Effect of plant density and water supply on wheat production

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Summary

A model is described to predict the dry matter production of a wheat crop. The
photosynthetic rate of the crop surface is calculated from the amount of light and
certain influences of the physical environment on photosynthesis, as crop density,
water supply and meteorological conditions. The dominant role of the leaf surface
resistance with regard to the final yield to be reached is apparent. Lowering the
sowing density at limited water supply will give a more favourable grain/straw
ratio.

Introduction

Data of sprinkler irrigation experiments as well as plant density experiments with
wheat have been used in an analysis of the effect of crop density, water supply
and meteorological conditions on dry matter production.

The dry matter production at different plant densities and various conditions of
water supply can be calculated with a production model. Variations in crop den-
sity also affect the potential water requirements of the crop.

Stress conditions at a given water supply are present at an earlier stage of growth
with increasing plant densities, affecting the distribution of dry matter over the
various parts of the plant.

The given approach can be used for optimization of crop density and water supply
in relation to crop yield for dry farming systems as well as for irrigated areas with
a limited water supply.

Available experimental data

Available experimental data were taken from the logs of the Intitute's experimen-
tal station 'De Sinderhoeve' located at Renkum (province of Gelderland, the Neth-

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erlands). They concern winter wheat (cv. Tadorna) in an experiment during 1970/1971 and spring wheat (cvs Peko and Jufy 1) in trials during 1961, 1962 and 1964. Of the spring wheat experiments some results on the effect of sprinkling irrigation were published by Toussaint (1961, 1962, 1964) and de Vos & Toussaint (1966). For the present study use was made of the original experimental data. The Tadorna experiment was carried out with five sowing densities (72, 96, 120, 168 and 240 kg ha^{-1}), the spring wheat experiments in the different years had a sowing density of 160, 240 and 220 kg ha^{-1}, respectively.

The experimental field has a coarse sandy soil with 6.5 % organic matter in the 40 cm top-layer. The available moisture content at the beginning of the growing season in the top 1 m is 100 mm of which about 72 mm is available from the mentioned humic top-layer. Root penetration was approximately 70 cm.

Adequate and uniform fertilization and management practices were used to ensure healthy plant growth. The soil water content was determined weekly in the 1971 experiments by means of a gamma radiation transmission method during the growing season. The nature and method of soil density measurements were those described by Ryhiner & Pankow (1969). During the 1961, 1962 and 1964
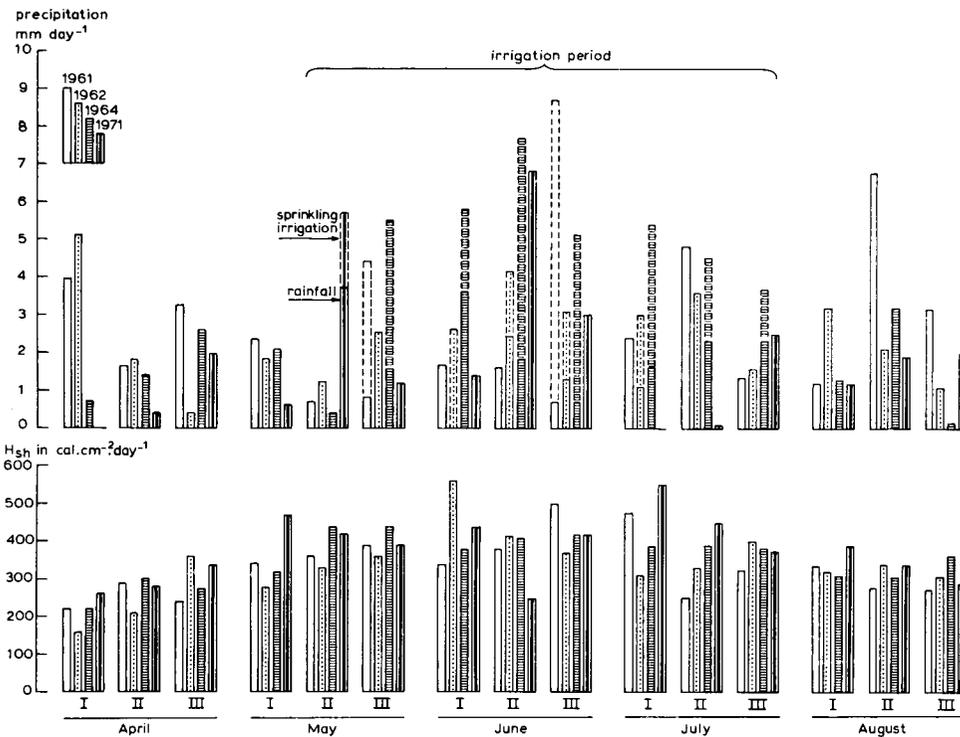
Fig. 1. Precipitation as well as sprinkling irrigation amounts expressed in mm day^{-1} per 10-day period and incident short wave radiation in cal cm^{-2} day^{-1} in the growing seasons of 1961, 1962, 1964 and 1971 at the Sinderhoeve experimental station (Netherlands).

experiments soil moisture determinations were performed by soil sampling. The meteorological data required for the calculations of potential evaporation such as short wave radiation, duration of bright sunshine, temperature, humidity, wind velocity and precipitation were measured daily at the meteorological observation field of the experimental station.

Fig. 1 gives some meteorological data and the amounts of sprinkling irrigation for the mentioned years. Crop growth was measured weekly as average height of the stand and the rate of development was estimated as the area of soil covered by plants. For the determination of dry matter production representative crop samples were obtained once per two weeks by random selection of a 1-metre row of plants. The results are presented as treatment averages.

Dry matter production of wheat

Dry matter production of field crops mainly depends on the intensity of solar radiation, the gross assimilation rate of individual leaves, the respiration rate, the size of the photosynthetic system, the nutritional status of the soil and the water supply. When a crop fully covers the soil surface and soil moisture is adequately available, photosynthesis can proceed at the potential rate under the prevailing environmental conditions. This potential production of a crop can be derived with de Wit's (1965) model, in which the potential production (P_{stand}) is taken to be a function of incident light energy (in the range 0.4 to 0.7 μ_m).

Considering physical limitations of the environment, Rijtema & Endrödi (1970) proposed the following expression for the actual dry matter production (P) per unit area of soil.

$$P = \alpha \frac{4.9}{r_a + 1.7\, r_s + r_m}\; S_c\, P_{stand} \; \text{dry kg ha}^{-1}\, \text{day}^{-1} \tag{1}$$

where: α = an efficiency factor depending on the crop, being the ratio of potential net dry matter production over gross production of the standard crop

r_a = exchange resistance between bulk air and the effective canopy surface in s cm^{-1}

r_s = canopy surface resistance for water vapour transport; 1.7 = ratio of the diffusion coefficients in air of water vapour and CO_2; multiplication gives the surface resistance for CO_2 transport in s cm^{-1}

r_m = diffusion resistance for CO_2 movement through the mesophyll in s cm^{-1}, including the resistance to carboxylation and biochemical restraints, as influenced by temperature and leaf age in s cm^{-1}

S_c = fraction of soil covered by the crop

P_{stand} = gross potential production of a standard crop, as defined by de Wit (1965) in kg ha^{-1} day^{-1},

4.9   = $r_a + 1.7\, r_s + r_m$ for de Wit's standard crop conditions

The efficiency factor α is related to the respiration rate and the ratio of the potential gross production of the actual crop over the gross standard crop production. Values of α for the wheat crops will be analysed in this study as the ratio net P_{pot} over gross P_{stand}.

The exchange resistance r_a is derived from tables given by Feddes (1971), using the data of crop height and wind velocity. It is assumed that in the turbulent moving air r_a is equal for both water vapour and CO_2 transport.

The surface resistance (r_s) can be split into partial resistances:

$$r_s = r_s^l + r_s^\psi \qquad \text{s cm}^{-1} \tag{2}$$

where r_s^l is a function of radiation intensity, and r_s^ψ is a function of leaf water potential. The resistance r_s^l was described in detail by Rijtema (1965) and Feddes (1971), and its values can be derived as a function of radiation intensity from their tables or graphs. In general, when a soil water stress is imposed a decrease in transpiration and an associated decrease in photosynthesis occurs. Rijtema (1965) did show that r_s^ψ depends on soil moisture content and soil water conductivity as well as plant properties and evaporative demand. For practical purposes r_s^l can be derived from actual evapotranspiration and the potential one by means of a formula given by Endrödi & Rijtema (1969):

$$r_s^\psi = \frac{\Delta r_a + \gamma (r_a + r_s^l + r_s^c)}{\gamma} \left[\frac{E_{pot} - E_I}{E_{ac} - E_I} - 1 \right] \text{s cm}^{-1} \tag{3}$$

where: Δ = the slope of the temperature-vapour pressure curve at air temperature in mm Hg °C^{-1}

γ = psychrometer constant in mm Hg °C^{-1}

r_s^c = canopy resistance for water vapour related to soil cover in s cm^{-1}

E_{pot} = potential evaporation in mm day^{-1}

E_{ac} = actual evaporation in mm day^{-1}

E_I = evaporation of intercepted precipitation in mm day^{-1}

Values of r_s^c, a resistance related to soil cover, are given by Rijtema & Ryhiner (1966) and Feddes (1971). The potential evaporation from a crop surface can be calculated from standard meteorological data and the aerodynamic nature of the evaporating surface. With the procedure introduced by Penman (1948) and modified by Rijtema (1965) the potential evapotranspiration can be calculated and according to Endrödi & Rijtema (1969) it can be expressed by:

$$E_{pot} = \frac{\Delta + \gamma}{\Delta + \gamma (1 + \dfrac{r_s^l + r_s^c}{r_a})} [E_{wet} - E_I] + E_I \qquad \text{mm day}^{-1} \tag{4}$$

where E_{wet} in mm day^{-1} is the evaporation of a wet surface with the same dimensions and shape as the crop considered.

The actual evapotranspiration (E_{ac}) is calculated from water balance data and E_I from the distribution of the precipitation during the balance period (Rijtema, 1965).

Returning to Eq. 1, r_m remains to be determined. In first instance it is assumed
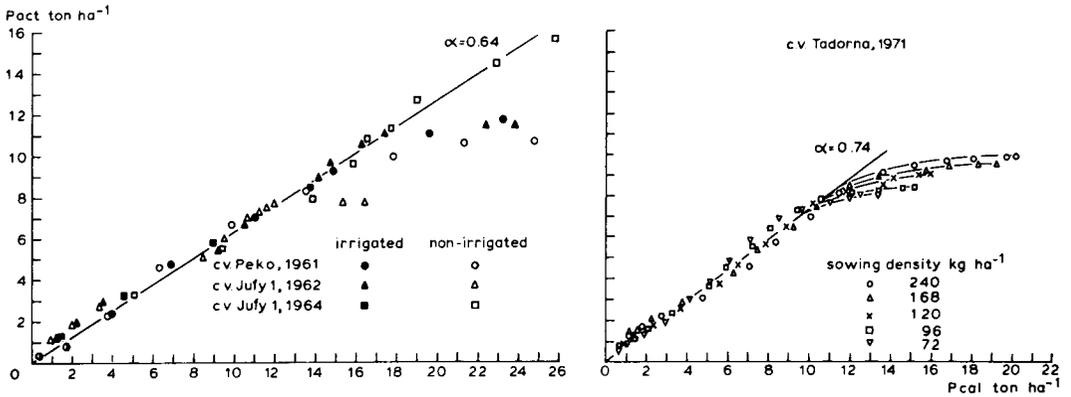
Fig. 2. The relation between calculated gross production and the data obtained from periodical harvests.

that it has the value of 4.4 s cm^{-1} (Rijtema & Endrödi, 1970). The actual production rate can provide a reasonable estimate of the mesophyll resistance especially towards the end of growth cycle when this resistance becomes a substantial one.

Plotting the data of actual dry matter production, as obtained from the periodical harvests, against $[4.9/(r_a + 1.7\,r_s + 4.4)]\,S_c\,P_{stand}$ gives the efficiency factor α as the tangent at the origin of the curve.

The dry matter production derived from periodical harvests is plotted in Fig. 2 against the calculated production. The slope of the linear part of the curves is α and equals 0.74 for winter wheat and 0.64 for spring wheat.

The various points at which the curves reach the inflexion agree with the production levels of the various treatments and correspond to the point in time at which the leaves began to senesce.

There is no indication that the results of any treatment departed from the general relationship. The value of the efficiency factor α ranges from 0.64 to 0.74. This variation must be ascribed to the fact that in the periodical harvests production of the root system was not taken into account. In the case of winter wheat the root system already develops in fall and early spring, so less assimilated dry matter is needed for the development of the root system in spring. As the calculations pertain to the period of April to August it is evident that α is larger for winter wheat than for spring wheat.
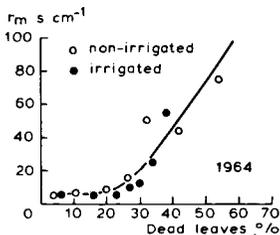
Fig. 3. The relation between r_m and the percentage of dead leaves in 1964.
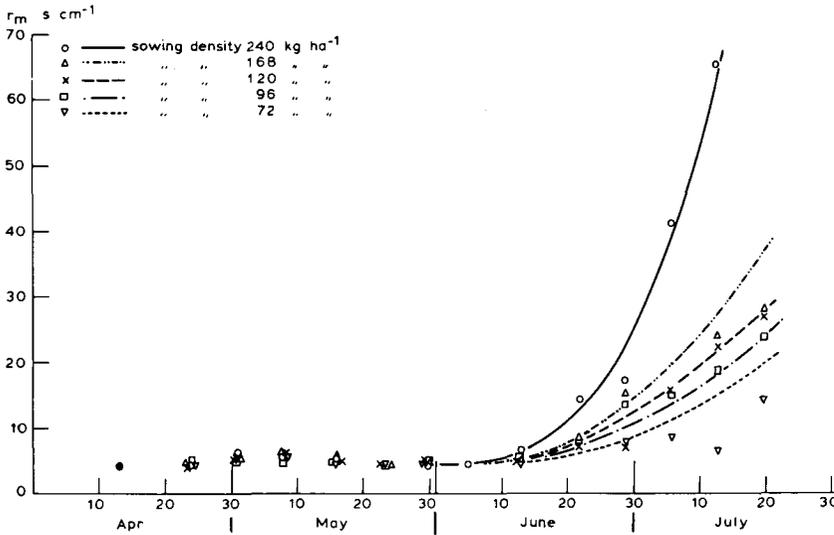
Fig. 4. Comparison of calculated mesophyll resistances for winter wheat in 1971 (r_m), as a function of time. The lines are calculated with the aid of dying-off data, from Fig. 3, whereas the points were calculated by back solution of Eq 1.

An analysis of the increase of r_m near senescence can be made by back solution of Eq. 1.

Relating the calculated r_m values with available dying-off data of the crop in 1964 (Fig. 3) offers the possibility to apply this relationship to the data of the Tadorna crop. The calculated course of r_m derived with the aid of Fig. 3 obtained from the dying-off data for the different Tadorna crop densities is given by the curves in Fig. 4, whereas the data obtained by back calculation of Eq. 1 are given by the points.

Although no great accuracy can be claimed for these calculated data, they reveal some interesting features. When the mature crop approaches ripening the magnitude of the mesophyll resistance increases considerably, whereas up to maturation the value remains constant at some 4.4 tot 5.0 s cm^{-1}.

A clear response of the seasonal course of r_m to population density is shown. Probably earlier maturation and a competition effect due to stress conditions may have contributed to these responses.

The given data indicate the dominant role of leaf surface resistances in the final yield to be reached. It must be remembered that the activity of the effective leaf surface, as well as its extent, is a determinant of grain yield. High densities alone may not compensate completely high leaf resistances, which confirms Matsuda's (1965) experimental results with a rice crop.

Crop density, water use and production

Plant growth is closely related to plant evaporation. Although the relationship be-tween production rate and evaporation rate is rather complicated, for practical purposes it is possible to use simple relations between accumulated photosynthesis product and cumulative plant evaporation. In a way similar as proposed by Bier-huizen & Slatyer (1965) and Rijtema (1966) a linear relationship between total dry matter production and the ratio total evapotranspiration over mean vapour pressure deficit is assumed, resulting in:

$$P_{ac.tot} = a \frac{E_{ac.tot}}{\Delta e} \qquad (5)$$

where: $P_{ac.tot}$ = accumulated dry matter production in kg ha^{-1}
$E_{ac.tot}$ = accumulated actual evapotranspiration in mm
Δe = mean vapour pressure deficit in mbars
a = crop constant

When assuming that potential production is achieved under conditions of poten-tial evaporation Eq. 5 can be reduced to:

$$P_{ac.tot} = P_{pot.tot} \frac{E_{ac.tot}}{E_{pot.tot}} \qquad (6)$$
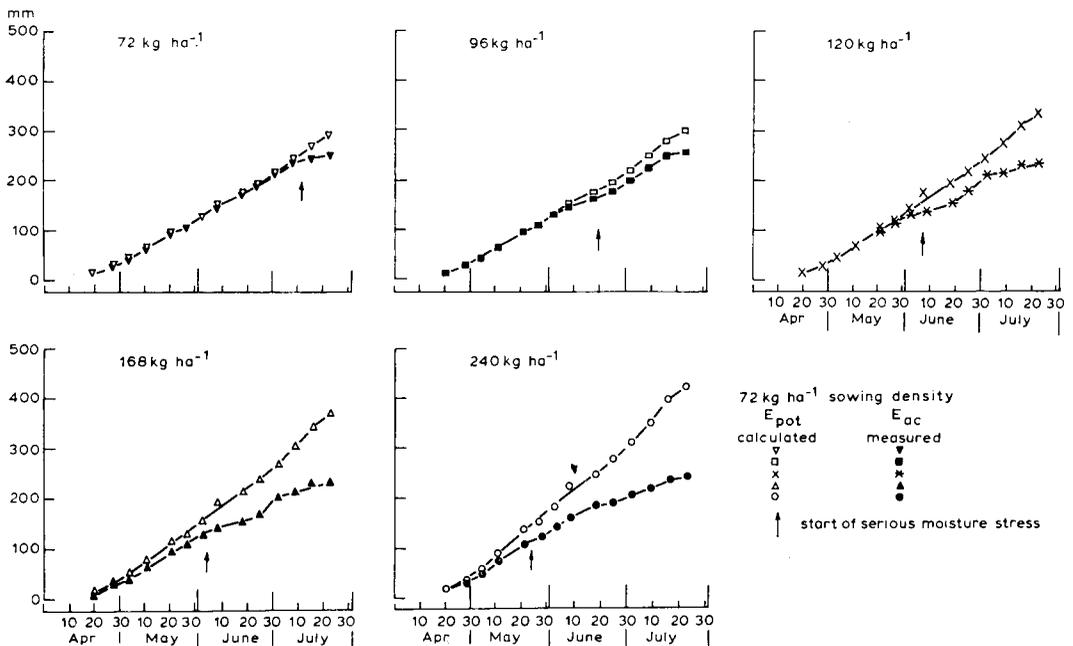
Fig. 5. Potential (E_{pot}) and actual (E_{ac}) evaporation of winter wheat during the growing season of 1971 for the given sowing densities.

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Values of $P_{pot.tot}$ can be calculated with Eq. 1 for conditions of optimum water supply, and $E_{pot.tot}$ with Eq. 4.

Decreasing crop density affects both $P_{pot.tot}$ and $E_{pot.tot}$ by the decreased soil cover. In particular under conditions of a limited water supply, for instance in dry farming or when irrigation water supply is limited, it is necessary to optimize the crop densities to the water resources.

The Tadorna experiment gives an example of the effect of crop density in relation to limited water supply. Fig. 5 gives the cumulated data of calculated potential and measured actual evapotranspiration in relation to crop density. With increasing density a serious moisture stress develops at an earlier date. It is shown in Table 1 that the mean soil cover during growth increases with sowing density, resulting in different values for $P_{pot.tot}$. It is interesting to note that although the minimum and maximum sowing densities differ a factor 3.3, the potential productions in these cases differ only a factor 1.7.

The values of $E_{pot.tot}$ also increase with increasing sowing density, whereas $E_{ac.tot}$ is almost constant because of the limited water supply.

The calculated $P_{ac.tot}$ values, obtained from Eq. 6, agree fairly well with the measure data. Since the severe moisture stress conditions at the high plant densities occured before anthesis (Fig. 5), the grain/straw ratio is unfavourably affected, resulting in an only slowly increasing grain production with increasing crop density. The additional grain production obtained by means of an increasing sowing density is minimal. It might even be expected that under more severe stress conditions the grain production would drop with increasing sowing densities.

Fig. 6 gives the course of the calculated dry matter production as curves, compared with the data of the periodical harvests as points, for both irrigated and non-irrigated spring wheat in the years 1961, 1962 and 1964. The deviation between irrigated and non-irrigated fields demonstrates clearly the effect of stress
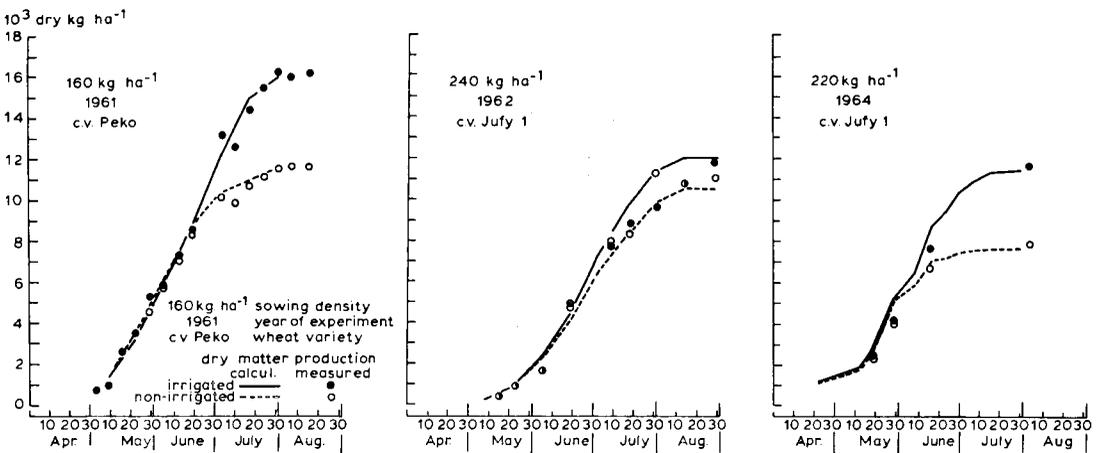
Fig. 6. Calculated and observed dry matter production of irrigated and non-irrigated spring wheat in 1961, 1962 and 1964.

Table 1. Relation between sowing density, soil cover, total evaporation and total production of winter wheat (cv. Tadorna, Sinderhoeve experimental station, Netherlands).

Sowing density (kg ha⁻¹)	Mean soil cover (%)	$E_{pot.tot}$ calcul. (mm)	$E_{ac.tot}$ water balance (mm)	$\dfrac{E_{ac.tot}}{E_{pot.tot}}$	$P_{pot.tot}$ calcul. (dry kg ha⁻¹)	$P_{ac.tot}$ (dry kg ha⁻¹) meas.	calcul.	Grain/ straw ratio	Grain production (dry kg ha⁻¹)
72	49	289	233	0.81	10091	7952	8174	0,673	3187
96	51	299	248	0.83	10724	8141	8901	0.646	3195
120	60	337	238	0.71	12518	8894	8888	0.640	3472
168	68	371	239	0.64	14377	9022	9201	0.628	3479
240	81	423	244	0.58	17234	9574	9996	0.598	3583

Table 2. Irrigation effect on the most important yield components of spring wheat (1961 cv. Peko; 1962, 1964 cv. Jufy 1), Sinderhoeve experimental station (Netherlands).

Year	Sowing density kg ha⁻¹	$E_{pot.tot}$ (mm)	$E_{ac.tot}$ (mm)	$\dfrac{E_{ac.tot}}{E_{pot.tot}}$	$P_{pot.tot}$ calcul. (dry kg ha⁻¹)	$P_{ac.tot}$ (dry kg ha⁻¹) meas.	calcul.	Grain/ straw ratio	Grain production (dry kg ha⁻¹)
Irrigated									
1961	160	419	360	0.86	18600	16038	15996	0.39	4500
1962	240	280	282	1.00	12350	12270	12350	0.70	5040
1964	220	444	435	0.98	13360	13352	13093	0.65	5260
Non-irrigated									
1961	160	419	251	0.60	18600	11570	11160	0.35	3000
1962	240	283	280	0.99	12350	11178	12227	0.83	5070
1964	220	444	271	0.61	13360	8998	8150	0.56	3230

conditions on dry matter production. In Table 2 the irrigation effects on the most important yield components of the spring wheat experiments are given. The data show that with the use of Eq. 6 a fair appraisal of dry matter production can be obtained. The grain/straw ratio is favourably affected by irrigation in the years with stress conditions. Irrigation in the wet summer of 1962 mainly resulted in a larger straw production.

Conclusions

The method for the calculation of photosynthesis of leaf canopies, as proposed by de Wit (1965) and modified by Rijtema & Endrödi (1970) gives a fair approach to the dry matter production of spring and winter wheat. Sowing densities affected both the potential water requirement of the crop and the potential production of dry matter.

Actual dry matter production could also be calculated from calculated potential production and the ratio $E_{ac.tot}$ over $E_{pot.tot}$.

Lowering crop density at a given water supply resulted in a more favourable distribution of dry matter over grain and straw due to less severe stress conditions.

The results are important for the optimization of the relation between crop density, water supply and dry matter and grain production in dry farming systems and irrigated areas with a limited water supply.

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