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Measurement and modelling of primary production and water use in a south Tunisian steppe

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Measurements carried out between 1971 and 1977 indicate the effect of rainfall on above-ground plant production. The site investigated consists of steppeland on sandy soil, dominated by the perennial dwarf shrub *Rhantherium suaveolens* with associated annual species. The average precipitation in this region (180 mm), produces about 1000 kg dry matter/ha. The ARFEJ model described, uses the most pertinent characteristics of the system so that production can be predicted under the assumption that water is the limiting factor. Seven model coefficients were calculated with the data of 1971–75. The results show (a) the considerable effect of rainfall distribution on evaporation from bare soil. The mean of this evaporation was 55 per cent (range 40–69 per cent) of total evapotranspiration; (b) during the short annual period of fast growth, the ratio of dry matter to water transpired would be about 1·26 g dry matter/kg H_2O for annuals, and 1·39 g dry matter/kg H_2O for perennial species. Over the whole year, the average efficiency of water use is 0·45 g dry matter/kg H_2O for all species; (c) above 250 mm precipitation, the availability of nitrogen and/or phosphorus becomes the limiting factor for plant production and efficiency of water use decreases.

Introduction

The primary production of ecosystems is affected by an array of interacting factors. In arid environments, water deficiency is commonly assumed to be the most important factor controlling the growth and survival of plants. Due to large annual rainfall fluctuations, long-term measurements of climate, soil water and standing biomass are necessary to establish the relationships between these data. Complementary modelling assists in clarifying these relationships and helps to evaluate and to predict plant production with different quantities and distributions of yearly rainfall. To reach this goal, the mathematical model takes into account the dynamic aspects of the system, and the processes essential to explain them. Ours is neither a large scale multiparameter model, which considers a great number of processes, as has been developed in the U.S. International Biological Program (Goodall, 1973*a*, *b*; Innis, 1978), nor a simplified version of it (Romane, 1974).

The Presaharan zone of Tunisia covers an area of about 20,000 km^2, lying between the 100- and 200-mm isohyets. In spite of a tendency for the nomadic population to settle and cultivate the land, this arid region still comprises vast ranges of steppe, used principally by grazing sheep, goats and a few camels.

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During the last 20 years, several ecological studies have been conducted in the region. Their purpose has been to characterise the main ecological systems in terms of plant production and dynamics and they have led to a better understanding of climate–soil–plant relationships (Floret & Pontanier, 1978). An attempt has also been made to evaluate primary and pastoral production at a regional level (Le Houérou, 1969; Floret, Le Floc'h *et al.*, 1977*a*, 1981). Schemes for managing, developing and conserving this densely populated territory, in which recent desertification is easily perceptible (Le Houérou, 1969; Floret, Le Floc'h *et al.*, 1977*b*), have been proposed.

In the different research programs, several ecological systems were studied in respect of (a) variations in standing phytomass, in order to evaluate primary production, and (b) fluctuations of soil water, to compute actual evapotranspiration; meteorological data were also collected. The measurements were carried out over six years.

The model and results presented in this article concern only one of the ecological systems investigated. The steppe under study is an homogeneous formation of *Rhantherium suaveolens* on deep sandy soil. The site is typical of areas which cover thousands of hectares in Tunisia. Similar steppes have been studied by Le Houérou (1959, 1969), Novikoff (1975, 1976, 1977) and Maniere (1975) in Algeria. Thalen (1979) has described closely related steppe vegetation (of *Rhantherium epapposum*) in Iraq.

Study site

The study site is located at 50 km north-west of Gabès, in the region of the 'Basses Plaines Méridionales Orientales'. It is a typical steppe range on sandy soil. The annual average rainfall is approximately 170–180 mm, of which 75 per cent falls in the cold season, between September and March. Large fluctuations occur: a range of 36–532 mm was observed over an 80-year period at Gabès. According to Emberger's (1955) classification, the climate of the region is very arid. The low rainfall and drying wind, which blows from the west during the growth season, yields a water deficit in the order of 1400 to 1500 mm (Damagnez, Riou *et al.*, 1963).

Soil

The Miopliocene substratum is formed from gypsous sandy clay. It is covered by early and middle Quarternary deposits, with marked wind action on the sand. Thanks to good porosity (40–50 per cent) in the upper horizons, almost all the rainfall penetrates the soil. The amount of organic matter (0·4–0·7 per cent) and the exchange capacity (5–7 mequiv./100 g), are very low. The base-exchange complex is saturated, mainly with calcium and the pH is approximately 8. Some physical properties for this soil are presented in Fig. 1.

Vegetation

The plant community is a homogeneous steppe formation of low (5–40 cm) woody species with a predominance of *Rhantherium suaveolens* Desf. with *Arthrophytum schmittianum* (Pomel) Mand W., *Helianthemum lippii* var. *sessiliflorum* (Desf.) Murb., *Salsola vermiculata* var. *brevifolia* (Desf.) M. & W., etc. The cover of the perennial species is about 35 per cent: *R. suaveolens* alone covers 30 per cent of the soil surface, with 26,500 tussocks/ha. The area between woody species is occupied by perennials such as *Stipa lagascae* R. & S. and *Aristida ciliata* Desf., and principally by *Plantago albicans* L. which covers about 5-6 per cent (Le Houérou, 1959).

Seeds of the annual species germinate at the beginning of the rainy season (September–October). They show maximum development during the spring (50 per cent of plant cover in favourable years). The relative amount varies according to season and the distribution of rainfall. The annual vegetation dries at the end of spring and

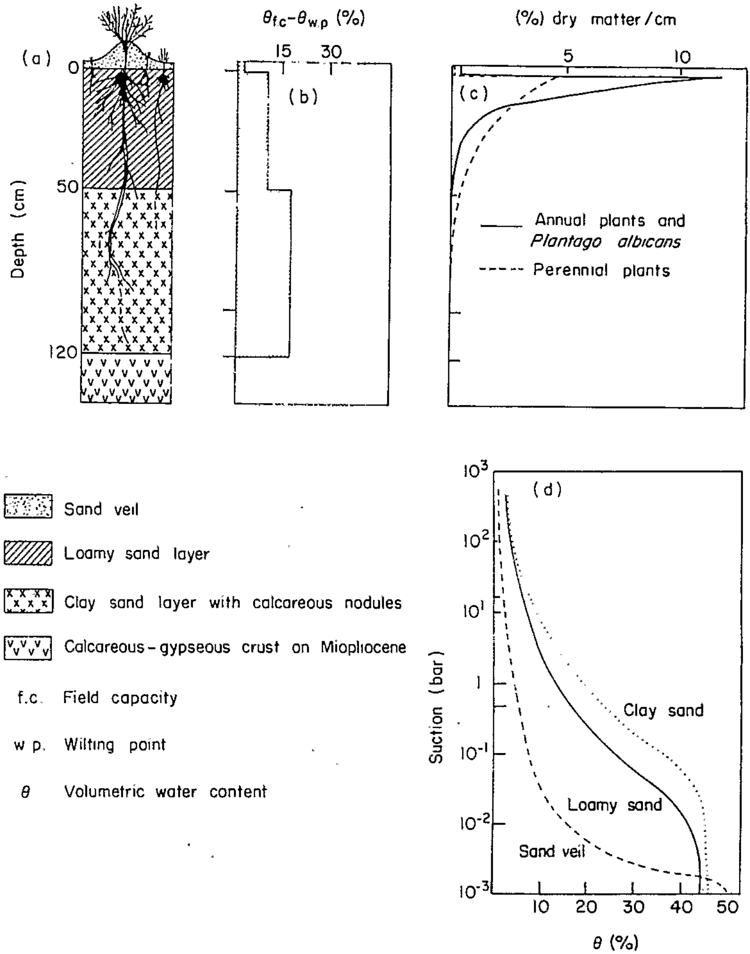

Figure 1. Some physical properties of the soil profile and the root distributions of the annual plants (plus *Plantago albicans*) and the perennial plants. (a) Pedological profile, (b) effective water supply distribution, (c) root distribution and (d) soil moisture retention curves.

disappears during summer. The perennial vegetation continues to grow for longer—occasionally until the end of July if water remains in the deeper layers of the soil. The average total above-ground phytomass, at the beginning of autumn, before the first rains and after the summer grazing, was approximately 1600 kg dry matter/ha. The corresponding average subterranean phytomass was approximately 45 per cent of the total. At the same time, there was approximately 50–80 kg dry matter/ha litter on the soil surface.

Experimental procedure

Net primary production was measured as follows: each year 0·25 ha were fenced for protection from large herbivores about a month before the beginning of the rainy season. The area was normally grazed until this time. The enclosures were subdivided into small plots. Between September and August, five to seven successive harvests were gathered at ground level in randomly selected plots. Each plot was only cut once. Large perennial species were sampled on nine replicates each of 32 m^2; annuals, small perennials and litter on 18 replicates of 4 m^2. The new shoots of perennial species were separated from the woody parts and weighed. The results were expressed as oven-dried matter. Each year, an enclosure was established on a new plot. The coefficient of variation for shoots and woody phytomass of perennial plants was 7·5 per cent and for the annual plants, plus *P. albicans* (a perennial herb), 40 per cent. At the same time, data on rainfall, temperature and Piche evaporation were collected daily at a meteorological station nearby, while solar radiation was measured at Gabès. Soil water was measured gravimetrically at approximately fortnightly intervals during the rainy season and immediately after each precipitation exceeding 10 mm, and monthly in the dry period. On each occasion three profiles were sampled at height different depths.

Evapotranspiration (*ET*) was calculated by difference using the water balance equation. Surface runoff and deep drainage were negligible, so that the equation was reduced to: $ET = P - \Delta S$ where P = precipitation and ΔS = change in soil water storage. All the water that infiltrated had either evaporated from bare soil or been transpired by plants before the end of the season. Table 1 summarises the climatic and plant data obtained from 1 October 1971 to 31 August 1976. Figures 3 to 5 show the variation of soil water content and the amount of phytomass.

Model development

The model presented here, named ARFEJ (from the Arabic name for *R. suaveolens*), is an attempt to take into account the characteristics of the soil, atmosphere and vegetation necessary to predict growth. These are not separated as they form interrelated parts of a whole. Soil fertility, atmospheric carbon dioxide concentration and grazing by animals are not, however, considered. The model is composed of three components: water flow, growth of annual plants and *P. albicans* and shoot growth from perennial plants (mainly *R. suaveolens*) (Rambal, 1980). A flow diagram is shown in Fig. 2.

The model simulates periods of one year from the beginning of the rainy season in September until the following August. Climatic data are entered daily, while

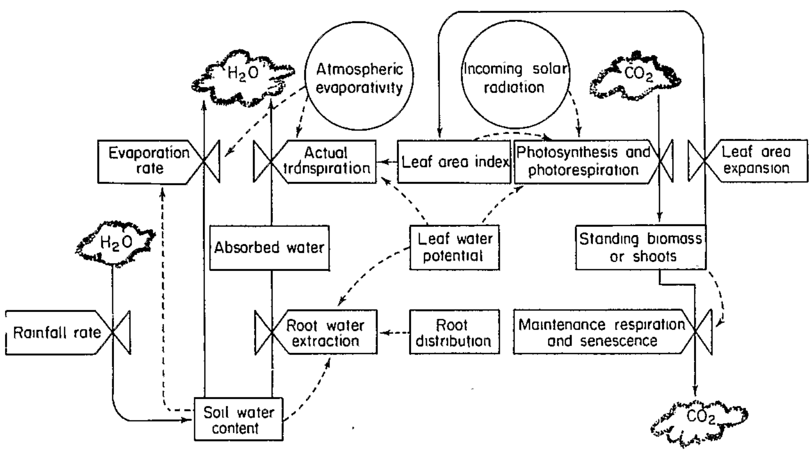

Figure 2. The ARFEJ model flow diagram.

Table 1. *Climate and measured plant production*

Season	Rainfall* (mm)		Number of rainy days	Temperature (°C)			Piche evaporation (mm)	Actual evapotranspiration (mm)	Annual plant production (kg dry matter/ha)			
	Annual	Spring (Feb–May)		t_{max}	t_{min}	$\bar{t}$			Annual plants	*Plantago albicans*	Perennial plants	Total
1971–72	191	116	32	34·4	3·0	—	—	194	87	48	883	1018
1972–73	210	59	35	37·8	3·5	17·8	2331	253†	532	97	531	1160
1973–74	316	42	18	34·8	6·4	19·4	2524	292‡	108	85	869	1062
1974–75	186	89	34	36·6	3·9	18·1	2421	186	284	215	512	1011
1975–76	295	145	44	34·7	4·1	18·2	2243	294	154	261	1130	1545
1976–77	84	27	15	34·7	6·3	19·1	2740	85	4	111	107	222
Average (Gabès)	183	61	31	32·7	5·9	19·3	2022					

* Climatic year is defined as 1 September to 31 August.
† Includes supplementation by runoff.
‡ Includes loss by runoff.

calculations of the simulation are made with a time increment of 1 day. Comparison between calculated and measured values was made approximately every 10 days (8 or 9 days in the last decade at February and 11 days in the last decade of months with 31 days). The model was calibrated with data of 1971 to 1975 according to Rosenbrock's method (1960) and by non-linear filtering (Rambal, Romane *et al.*, 1977); validation used the 1971 to 1977 data.

Water flow

The behaviour of soil water is simulated by storage at four levels: the first in superficial sand, the next two in loamy sand, and the last in clay sand. Outflow rates and deep percolation are proportional to the difference between the actual soil water content and the soil water content at 0·5 bar suction, i.e. field capacity. For each layer

$$\begin{aligned} D_i &= (S_i - CR_i)/T_i \quad \text{if} \quad S_i > CR_i, \\ D_i &= 0 \quad \text{if} \quad S_i \leqslant CR_i, \end{aligned} \qquad (1)$$

where D_i = outflow rate or deep percolation (mm/day), S_i = actual soil water content (mm), CR_i = soil water content at 0·5 bar suction (mm), and T_i = time constant of the redistribution of soil moisture following infiltration (day). The time constants (T_i) per cm are equal to $8{\cdot}33 \times 10^{-3}$ days and $12{\cdot}5 \times 10^{-3}$ days, respectively, for the loamy and clay sand layers. Redistribution is considered instantaneous in the superficial sand.

The water balance equation for each soil layer is indicated in the following differential equation:

$$\mathrm{d}S_i/\mathrm{d}t = (P \text{ or } D_{i-1}) - ET_i - D_i,$$

where ET_i is the contribution of the ith soil layer to actual evapotranspiration.

Actual evaporation from bare soil

The potential rate of evaporation (E_{pot}) is calculated from atmospheric evaporation. It is assumed to be proportional to Piche evaporation (PICHE) (Bouchet, 1965). The actual evaporation rate (E) is then determined by the water content of the top soil. The energy intercepted by vegetation is negligible because of the low plant cover. In summer, when the soil surface is air dry, the evaporation rate is mainly controlled by temperature gradients and is assumed to be 8 per cent of the potential evaporation (Gardner & Fireman, 1957). The ratio between the water content of upper horizon and actual and potential evaporation is taken from the Van Keulen (1975):

$$E_{pot} = k_1 \text{ PICHE (mm/day)} \qquad (3)$$

where k_1 = calibration coefficient (to use Piche evaporation as an estimation of the atmospheric evaporativity)

$$E/E_{pot} = F(\text{SVE}') \qquad (4)$$

where SVE′ is the dimensionless soil water content of the upper horizon defined by:

$$\text{SVE}' = (\text{SVE} - \text{SVE}_A)/(\text{CRVE} - \text{SVE}_A)$$

where SVE = actual soil water content of the upper horizon (mm), SVE_A = soil water content at atmospheric humidity of this layer (mm), and CRVE = soil water content at 0·5 bar suction (mm). Water loss through evaporation is distributed throughout the various layers of the soil by means of an extinction coefficient α (Van Keulen, 1975) computed as follows:

$$\alpha_i = S_i'.\exp(-KE.z_i) \qquad (5)$$

where S_i' is the dimensionless soil water content of the ith layer, z_i is the depth of the center of the ith soil layer (cm) and KE is the extinction coefficient for moisture withdrawal (cm^{-1}). A KE value of 0·125 cm^{-1} was used.

$$\text{If} \quad \alpha = \sum_i \alpha_i, \quad \text{then} \quad \alpha_i' = \alpha_i/\alpha, \tag{6}$$

where α_i' is the extinction coefficient of actual evaporation

$$E_i = \alpha_i' E \tag{7}$$

and where E_i is the contribution of the ith soil water layer to the total evaporation (mm/day).

Actual transpiration

A first approximation of the total transpiration of vegetation subjected to substantial water stress is given by Thom (1975). Piche evaporation is related linearly to the vapour pressure deficit of the air (Stanhill, 1962). Consequently the equation for actual transpiration is

$$TR = k_1 \text{PICHE} \times \text{LAI} \times K_S \text{ (mm/day)}, \tag{8}$$

where LAI is the leaf area index (ha/ha) and K_S the stomatal conductance (per cent). The relation between stomatal conductance and the leaf water potential Ψ_f is the following:

$$K_S = 1/(1 + (\Psi_f/k_2)^5), \tag{9}$$

where k_2 = critical leaf water potential (bar) (coefficient to be estimated). To satisfy the TR demand, the roots extract Q_i from each soil layer (Gardner & Ehlig, 1962).

$$\begin{aligned} Q_i &= (\Psi_f - \Psi_i)/R_i \quad \text{if} \quad \Psi_f > \Psi_i, \\ Q_i &= 0 \quad \text{if} \quad \Psi_f < \Psi_i, \end{aligned} \tag{10}$$

where Ψ_i is the suction (bar) at S_i water content (mm), and R_i is the hydraulic resistance of the roots associated with the percentage of the total root system in the ith layer (bar/day/mm). In the macroscopic model, the hydraulic resistance to flow in the soil (rhizospheric resistances) is assumed to be negligible.

The hydraulic resistance of the roots (R_i) is inversely proportional to the percentage of the total root system in the ith soil layer, with a total resistance equal to 1·03 bar/day/mm. The leaf water potential Ψ_f is unknown. We assume that plants generate a Ψ_f value just sufficient to satisfy TR as the summation of all individual root extraction terms:

$$TR = \sum_i Q_i. \tag{11}$$

The search for an appropriate Ψ_f value, at any point in time is made by an iterative procedure.

These mathematical expressions are applied to the annual plants (plus *Plantago albicans*) and the perennial plants. k_1 is the same coefficient for these two groups of species.

Carbon flow

Photosynthesis

Gross photosynthesis is assumed to be a function of water status, leaf area index and incoming solar radiation. The equation for gross photosynthesis, derived from Feddes

(1971), is

$$dP/dt = k_3 \times 4{\cdot}9\ K_S \times \mathrm{LAI} \times \mathrm{RAYGL}/(4{\cdot}4\ K_S + 1{\cdot}64), \quad (12)$$

where dP/dt is the gross photosynthetic rate (kg dry matter/ha/day), LAI is the leaf area index (ha/ha), K_S is stomatal conductance (per cent) and RAYGL in the incoming solar radiation (W/m^2). Leaf area index is linearly proportional to standing biomass (*BM*).

$$\mathrm{LAI} = KF \times BM \quad (13)$$

where *BM* is the standing biomass (kg/ha), and *KF* the leaf area index conversion factor (ha/kg). In our study we took a *KF* value of 0·0025 ha/kg.

Respiration and senescence

Respiration has two components: one proportional to the rate of photosynthesis and the other, a maintenance component, proportional to the standing biomass (McCree, 1970). No distinction is made between weight loss due to senescence and through respiration. Respiration and leaf loss are assumed to be independent of temperature. For the growth of perennial shoots, this term includes lignification:

$$dR/dt = k_4\ dP/dt + k_5\ BM, \quad (14)$$

where dR/dt is the weight lost through respiration and senescence (kg dry matter/ha/day).

Dry matter production

The estimation of carbohydrate balance takes into account only the processes of photosynthesis, respiration and dry matter production

$$dBM/dt = dP/dt - dR/dt, \quad (15)$$

where dBM/dt = dry matter production (kg/ha/day). Hence, combining equations (12), (13), (14) and (15),

$$dBM/dt = (k_6 \times 4{\cdot}9\ K_S \times KF \times BM \times \mathrm{RAYGL}/(4{\cdot}4\ K_S + 1{\cdot}64)) - k_5\ BM \quad (16)$$

with

$$k_6 = k_3(1 - k_4).$$

Model verification

The ARFEJ model is written in Fortran IV and runs on the Mitra 125 CII of the 'Ecothèque Méditerranéenne du Centre National de la Recherche Scientifique'. The program, including comments, is approximately 800 cards in length and requires approximately 30 CPU sec for a 4-year simulation run. Calibration yielded the following model coefficients:

$k_1 = 0{\cdot}2$,

annuals: $k_2 = 5$ bars,

$k_5 = 81{\cdot}0 \times 10^{-4}$ day^{-1},

$k_6 = 12 \times 10^{-2}$ m^2/W/day,

perennials: $k_2 = 8$ bars,

$k_5 = 67{\cdot}4 \times 10^{-4}$ day^{-1},

$k_6 = 7{\cdot}9 \times 10^{-2}$ m^2/W/day.

Comparison between observed and simulated data of soil water content, and annual and perennial standing biomass for the 1971–77 period (Figs 3–5).

In the model, growth of perennial species is generally too fast in spring. In reality, maximum spring growth of annual species is distinct from the late maximum of the perennials. This delay is probably because the model does not take into account the transfer of the products of photosynthesis into the ligneous parts of the perennial species.

Simulated senescence is too slow. Indeed, in the model, the term for respiration-

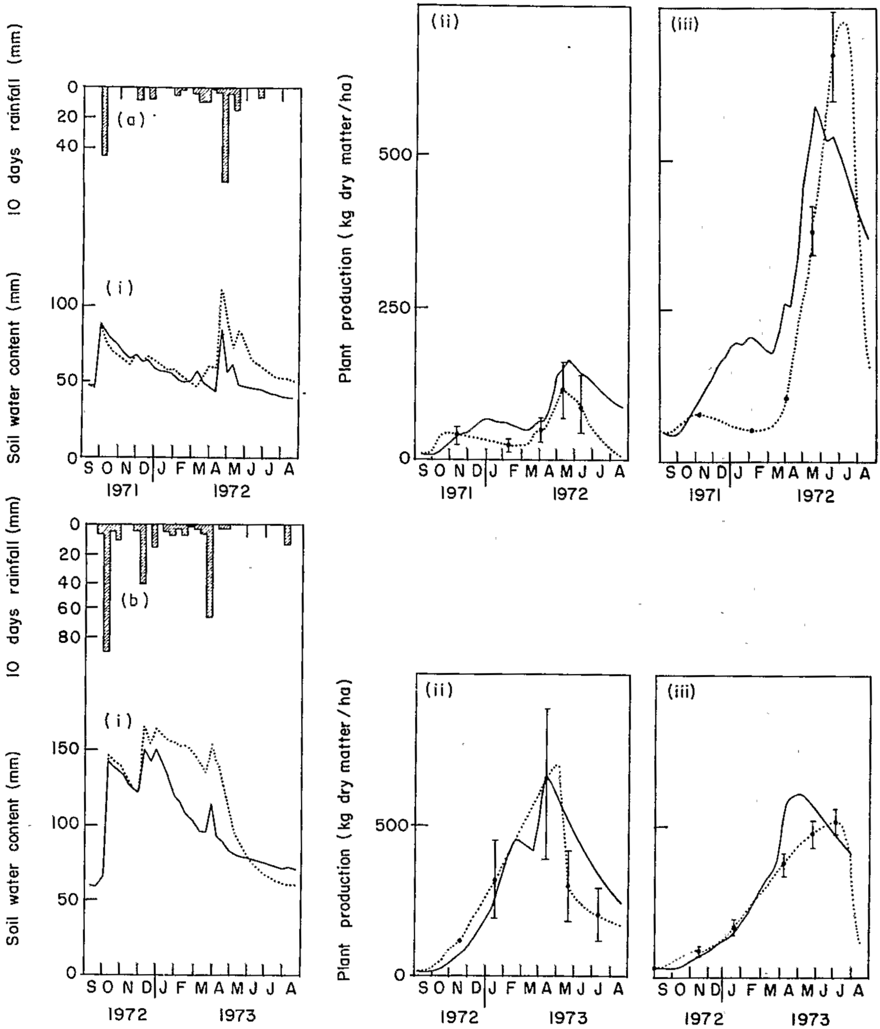

Figure 3. Simulated (———) and observed (– – –) values of (i) soil water content and plant production for (ii) annual plants and *Plantago albicans* and (iii) perennial plants in (a) 1971–72 and (b) 1972–73. Solid circles and vertical bars represent measurements and 68 per cent confidence limits.

senescence is independent of temperature. Moreover, wind blows away a considerable portion of the yearly dry phytomass but this is not taken into consideration.

Soil water consumption by plants is faster in the model than in reality. This may be related to the phenomenon of slow senescence.

The simulation is better for dry years or moderately wet years than for very wet years. Indeed, it has been shown (Floret & Pontanier, 1978) that the efficiency of soil water use is maximum at an annual rainfall of near 250 mm. Above this, the low level of nutrients (probably nitrogen and/or phosphorus) limits the efficient use of water. Van Keulen (1975) presents similar results for the northern Negev desert; however, in this case production/mm of rainfall is much higher than in Tunisia, due to several causes (distribution and intensity of rainfall, soil characteristics and nutrient statute).

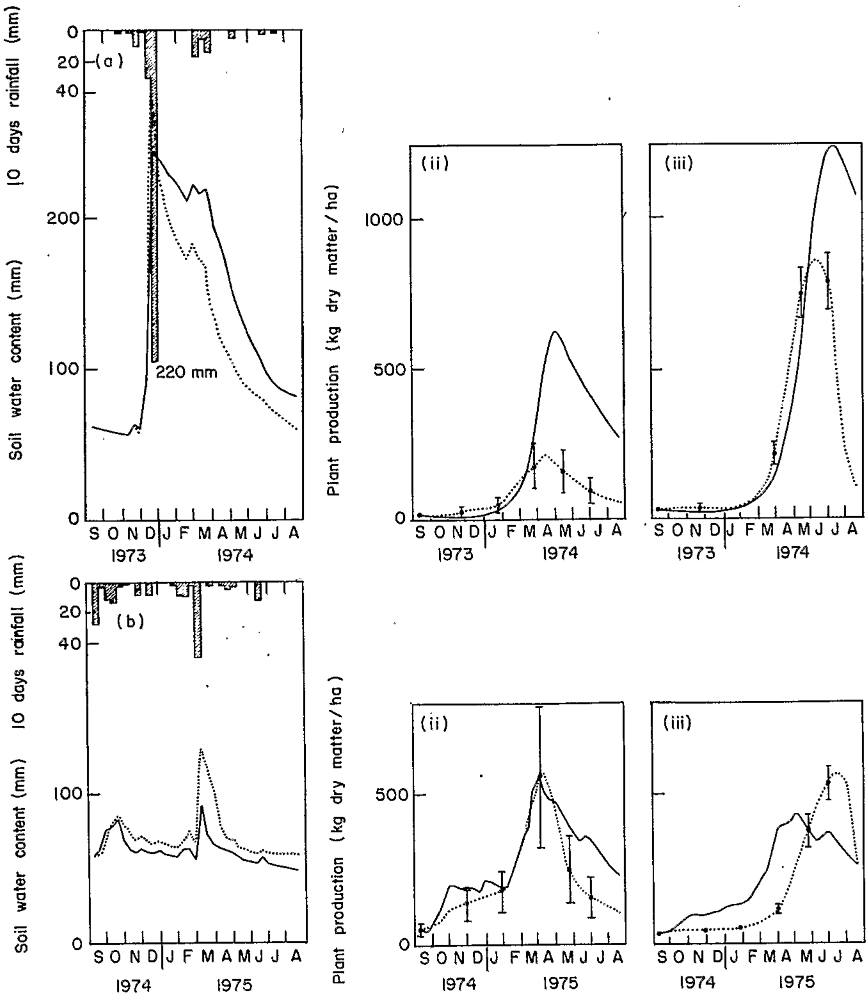

Figure 4. Simulated (———) and observed (— — —) values of (i) soil water content and plant production for (ii) annual plants and *Plantago albicans* and (iii) perennial plants in (a) 1973–74 and (b) 1974–75. Solid circles and vertical bars represent measurements and 68 per cent confidence limits.

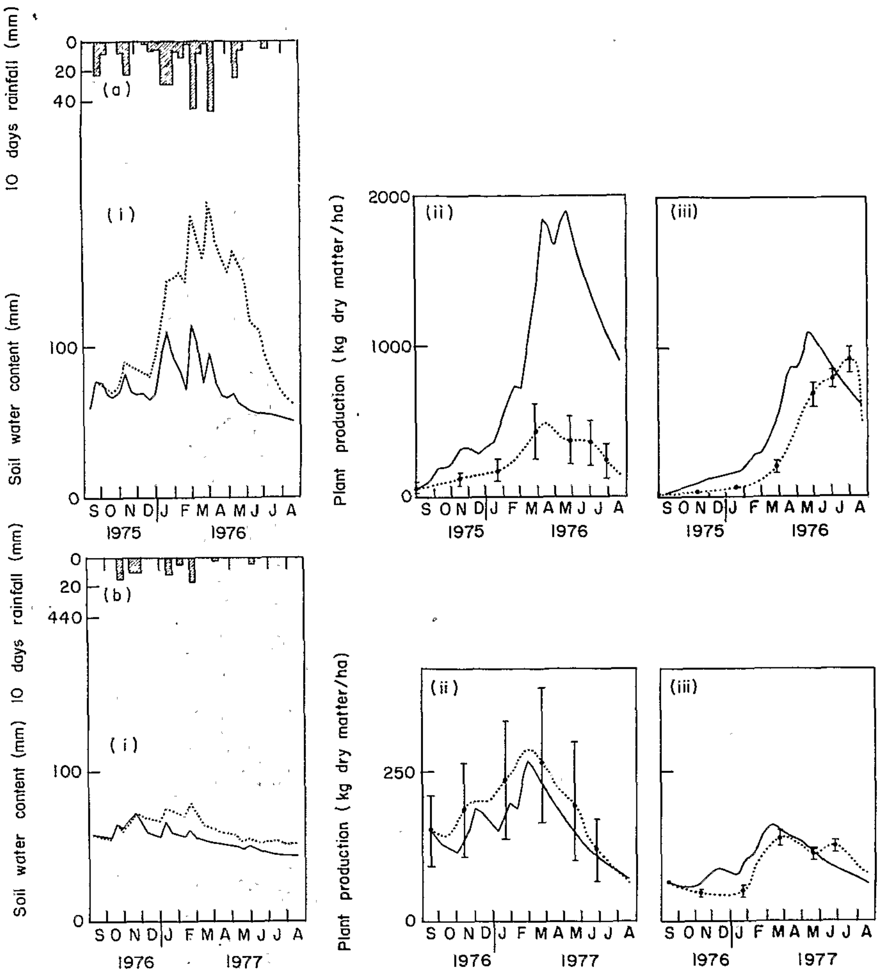

Figure 5. Simulated (———) and observed (— — —) values of (i) soil water content and plant production for (ii) annual plants and *Plantago albicans* and (iii) perennial plants in (a) 1975–76 and (b) 1976–77. Solid circles and vertical bars represent measurements and 68 per cent confidence limits.

Discussion and conclusions

Production and rainfall distribution

The net plant production of the Tunisian steppe is approximately 1000 kg dry matter/ha (for a mean year, rainfall 180 mm) (Table 1). Wet years, with about 300 mm rain, produced 1550 kg dry matter/ha (1975–76) and 1060 kg dry matter/ha (1973–74). The difference between these seasons is caused by rainfall distribution (in 1973–74, 80 per cent fell in 24 h). This distribution is all the more important as the growth periods of the annual and perennial species are different. For maximum production of annuals rainfall should be distributed regularly between autumn and the end of spring; while *R. suaveolens* grows till the end of July if the deep soil layers are still wet in mid-May.

We have conceived two ideal imaginary years with 250 mm annual rainfall, one of them with a distribution suggested by Tadmor, Eyal *et al.* (1974) (100 mm: October–November rain, falling in 3–4 days followed in monthly intervals by 3 or 4 rains of 50 mm, each falling over a 2–3-day period till the middle of March); the other distribution (60 mm rain in September falling in 2 days, followed by 15–35 mm monthly in 2–3 days till the end of February and by 80–90 mm spring rain falling in 6 days till the middle of May) as suggested by Floret & Pontanier (1978) for *R. suaveolens* steppe. The simulated results of these two imaginary years, compared with measured data from the 1972–73 period with 250 mm rainfall, are presented in the Table 2. The Tadmor distribution promotes maximum plant production. The Floret & Pontanier distribution promotes a regular production throughout the year.

Table 2. *Simulated results for three types of annual rainfall repartition (total = 250 mm)*

Repartition	Number of rainy days	Transpiration (mm)	Evaporation (mm)	*E/ET* (%)	Plant production (kg dry matter/ha): Annual plants and *Plantago albicans*	Perennial plants	Total
Ideal repartition in south Tunisia (Floret & Pontanier, 1978)	21	141	114	45	983	844	1827
Ideal repartition in north Negev (Tadmor, Eyal *et al.*, 1974)	15	146	89	38	742	1267	2009
Observed repartition in south Tunisia 1972–73	35	106	137	56	668	620	1288

Water efficiency for plant production

Much of the infiltrated water is lost by evaporation. In 1975–76, measurements on bare sterilised soil showed that 70 per cent of the infiltration water evaporated. The components of the actual evaporation (*ET*) could not be measured in the field. But, in the model, the evaporation *E* was calculated. For the six observed years, the fractions evaporated were 54, 56, 50, 59, 40 and 69 per cent, while the average calculated evaporation and transpiration ($TR = ET - E$) represented, respectively, 55 and 45 per cent of infiltrated water. During the dry years, the fraction evaporated was about 25 per cent higher while the fraction transpired decreased in wet years.

Viets (1962) defines water use efficiency (WUE) as the ratio between the amounts of dry matter produced and evapotranspiration. The calculation of WUE for the six measured periods shows values from 0·263 g dry matter/kg H_2O in 1976–77 to 0·544 in 1974–75, with an average of 0·446. The calculation made with 11 years of Tadmor's data gives an average value of 0·887. Nevertheless, the WUE concept does not take into account the fact that the E/ET ratio is very variable and also that the period of growth is about 4 months at Tadmor's site, whereas, in our case, it was 9 to 11 months. Using the ratio produced phytomass/transpiration for spring when growth is fast, we obtained figures of 1·26 g dry matter/kg H_2O for annual species and 1·39 for the perennial species.

These values are similar to those of Downes (1969) who gives 1·49 g dry matter/kg H_2O for grasses and 1·59 for dicotyledons, under controlled conditions.

Use of the model

The accuracy of growth trends in general indicates that the model has considerable predictive value. It is therefore possible, knowing the initial standing phytomass, the daily rainfall and Piche evaporation, to calculate not only the dynamics of the phytomass of annual and perennial species but also variations in soil water content. Seasons or years for which data are not available can be simulated. If probabilities of the recurrence of rainy days are known, estimates of plant production can be obtained. Although the model simulates plant growth only when grazing animals are excluded, it could also help in range management, by forecasting carrying capacity consistent with plant production, the quantity of fodder reserves necessary and the time when they must be available. It must, nevertheless, be stressed that the model is not effective for very wet years (above 250 mm precipitation) when water is not the principal limiting factor.

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