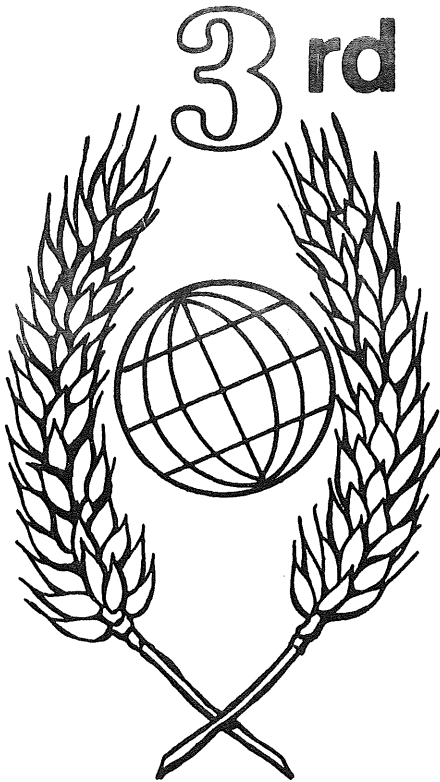


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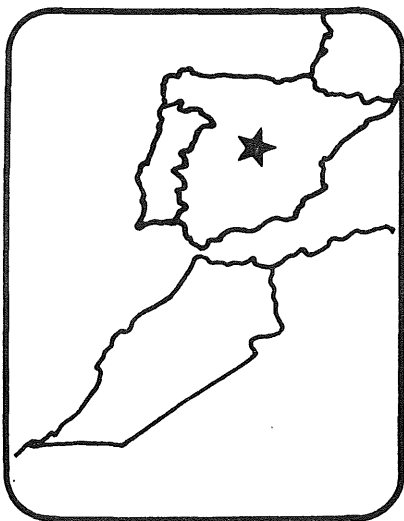
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NORTH CENTRAL REGION

UNIVERSITY OF NEBRASKA-LINCOLN
INSTITUTE OF AGRICULTURE AND
NATURAL RESOURCES
THE AGRICULTURAL EXPERIMENT STATION
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MODELING GRAIN PRODUCTION OF WHEAT UNDER CONDITIONS OF
LIMITING WATER SUPPLY: A CASE STUDY.

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The basis for the calculation is the photosynthesis light response curve of individual leaves, characterized by an initial light use efficiency at low light intensities and a maximum level, where CO₂ diffusion is the limiting factor. When experimentally-determined relations of this type are available in combination with the spatial arrangement of the leaves in the canopy and their optical properties, the gross rate of CO₂ assimilation may be obtained at any moment from the level of irradiance. Integration of these values over the day yields the daily potential gross CO₂-assimilation. Values of this variable have been tabulated by Goudriaan and Van Laar (1978) for different saturation levels as a function of latitude and time of the year. They hold for closed green crop surfaces (where all irradiance is intercepted). In the calculation scheme, incomplete cover is accounted for by assuming exponential extinction in the canopy with an extinction coefficient of 0.5. For any given situation, gross canopy photosynthesis can be derived in this way. Potential canopy photosynthesis may not be achieved due to insufficient moisture supply. To account for water shortage, a simple soil water balance is administered in which the available soil moisture, that is the amount of soil water between "field capacity" and "wilting point", is tracked.

Available water may increase by rain or by irrigation and decreases by soil evaporation and transpiration by the canopy. The latter two terms are combined into total evapotranspiration. The basic assumption is that, when sufficient soil moisture is available, total evaporative demand will be satisfied either through the plant or from the soil surface. That is an oversimplification since, especially at incomplete soil cover, the top soil may be dry, thus effectively preventing direct surface evaporation, while moisture still remains available at greater depth. In the present simplified approach no attempt has been made to incorporate a more sophisticated assumption.

It appeared necessary to take the rooting depth into account, since soil moisture stored at greater depth may not be available for plant uptake in the early stages of the growing season. It is assumed, therefore, that the plant roots extend vertically at a rate of 1.2 cm per day, thus gradually increasing the availability of soil moisture at greater depth.

The evaporative demand (potential evapotranspiration) is obtained from the Penman formula using the coefficients originally defined by the author (Penman, 1948).

When the total amount of available moisture in the soil, augmented by rain or irrigation in the relevant period, is insufficient to satisfy the evaporative demand, actual evapotranspiration is equal to the sum of these terms. Actual gross canopy photosynthesis is then calculated under the assumption that a direct proportionality exists between the ratio of actual and potential evapotranspiration and that of actual and potential gross photosynthesis. Any possible modifications in water use efficiency are thus disregarded in this way.

Part of the carbon fixed in the photosynthetic process is respired to provide energy for biological functioning of the plant. Two main components are distinguished in the scheme: maintenance respiration which is proportional to the amount of dry matter present in the field. Temperature and chemical composition of the material are influencing the maintenance respiration, but in the present simplified approach these factors have been ignored and the maintenance requirement is assumed to be 0.02 kg kg^{-1} (dry matter) before anthesis and 0.015 after that time.

Growth respiration is taken into account by means of a conversion efficiency of primary photosynthates into structural plant material. Here again the chemical composition of the material formed is the major determinant of the overall efficiency, but an average value of $0.7 \text{ kg (dry matter) kg}^{-1}$ (photosynthates) is used for the vegetative plant material and 0.8 for the grains having on the average a somewhat lower protein content.

The total amount of dry matter produced during one period is divided between leaves, stems (including the leaf sheaths) and grains. The partitioning coefficients vary with the phenological stage of the canopy. In the first one third of the growth period only leaves are formed. From that moment until anthesis the newly formed material is divided equally between leaves and stems whereas after anthesis all current photosynthates are used for grain filling. The green leaf area of the canopy is obtained from the weight of the leaves assuming a specific leaf area of $15 \text{ m}^2 \text{ kg}^{-1}$ dry matter.

The leaves of a plant have a limited life span, hence after some time they die off. This process is ignored in the early stages of crop development but after anthesis a constant relative death rate, due to senescence, of 0.03 day^{-1} is assumed. Application of this value reduces the green leaf area by a factor of two in about three weeks. When water shortage occurs during that period accelerated senescence is assumed, the relative death rate increasing in proportion to the transpiration deficit.

The phenological development of the crop is introduced in the present example as a forcing function, the onset of stem formation and the moment of anthesis being taken from field observations. For the purpose of comparing different sowing dates or various

years at the same site it should be possible to define these events on the basis of accumulated heat sums, as was done for banded rice (van Keulen, 1976).

The calculation scheme is executed for time intervals of ten days. In the above-mentioned example of rice it was shown that the results are not very sensitive to the magnitude of the time-interval.

The scheme outlined in the previous section was tested on data collected near Sde Boker in the Negev Desert of Israel, (Long. $34^{\circ} 41^1$ E., Lat. $30^{\circ} 51^1$ N) in the framework of a joint Dutch-Israeli research project on dry land agriculture. Annual rainfall in the area is too low (long-term average 92 mm yr) for arable cropping which can only be practiced with irrigation. Different irrigation treatments were imposed so that water stress in the canopy developed at different stages of development. Detailed information on the experiments and its results will be published elsewhere (Hochman and van Keulen, in prep.).

Measured and calculated dry matter accumulation for three irrigation regimes are given in Figure 1.

For the non-stressed treatment, the calculated curve coincides closely with the measured one until about 120 days after emergence, well into the grain filling stage. Towards the end of the growing period the calculated growth rate is about 10% below the measured one. This could be due to the fact that leaf senescence is overestimated in the calculation scheme, since the crop, which was also well supplied with nutrients, showed a healthy appearance for an extended period. This cannot be verified with experimental data, however, since determination of green leaf area was discontinued at anthesis.

The calculated grain yield (Table 1) is somewhat lower than the measured value, but is situated within the 5% accuracy limit. In the present formulation no contribution of pre-anthesis photosynthesis to grain yield is taken into account, but that is probably counterbalanced by the fact that in reality a small proportion of post-anthesis assimilation is required for growth of vegetative tissue (e.g. roots). In treatment 2 waterstress was allowed to build up in the late vegetative stage between day 60 and 90 after emergence. Again the calculated curve agrees very well (Figure 1) with the measured one. These results indicate that the assumption that water use and dry matter production are proportional holds also in this situation. Any change in water use efficiency under water stress cannot be detected from the experimental data. The lower grain yield for this treatment can be explained fully by the accelerated senescence of leaves during stress resulting in a smaller green leaf area and, hence, less intercepted irradiance during the reproductive stage.

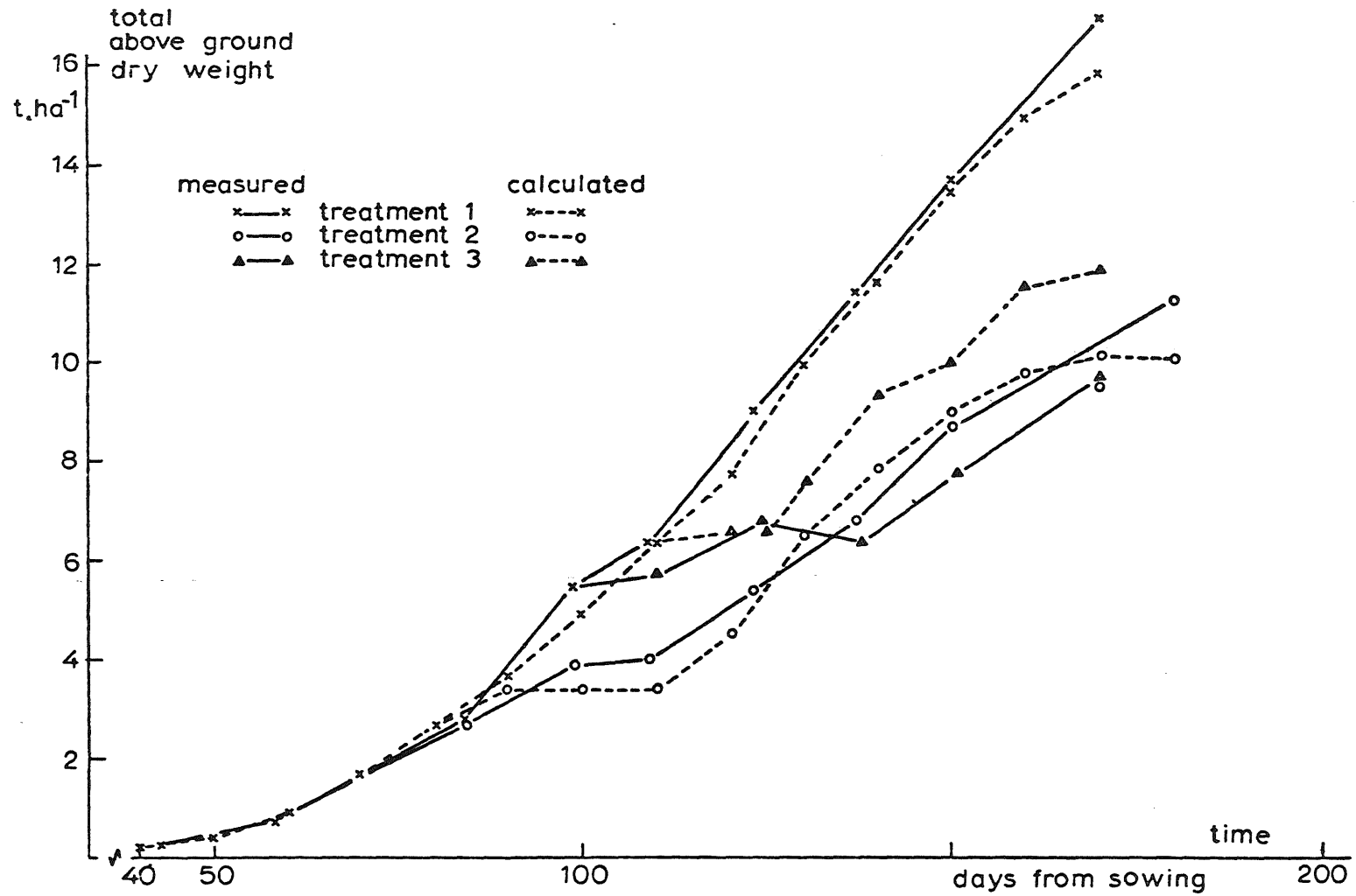


Figure 1. Course of measured and calculated DM growth for three irrigation treatments.

Table 1. Calculated and measured grain yield (kg ha^{-1}).

Treatment	Measured	Calculated
1	7790	8081
2	5590	5580
3	4980	5072

The results of treatment 3, where moisture stress developed between day 90 and day 110 coinciding with period of flowering and pollination, are contradictory to the previous one. The calculated growth rates after restoration of soil moisture are far higher than the measured ones, especially in the first ten-day period. The reason for this discrepancy is not clear, although one could speculate that the stress treatment not only resulted in accelerated senescence of leaves but also affected the photosynthetic capacity of the remaining green leaf area. A similar phenomenon of a lag in the recovery after water stress was observed in a natural pasture situated in the same environment (van Keulen et al., 1980). This seems a more likely explanation than one of sink-size limiting the growth rate of the grains, since after day 120 the measured growth rate is practically identical to the calculated one.

The calculated and measured grain yields are hardly different, which is unexpected in view of the difference in total dry matter accumulation. In this case post-anthesis assimilates must have supplied a substantially larger part of the final grain weight in reality. It could be speculated that most of the photosynthates produced during the stress period could not be used for growth, but were stored and available for translocation to the grain.

In Table 2 some variables pertaining to the calculated water balance are given. The partitioning between transpiration and evaporation is calculated under the assumption that in each period the ratio between the two terms is equal to the ratio of absorbed and transmitted radiation. The results show that in all cases direct soil surface evaporation ranging between 20 and 36% of the total evapotranspiration constitutes a major source of water loss under these semi-arid conditions. The transpiration coefficients of slightly over $200 \text{ kg H}_2\text{O kg}^{-1}$ (dry matter) are virtually identical for all treatments. These values are substantially lower than the ones reported for other C3 species growing in the same environment (van Keulen, 1975). This observation suggests that the wheat crop under consideration must have shown stomatal regulation through the internal CO_2 -concentration for at least part of its growth period.

Table 2. Calculated values of evapotranspiration (ET), evaporation (E), transpiration (T), and transpiration coefficient (TRC = T/DM).

Treatment	ET mm	E mm	T mm	TRC kg H ₂ O kg ⁻¹ (DM)
1	421	85	336	211
2	347	126	221	218
3	332	88	244	211

The results presented here show that a simple method, based on available physiological and physical knowledge, may be used to calculate yields under varying climatic conditions. Combination with a simple waterbalance provides an opportunity to take into account periods of suboptimum water supply leading to reduced transpiration and lower growth rates. It seems, however, that when periods of severe stress are encountered, reduced transpiration and stress-induced leaf death cannot account for all the observed effects. A more extensive testing in different situations is necessary, however, to arrive at firm conclusions in this respect.

This simulation approach will be improved by including the plant and soil processes which are involved in the crop response to nitrogen supply. Further study is required on the nature of interactions between water use, nutrient uptake and root activity, especially during the grain-filling period.

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