. Such a description takes into account
mass transport and (part of) the effects of mathematical disper-
sion, inherently present in such compartmentalized models
(Goudriaan, 1973). Upward transport of solutes with the soil
evaporative flow or diffusion along developing concentration
gradients is not taken into account. The present description is
satisfactory for our purpose, where the main interest is in the
availability of nitrogen to the vegetation, rather than in its
exact distribution within the profile.

Ammonium fertilizers, especially when applied to soils, with
a high pH may lead to considerable losses of nitrogen through vol-
atilization. Again the time constant of the chemical processes
involved are lower than the time resolution of the model. Am-
monium when present in the top soil compartment is assumed to
volatilize at a constant relative rate, whereas at the same time
nitrification proceeds. The relative rates for these processes
are of the order of 5-10 day^{-1}, so that appreciable losses only
occur during the first week after application when no precipitation

occurs during that period. This is a rather crude description and a more realistic one would increase the generality of the model.

Processes Not Considered. Some of the processes taking place in the soil-plant system have not been included in the model:

1) Denitrification is disregarded for the moment, because anaerobic conditions are unlikely to occur in the semi-arid regions for which the model is mainly developed. The possibility that through intensive biological activity anaerobic pockets may occur around plant roots or inside soil structural elements is recognized, but simulation of such situations is extremely complex (Leffelaar, 1979).

2) Adsorption of NH_4^+ onto the exchange complex or fixation into the lattice of clay minerals has not been taken into account. In most situations these processes play a minor role in the annual nitrogen balance. In specific cases however, especially when nitrification is hampered, they could be of importance. Appropriate process models would have to be developed then.

Soil Water Balance

The description of the soil moisture balance in this model is essentially identical to that used in the model ARID CROP (van Keulen, 1975; van Keulen et al., 1980a) and will be treated here only briefly. For the description of the water balance, the soil depth is divided into homogeneous compartments. Both their number and their thickness can be easily adapted.

Infiltration. Infiltration into the soil either from rain or irrigation is obtained from the rate of moisture supply, taking into account possible run-off effects. The latter has been treated rather rudimentary. A more detailed treatment has been elaborated (Rietveld, 1978) but as yet not been applied in lower resolution models.

When water is added to the soil, the change of moisture content in each compartment is set equal to the difference between the moisture content at field capacity and the current moisture content. Instantaneous 'equilibrium' is thus assumed. The compartments are filled in this way from the top one downwards.

Soil Surface Evaporation. Under semi-arid conditions evaporation from the soil surface is the most important source of non-productive water loss. In the model potential evaporation follows from a Penman-equation. Subsequently that is modified by taking

into account the effects of shading by the vegetation and of drying
of the topsoil. The total water loss is proportioned over the dif-
ferent compartments by means of a mimicking procedure (van Keulen,
1975). This procedure yields reasonable results in winter rain-
fall conditions, but seems not to be applicable without modifica-
tion under summer rainfall conditions, probably because of the
steep temperature gradients that may develop in such situations.

Root Water Uptake. From the potential rate of transpiration
and the total rooted depth, the required rate of water uptake per
unit root length is calculated. In each compartment that rate may
be reduced due to low moisture contents or due to low soil temper-
atures. The relation between soil moisture content and root water
uptake is of the Viehmeyer-type: water remains freely available
until about 70% of the available water has been used. After that
a sharp reduction follows until the permanent wilting point. Par-
tial compensation is accounted for, when a portion of the root
system is in dry soil layers. Temperature effects on root water
uptake take into account both the change in viscosity of the water
and in activity of the root system.

RESULTS AND DISCUSSION

The performance of the model was studied by analyzing its be-
havior under conditions prevailing in the northern Negev desert of
Israel. In this semi-arid region (average annual rainfall 250 mm)
long-term experiments on the productivity of natural pastures have
been carried out (Tadmor et al., 1974; van Keulen, 1975) both with
and without the application of nitrogenous fertilizers. For the
simulation runs actual weather data were used, collected at a
nearby station of the Israeli Meterological Service, with the ex-
ception of rainfall which was recorded at the site.

The initial conditions at the onset of the rainy season were
assumed identical for all years: a total amount of 3000 kg of
fresh organic material, consisting of roots, stubble, etc., of
last year with a nitrogen content of 0.01 kg N kg^{-1} (dry matter)
present in the upper 60 cm of the soil profile. When fertilizer
was applied, this was assumed to be evenly distributed in the
upper 10 cm of the profile in ammoniacal form.

The results of the simulations (Figs. 2, 3, 4) do not show a
consistent picture:

1) For the 1966/1967 growing season only application-yield
data are available for testing. The yield without fer-
tilizer application is reasonably well estimated, but
the simulated fertilizer response curve deviates con-
siderably from the measured one. Since no nitrogen up-
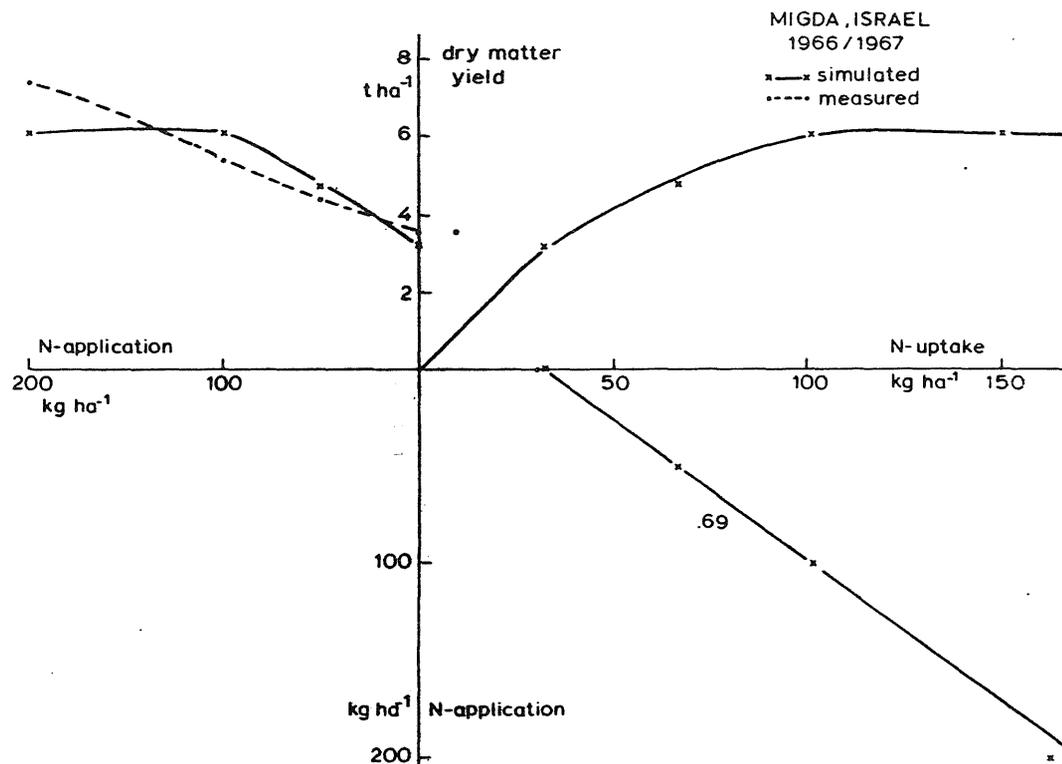take data are available it is impossible to determine

Fig. 2. Comparison between simulated and measured results of fertilizer experiments on natural vegetation in Migda, Israel in the 1966/1967 growing season (right hand quadrants only simulated).
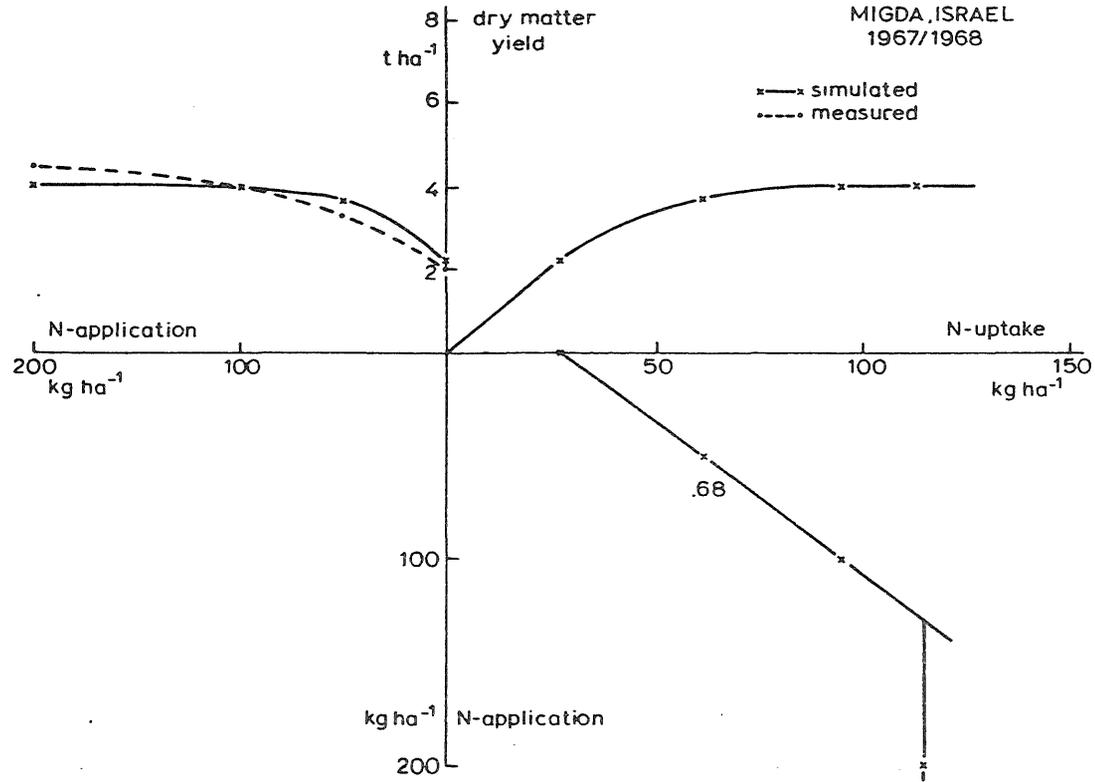
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Fig. 3. Comparison between simulated and measured results of fertilizer experiments on natural
vegetation in Migda, Israel in the 1967/1968 growing season (right hand quadrants only
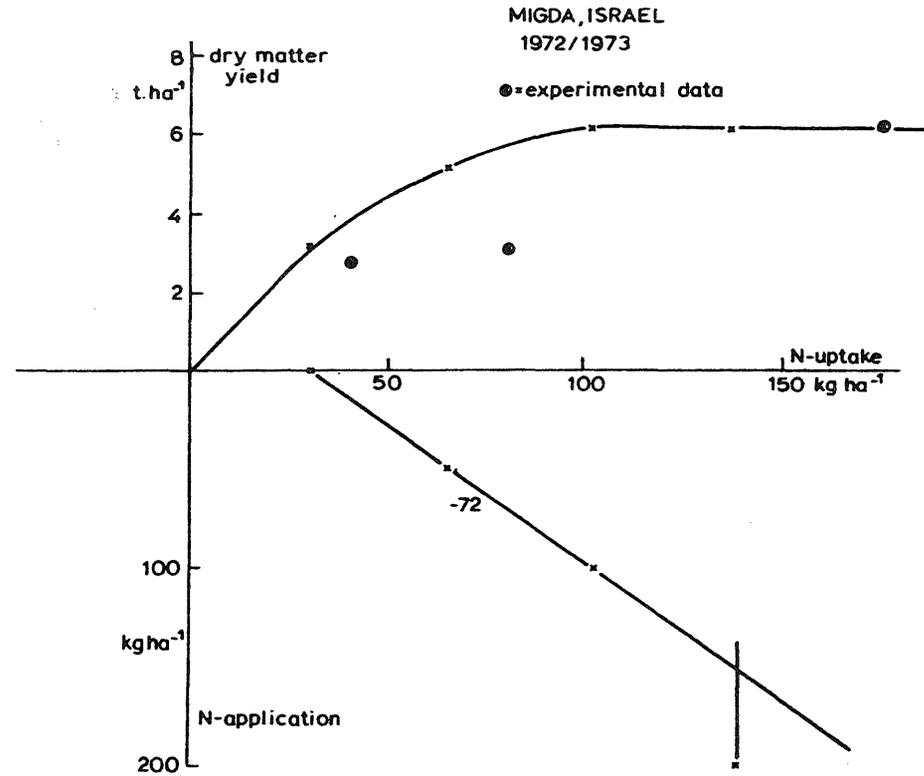simulated).

Fig. 4.   Comparison between simulated and measured influence of nitrogen uptake on dry matter production of natural pasture in Migda, Israel in the 1972/1973 growing season.

whether the discrepancies in the fertilizer response are the result of inaccuracies in the description of the response of the vegetation to increased nitrogen availability or of a misrepresentation of the application-uptake relation.

2) For 1967/1968, a drier year than the previous one (mainly as a result of a much more unfavorable distribution of the rainfall), the simulated yield-application curve is fairly close to the measured one over the full range of applications. In such years there is only limited benefit of the application of nitrogenous fertilizer. However under these semi-arid conditions where neither leaching nor denitrification play an important role, the applied nitrogen will largely remain in the soil and become available in subsequent years. When the soils are sufficiently deep and fertilizer is applied in nitrate form, all applied nitrogen should eventually be recovered in the vegetation. Whether this is also true in the short run is questionable, since inputs of fertilizer N will result in the creation of a non-equilibrium, where part of the applied N may temporarily be tied up in the soil organic matter.

3) The simulated yield-uptake curve for 1972/1973 deviates considerably from the measured one. Part of the explanation must be the leguminous component, which, at peak biomass, comprised about 25% of the total dry matter yield. Even when that is taken into account, the measured yield is low in relation to the amount of N absorbed. The reason for this lack of dilution is not clear.

The influence of nitrogen shortage on the transpiration/assimilation ratio and hence the water use efficiency is subject to debate. There are, on the one hand, many reports showing improvements in water use efficiency at optimum N-levels (c.f., Viets, 1965). More recent experimental evidence suggests however a constant ratio irrespective of the nutritional level of the plant (Goudriaan and van Keulen, 1979). The results of the model (Fig. 5) strongly indicate that total water loss under the Negev conditions is virtually identical with and without N-application. Results obtained under Sahelian conditions (PPS, 1980) however show that under N-limiting conditions more moisture remains in the soil at the end of the growing season. This aspect of plant physiology certainly warrants more attention.

The results presented here indicate that the performance of the model when compared to the real-wold is rather variable. One of the major drawbacks is, that for a model of this complexity
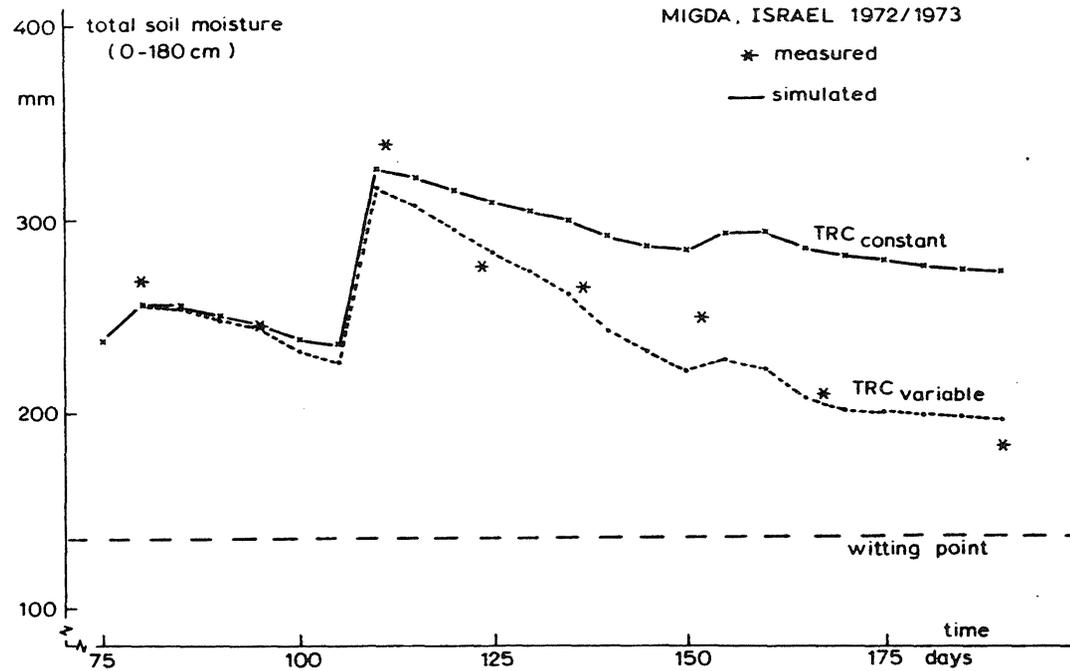
Fig. 5. The influence of two alternative hypotheses with respect to transpiration/photosynthesis
ratio, on the simulated moisture balance below the natural vegetation in Migda, Israel
in the 1972/1973 growing season, in comparison to the measured data.

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the use of only gross output data for validation is hardly suffici-
ent.   It contains so many relations and parameters that almost any
result can be obtained by changing their value.   On the other hand,
however, data sets, to validate separate elements of the model are
extremely scarce.   This again stresses the point that systems
analysis, model development and simulation can never be a substi-
tute for experimental work.   It should be used as a framework by
which problems can be more clearly recognized and analyzed, and
hence may lead to the design of more relevant experiments.

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