ACKNOWLEDGEMENTS

Thanks are due to A. Blatz and B. Petit for technical assistance.

REFERENCES

Bloom A. J., Jackson L. E. and Smart D. R. (1993). Root growth as a function of ammonium and nitrate in the root zone. *Pl. Cell Envir.*, **16,** 199-206.

Bonhomme R., Ruget F., Derieux M. and Vincourt P. (1982). Relations entre production de matière sèche aérienne et énergie interceptée chez différents génotypes de maïs. *C. R. Acad. Sci.*, Ser. III, **294,** 393-398.

Comfort S. D., Malzer G. L. and Busch R. H. (1988). Nitrogen fertilization of spring wheat genotypes : Influence on root growth and soil water depletion. *Agron. J.*, **80,** 114-120.

Delphin J. and Gassmann B. (1992). Comparison of three methods for assessing mineral nitrogen released by soil under maize. *Eur. J. Agron.*, **1,** 221-226.

Demotes-Mainard S. and Pellerin S. (1992). Effect of mutual shading on the emergence of nodal roots and the root/shoot ratio of maize. *Plant Soil,* **147,** 87-93.

Diggle A. J. (1988). ROOTMAP - a model in three-dimensional coordinates of the growth and structure of fibrous root systems. *Plant Soil,* **105,** 169-178.

Durand R., Bonhomme R. and Derieux M. (1982). Seuil optimal des sommes de températures : Application au maïs (*Zea mays* L.). *Agronomie,* **2,** 589-597.

Geisler G. and Krützfeldt B. (1983). Investigations into the effect of nitrogen on the morphology, dry matter formation and nutrient uptake efficiency of the root systems of maize, spring barley and field bean varieties, having regard to temperature conditions. I. Root morphology. *J. Agron. Crop Sci.*, **152,** 336-353.

Giauffret C., Bonhomme R., Dorvillez D. and Derieux M. (1991). Conversion of intercepted radiation into aerial dry biomass for three maize genotypes : influence of plant density. *Maydica,* **36,** 25-27.

Girardin P. (1992). The « funnel effect » of a maize canopy. In : Scaife A. (Eds.) *Proc. 2nd ESA Congress, Warwick Univ.*, Colmar : European Society of Agronomy, 76-77.

Girardin P., Jordan M. O., Picard D. and Trendel R. (1986). Harmonisation des notations concernant la description morphologique d'un pied de maïs (*Zea Mays* L.). *Agronomie,* **6,** 873-875.

Girardin P., Morel-Fourrier B., Jordan M. O. and Millet B. (1987). Développement des racines adventives chez le maïs. *Agronomie,* **7,** 353-360.

Greenwood D. J., Lemaire G., Gosse G., Cruz P., Draycott A. and Neeteson J. J. (1990). Decline in percentage N of C3 and C4 crops with increasing plant mass. *Ann. Bot.*, **66,** 425-436.

Hill R. W. (1991). Irrigation scheduling. In : Hanks J. and Ritchie J. T. (Eds.) *Modeling plant and soil systems.* Madison : Amer. Soc. Agron., Crop Sci. Soc. Amer., Soil Sci. Soc. Amer., 491-509.

Hoppe D. C., McCully M. E. and Wenzel C. L. (1986). The nodal roots of Zea : their development in relation to structural features of the stem. *Can. J. Bot.*, **64,** 2524-2537.

Ilgen B. and Stamp P. (1993). Nitrogen effects on seedling roots of crucifers and legumes. *J. Agron. Crop Sci.*, **170,** 18-24.

Jordan M. O., Girardin P., Varlet-Grancher C., Picard D. and Trendel R. (1988). Rythme d'apparition des racines primaires du maïs (*Zea mays* L.). 3. Variations observées au champ. *Agronomie,* **8,** 37-46.

Klepper B., Belford R. K. and Rickman R. W. (1984). Root and shoot development in winter wheat. *Agron. J.*, **76,** 117-122.

Lemaire G. and Salette J. (1984). Relation entre dynamique de croissance et dynamique de prélèvement d'azote pour un peuplement de graminées fourragères. I. - Étude de l'effet du milieu. *Agronomie,* **4,** 423-430.

Maizlish N. A., Fritton D. D. and Kendall W. A. (1980). Root morphology and early development of maize at varying levels of nitrogen. *Agron. J.*, **72,** 25-31.

Mawaki M., Harada J., Iwata T. and Yamazaki K. (1990). Effect of shading on root system morphology and grain yield of rice plants (*Oryza sativa* L.). II. An analysis on primary roots. *Jpn. J. Crop Sci.*, **59,** 95-99.

Pagès L., Jordan M. O. and Picard D. (1989). A simulation model of the three-dimensional architecture of the maize root system. *Plant Soil,* **119,** 147-154.

Pellerin S. (1993). Rate of differentiation and emergence of nodal maize roots. *Plant Soil,* **148,** 155-161.

Picard D., Jordan M. O. and Trendel R. (1985). Rythme d'apparition des racines primaires du maïs (*Zea mays* L.). 1. Étude détaillée pour une variété en un lieu donné. *Agronomie,* **5,** 667-676.

Sadras V. O., Hall A. J., Trapani N. and Vilella F. (1989). Dynamics of rooting and root-length : leaf-area relationships as affected by plant population in sunflower crops. *Field Crops Res.*, **22,** 45-57.

SAS Institute Inc. (1989). *SAS/STAT Users' guide,* Version 6, Fourth edition, Volume 1, Cary, NC : SAS Institute Inc., 943 pp.

Stone J. A. and Buttery B. R. (1985). Effects of nitrate level and soil texture on soybean root growth and nodulation. In : Evans H. J., Bottomley P. J. and Newton W. E. (Eds.) *Nitrogen fixation research progress.* Dordrecht, The Netherlands : Martinus Nijhoff, 321.

Tanaka S., Yamauchi A. and Kono Y. (1993). Cultivar difference in the response of root system to nitrogen application in rice plant. *Jpn. J. Crop Sci.*, **62,** 447-455.

Tardieu F. and Pellerin S. (1990). Trajectory of the nodal roots of maize in fields with low mechanical constraints. *Plant Soil,* **124,** 39-45.

Thoms K. and Sattelmacher B. (1990). Influence of nitrate placement on morphology and physiology of maize (*Zea mays*) root systems. In : Van Beusichem M. L. (Ed.) *Plant nutrition-physiology and applications.* Doordrecht : Kluwer Academic Publishers, 29-32.

Varlet-Grancher C., Bonhomme R., Chartier M. and Artis P. (1982). Efficience de la conversion de l'énergie solaire par un couvert végétal. *Acta oecol.*, **3,** 3-26.

Yamazaki K. (1989). Root system formation and its relation to grain yield in rice plants. *Korean J. Crop Sci.*, **34,** 449-459.

Eur. J. Agron., 1994, **3**(2), 111-116

Photosynthesis of flag leaves and ears of field grown barley during drought

V. O. Mogensen*, G. Mortensen and C. R. Jensen

The Royal Veterinary and Agricultural University, Department of Agricultural Sciences, Soil and Water and Plant Nutrition, Agrovej 10, 2630 Taastrup, Denmark.

Received 21 September 1993 ; accepted 2 November 1993.

* To whom correspondence should be addressed.

Abstract

A barley crop (*Hordeum distichum* L., *cv.* Corgi) was grown in sandy loam soil in lysimeters. The lysimeter installation was placed in the field and automatically protected from rain by a mobile glass roof. During the grain filling period, the plants were exposed to different levels of water stress expressed as the number of stress days (SD) calculated from the evapotranspiration of the water stressed and the fully irrigated crop. During this period, net photosynthesis of flag leaves and ears was measured between 1000 h and 1500 h. When the crop had utilized 2/3 of the available soil water content net photosynthesis began to decrease. With further decrease in soil water content, the relationship between photosynthesis of fully irrigated plants (Pr) and water stressed plants (Pa) decreased by 3 per cent for a decrease of 1 per cent in relative soil water content. When SD exceeded 1.8, Pa/Pr decreased by 7.1 per cent per SD. Relative grain dry matter and relative total dry matter yield decreased by 2.2 and 1.9 per cent per SD, respectively.

Key-words : water stress, grain yield, stress days, soil water.

INTRODUCTION

Net photosynthesis of ears and flag leaves between ear emergence and maturity accounts for the major part of the final grain dry weight of field grown barley and wheat (Thorne, 1965). For a wheat crop grown in lysimeters Brar *et al.* (1990) found a decreasing photosynthetic rate with increasing soil water deficit. In a growth chamber experiment Johnson *et al.* (1974) found decreasing photosynthetic rates and transpiration of flag leaves and spikes of barley with decreasing leaf water potential of the flag leaves. In wheat and barley the decrease in stomatal conductance is probably the main cause of reduction in photosynthesis and transpiration at low leaf or ear water potentials.

Drought or water stress can be defined in various ways. For a barley crop Mogensen (1980) found that relative evapotranspiration was a sensitive expression of water stress. The term stress days as defined by Hiler and Clark (1971) combines the effect of the severity and the duration of water stress.

In earlier studies under field conditions we found that drought during the grain filling period decreased the grain yield in proportion to the number of stress days (Mogensen, 1980). Thus, these results suggest that the reduction in photosynthesis in ears and flag leaves is proportional to the severity and duration of water stress.

The purpose of the present study was to investigate how drought, imposed during the grain filling period of a barley crop, influenced the rate of photosynthesis of awned ears and flag leaves, grain yield, and total dry matter yield.

MATERIALS AND METHODS

The experiment was conducted in a lysimeter installation situated 20 km west of Copenhagen (55° 40' N ; 12° 18' E ; 28 m above MSL). The lysimeter facility (Kristensen and Aslyng, 1971) consists of 36 tanks, each 2 × 2 m by 1 m in depth. In the field, the lysimeter tanks are positioned in two rows divided

ISSN 1161-0301/94/02/$ 4.00/ © *Gauthier-Villars - ESAg*

by a drainage tunnel. A mobile glass roof automatically protects the crop against rain and when rain ceases the roof is automatically removed. Each tank is supplied with an individually operated trickle irrigation system. The present investigation was conducted in 18 tanks containing sandy loam soil with 33 per cent (clay + silt) in the topsoil. Soil water content in the tanks was 260 mm at field capacity (FC : pF = 2) and 115 mm at permanent wilting (PW : pF = 4.2), thus the amount of available water was 145 mm. The weather conditions during the growing seasons were recorded at the climate station situated close to the lysimeter installation.

The crop, two-rowed awned spring barley (*Hordeum distichum* L., *cv.* 'Corgi') was sown on April 3, 1989 and on March 27, 1990. Both years the seed rate was equivalent to 230 kg ha^{-1} and the distance between rows was 11 cm. In both years, fertilizer was applied as top dressing to provide, in kg ha^{-1}, 117 N, 37 P and 88 K. The crop emerged on 16 April, 1989 and on 14 April, 1990 and the numbers of days after emergence, DAE, were counted from these dates. The weather conditions during the growing seasons are given in Figure 1 as weekly means. In both years heading began on DAE 62 and terminated on DAE 70.

Soil water content was measured twice a week by the neutron moderation method at depths of 10, 20, 30, 40, 50, 70 and 90 cm. The calculated water deficit was restored at weekly intervals to the fully irrigated reference treatment (A). The drought treatments B, C, D, and E were irrigated with 2/3, 1/2, 1/3, and 1/4, respectively, of the amount applied to treatment A. Actual evapotranspiration (E*a*) was calculated from change in soil water content, and the supplied and drained water. Evapotranspiration (E*r*) from the fully irrigated treatment was taken as the reference. The number of stress days (Hiler and Clark, 1971) was calculated from equation 1 :

$$\mathrm{SD}_j = [1 - \mathrm{E}a_j/\mathrm{E}r_j]\,\mathrm{N}_j \qquad (1)$$

where Er_j and Ea_j are evapotranspiration from the fully irrigated treatment and the drought treatment, respectively, and N_j is the number of days in the period *j* between two measurements of soil water content. The number of stress days (SD_i) in the drought period corresponding to the development stage of *i* is :

$$\mathrm{SD}_i = \sum_{j=1}^{n_i} \mathrm{SD}_j \qquad (2)$$

where n_i is the number of periods in which SD_j is calculated.

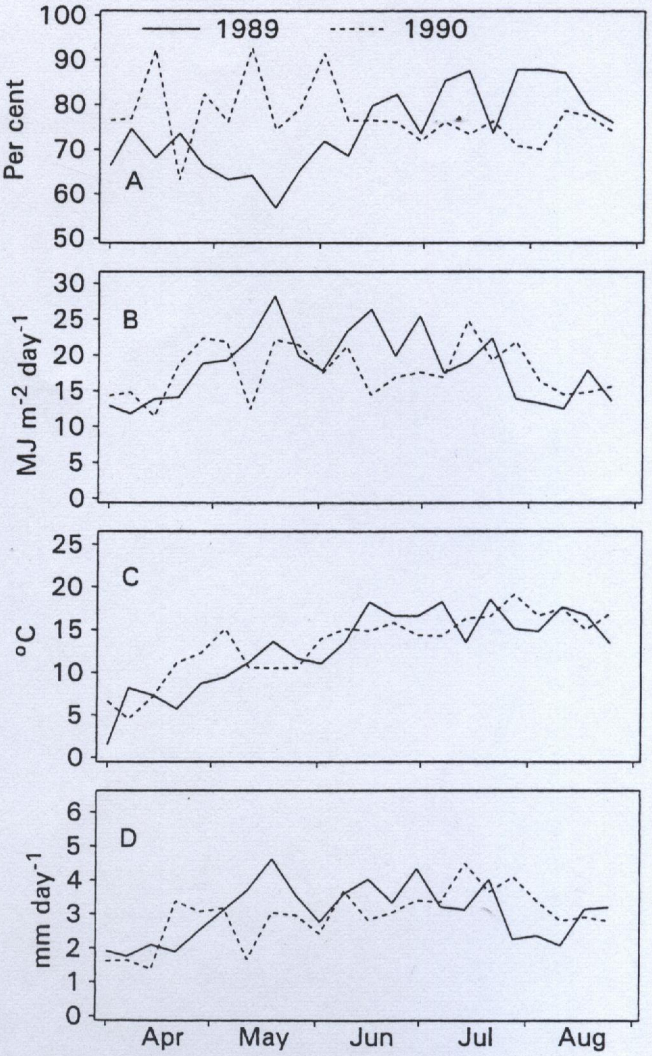

Figure 1. *Weather conditions during the two growing seasons. A, relative humidity ; B, solar radiation ; C, mean air temperature ; D, evapotranspiration. All values are weekly means.*

Relative available soil water content (RASW) was calculated from actual soil water content (SW), the soil water content at field capacity (FC) and at permanent wilting (PW) :

$$\mathrm{RASW} = (\mathrm{SW} - \mathrm{PW})/(\mathrm{FC} - \mathrm{PW}) \times 100 \qquad (3)$$

In 1989 relative available soil water content (RASW) of the reference treatment decreased to 50 per cent at the end of the grain filling period. In 1990, it did not decrease below 67 per cent. Decrease of RASW during the drought treatments (Figure 2) resulted in a decrease in the evapotranspiration rate and consequently the number of stress days (SD) increased, as formulated in equation 1 (Figure 3).

The photosynthetic rate was measured during the grain filling period in flag leaves and ears. In the field, measurements were carried out on intact plants between 1000 h and 1500 h using a LI-6200 portable

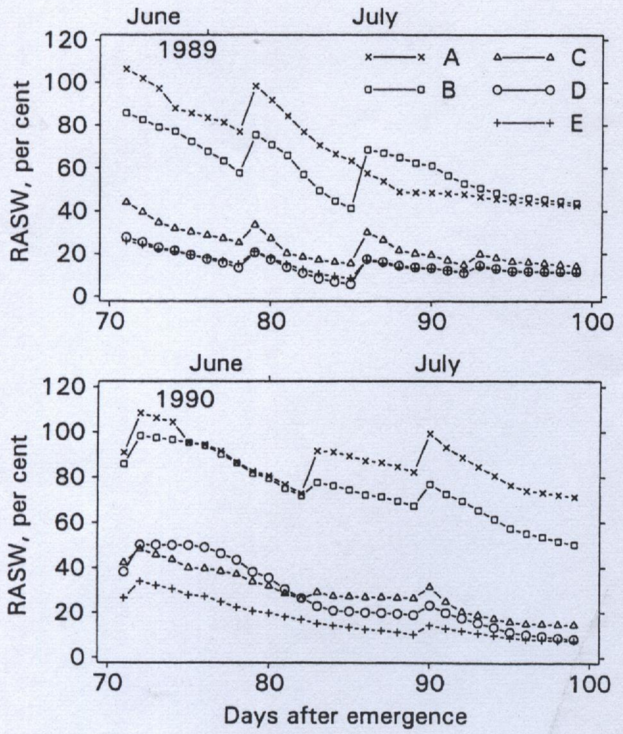

Figure 2. *Relative available soil water content (RASW) in the treatments during the grain filling phase. The letters A-E refer to the treatments (see text for details).*

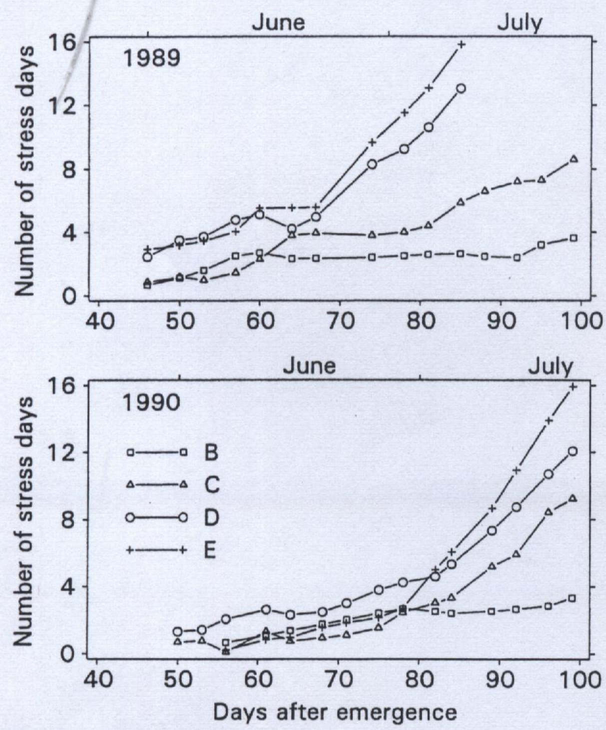

Figure 3. *Cumulative number of stress days SD in the treatments B-E (see text for details).*

photosynthesis system with a 1 litre chamber (LI-COR Inc. Lincoln, NE). The photosynthetic rate (P*a*) of the drought treatments was compared to that of the fully irrigated plants (P*r*). Individual ears were fully exposed and held in an approximately normal position to the direction of the sun. Flag leaves were placed across the chamber, so that only part of the leaves were measured, whereas whole ears were enclosed lengthwise in the chamber.

Because of overcast weather with frequent showers during the grain filling stage in 1989 and technical problems, it was only possible to obtain measurements of net photosynthesis on four days, 5-8 July. In 1990 net photosynthesis was measured between 26 June and 13 July, only with few interruptions. However, in the period between 27 June and 9 July there were scattered clouds and great variation in radiation intensity.

RESULTS AND DISCUSSION

On DAE 76-90 in non-senescent plants net photosynthesis of flag leaves was increasing with photosynthetically active radiation (PAR) until 1200 µmol photons $m^{-2} s^{-1}$ in the fully irrigated treatment (A). For the ears, photosynthesis continued to increase up to 2400 µmol $m^{-2} s^{-1}$. However, there was only a slight

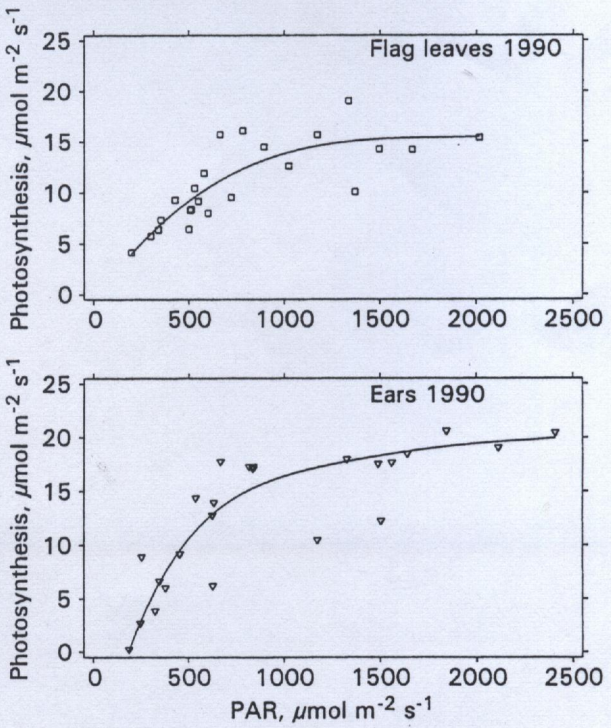

Figure 4. *Photosynthesis of flag leaves and ears in relation to photosynthetically active radiation intensity, PAR (400-700 Nm), in non-senescent plants of the fully irrigated treatment A.*

increase from 1200 to 2400 (Figure 4). For spring wheat, Hurry and Huner (1991) found no increase in net photosynthesis for PAR above 500. For the third leaf of wheat, Lawlor *et al.* (1987) found results similar to those in the present investigation.

Midday net photosynthesis for PAR values above 500 μmol m^{-2} s^{-1} in ears and flag leaves are shown in Figure 5 for the fully irrigated treatment. On DAE 76-88 the photosynthesis of flag leaves was measured at low intensity of PAR between 500-700 μmol m^{-2} s^{-1} due to scattered clouds. It should be mentioned that, based on the relations given in Figure 4, a correction of the photosynthesis for the days 76-88 to a PAR value of 1200 μmol m^{-2} s^{-1} gives a photosynthesis of approximately 14 μmol CO$_2$ m^{-2} s^{-1}. Correspondingly, net photosynthesis of the ears on DAE 88 would be 18 μmol CO$_2$ m^{-2} s^{-1}. Due to senescence the net photosynthetic rate decreased with time (Figure 5). For the fully irrigated treatment the decrease began on DAE 90, three weeks after heading had terminated. A corresponding decrease in photosynthesis as an effect of senescence as found in this experiment was found to be proportional to the carboxylation efficiency (Lawlor *et al.*, 1989).

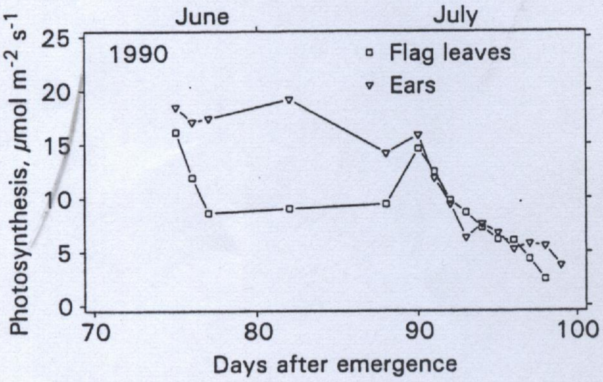

Figure 5. *Photosynthesis of flag leaves and ears in relation to age for the fully irrigated treatment A.*

To allow for the effect of senescence, when analyzing the effect of water stress on photosynthesis, relative photosynthesis (P*a*/P*r*) was calculated. Water stress was increasing during the later part of the grain filling period (Figure 3). For RASW less than 33 per cent, the relative photosynthesis (P*a*/P*r*) of flag leaves and ears was decreasing with decreasing RASW (Figure 6). Below a critical value of 33 per cent (RASW$_c$) the decrease in photosynthesis was analysed by applying linear regression analysis, with RASW as the independent and 100 × P*a*/P*r* as the dependent variable. The decrease was found to be 3 per cent for a decrease of 1 per cent in RASW. Similarly, the relationship between relative photosynthesis (P*a*/P*r*) and the number of stress days (SD) was analyzed by linear regression with SD as the independent and 100 × P*a*/P*r* as the dependent variable. No significant difference was found between years, nor between flag leaves and ears (Table 1 and Figure 7). For both years, the calculated regression for leaves and ears showed that the linear decrease in P*a*/P*r* began when the water stress exceeded a critical number of stress days (SD$_c$) equal to 1.8 stress days. Beyond SD$_c$, P*a*/P*r* decreased 7.1 per cent per SD.

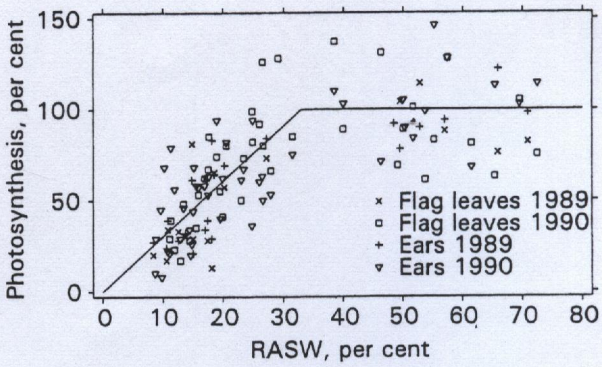

Figure 6. *Relative photosynthesis (Pa/Pr) in relation to relative available soil water content (RASW).*

When comparing relative evapotranspiration (E*a*/E*r*) and leaf water potential for a barley crop at heading, Mogensen (1980) found a critical leaf water potential of − 1.5 MPa measured on leaf 4. At this time the number of SD was 0.5. Correspondingly, Gupta *et al.* (1989) found no decrease in net photosynthesis of wheat leaves until the leaf water potential decreased below − 1.5 MPa, whereas Johnson *et al.* (1974) did not find any critical value.

The yield was greater in 1989 than in 1990. In both years, the grain dry matter yield as well as the total dry matter yield decreased with decreasing water

Table 1. *Regression of relative photosynthesis on the number of stress days (SD) and relative available soil water content (RASW). Regression coefficients b, intercepts a, and their standard deviations s are given. SD$_c$ is the critical number of stress days.*

	b	s_b	*a*	s_a	SD$_c$
Flag leaves 1989	− 5.9	0.8	100	7	0.1
Flag leaves 1990	− 7.9	1.2	115	8	1.9
Ears 1989	− 6.4	0.6	109	5	1.4
Ears 1990	− 7.7	0.7	119	5	2.4
Ears and leaves 1989 and 1990	− 7.1	0.4	113	3	1.8
RASW (*)	3.0	0.1			

* for RASW < 33 per cent.

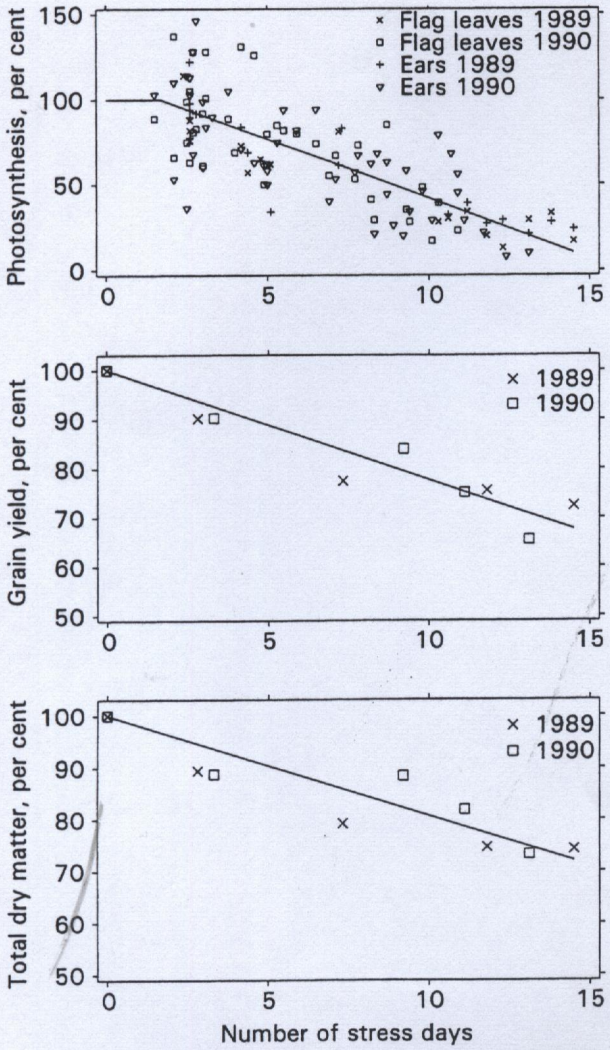

Figure 7. *Relative photosynthesis, relative grain yield, and relative total dry matter yield in relation to number of stress days.*

Table 2. *Dry matter yields, g* m^{-2}.

	1989			1990		
Treatment *	Grain	Straw	Total	Grain	Straw	Total
A	815	715	1530	711	634	1345
B	735	634	1369	642	553	1195
C	632	581	1213	597	593	1190
D	615	527	1142	534	568	1102
E	590	546	1136	465	493	958

* See text for details.

Table 3. *Regression of relative dry matter yield (per cent) on the number of stress days (SD). Regression coefficients b, intercepts a, and their standard deviations s, are given.*

	b	s_b	a	s_a
Model $y = a + bx$				
Total dry matter	− 1.7	0.3	97	2
Grain dry matter	− 2.1	0.2	98	2
Model $y = 100 + b$				
Total dry matter	− 1.9	0.1		
Grain dry matter	− 2.2	0.1		

supply (Table 2). Linear regression was applied with SD as the independent and relative dry matter yield in per cent as the dependent variable. As the intercepts (*a*) did not differ significantly from 100 per cent (Table 3), no critical values of SD could be determined and the model $y = 100 + bx$ was applied. When calculated with this model, relative grain yield decreased by 2.2 per cent per SD (Table 3 and Figure 7) and relative dry matter yield decreased by 1.9 per cent per SD (Table 3 and Figure 7).

For a grain filling period of 25 days (Gallagher *et al.*, 1976 ; Mogensen, 1991) the daily grain production is 4 per cent of the final grain yield. In the present study, the relative grain yield decreased by 2.2 per cent per SD whereas Mogensen and Jensen (1989) found a decrease of 3.7 per cent per SD and concluded that one SD corresponds to one day without grain growth. The possible reason for the smaller decrease found in this experiment was a slower developing drought because some irrigation was applied in the drought period, in contrast to the experiment by Mogensen and Jensen (1989).

In the present study, drought occurred mainly during the grain filling period. During this period 1/4-1/3 of the total dry matter is accumulated (Andersen *et al.*, 1992, and unpublished data from the crops reported by Mogensen, 1991). Therefore, the effect of drought on photosynthesis during grain filling may be expected to be between 4 and 3 times that on total dry matter production. The P*a*/P*r* decreased 7.1 per cent per SD (Table 1) and the relative dry matter yield decreased 1.9 per cent per SD (Table 3). Thus, in the present investigation the ratio is found to be 7.1/1.9 = 3.7 which is within the range mentioned above. Furthermore, during grain filling between 13 and 28 per cent of the net photosynthesis is lost by dark respiration (Mogensen, 1977 ; Morgan and Austin, 1983 ; Araus *et al.*, 1993). However, as dark respiration has an effect on both P*a* and P*r* it was not taken into account when calculating the ratio of relative photosynthesis to relative dry matter yield.

REFERENCES

Andersen M. N., Jensen C. R. and Lösch R. (1992). The interaction effects of potassium and drought in field-grown barley. I. Yield, water-use efficiency and growth. *Acta Agric. scand.*, **42,** 34-44.

Araus J. L., Brown H. R., Febrero A., Bort J. and Serretv M. D. (1993). Ear photosynthesis, carbon isotope discrimination and the contribution of respiratory CO_2 to differences in grain mass in durum wheat. *Plant Cell Environ,* **16,** 383-392.

Brar G. S., Kar S. and Singh N. T. (1990). Photosynthetic response of wheat to soil water deficits in the tropics. *J. Agron. Crop Sci,* **164,** 343-348.

Gallagher J. N., Biscoe P. V. and Scott R. K. (1976). Barley and its environment VI. Growth and development in relation to yield. *J. appl. Ecol,* **13,** 563-583.

Gupta A. S., Berkowitz G. A. and Pier P. A. (1989). Maintenance of photosynthesis at low leaf water potential in wheat. *Plant Physiol,* **89,** 1358-1365.

Hiler E. A. and Clark R. N. (1971). Stress day index to characterize effects of water stress on crop yields. *Trans. ASAE,* **14,** 757-761.

Hurry V. M. and Huner N. P. A. (1991). Low growth temperature effects a differential inhibition of photosynthesis in spring and winter wheat. *Plant Physiol.,* **96,** 491-497.

Johnson R. R., Frey N. M. and Moss D. N. (1974). Effect of water stress on photosynthesis and transpiration of flag leaves and spikes of barley and wheat. *Crop Sci.,* **14,** 728-731.

Kristensen K. J. and Aslyng H. C. (1971). Lysimeters with rainfall and soil water control. *Nord. Hydrol.,* **2,** 79-92.

Lawlor D. W., Boyle F. A., Young A. T., Keys A. J. and Kendall A. C. (1987). Nitrate nutrition and temperature effects on wheat: Photosynthesis and Photorespiration of leaves. *J. exp. Bot.,* **38,** 393-408.

Lawlor D. W., Kontturi M. and Young A. T. (1989). Photosynthesis by flag leaves of wheat in relation to protein, ribulose bisphosphate carboxylase activity and nitrogen supply. *J. exp. Bot.* **40,** 43-52.

Mogensen V. O. (1977). Field measurements of dark respiration rates of roots and aerial parts in Italian ryegrass and barley. *J. appl. Ecol,* **14,** 243-252.

Mogensen V. O. (1980). Drought sensitivity at various growth stages of barley in relation to relative evapotranspiration and water stress. *Agron. J.,* **72,** 1033-1038.

Mogensen V. O. (1991). Growth rate of grains of barley in relation to drought. *Acta Agric. scand,* **41,** 345-353.

Mogensen V. O. and Jensen H. E. (1989). The concept of stress days in modelling crop yield response to water stress. In : Ph. Plancquaert (Ed.) *Agriculture, Management of water resources in cash crops and in alternative production systems. EUR 11935 EN Paris : ITCF* 13-23.

Morgan C. L. and Austin R. B. (1983). Respiratory loss of recently assimilated carbon in wheat. *Ann. Bot,* **51,** 85-95.

Thorne G. N. (1965). Photosynthesis of ears and flag leaves of wheat and barley. In : *Ann. Bot., N. S. Vol. 29, No. 115,* 318-329.

Eur. J. Agron., 1994, **3**(2), 117-123

The effect of daylength on yield and quality of fibre hemp (*Cannabis sativa* L.).

H. M. G. van der Werf [1, 2, 3, *], H. J. Haasken [2], M. Wijlhuizen [1]

[1] *DLO Research Institute for Agrobiology and Soil Fertility (AB-DLO), PO Box 14,*
6700 AA Wageningen, The Netherlands.
[2] *Department of Agronomy, Wageningen Agricultural University, Wageningen, the Netherlands.*
[3] *Research Station for Arable Farming and Field Production of Vegetables, Lelystad, the Netherlands.*

Received 16 December 1993 ; accepted 14 January 1994

* To whom correspondence should be addressed.

Abstract

Stem growth of the short-day plant fibre hemp (*Cannabis sativa* L.) decreases after flowering. In the Netherlands, the hemp cultivars currently available flower in August. In 1990 and 1991 the ambient daylength was compared with a 24-hour daylength in field experiments on two cultivars. Crop development, interception of photosynthetically active radiation, dry matter accumulation, stem yield and stem composition were recorded. The 24-hour daylength did not totally prevent flowering, but did greatly reduce the allocation of dry matter to floral parts. It enhanced the efficiency of post-flowering radiation use, and increased stem dry matter yield by 2.7 t ha^{-1}. The continued stem growth resulted in higher yields, which in one cultivar were accompanied by a lower bark content of the stem. At final harvest, the 1 per cent NaOH solubility indicated a lower fibre content in the bark of plants from the 24-hour daylength. Breeding late-flowering hemp may be a promising strategy to improve the potential stem yield of hemp in the Netherlands, but the stem quality of such cultivars may be slightly poorer.

Key-words : *Cannabis sativa* L., fibre hemp, photoperiod, daylength, flowering, stem yield, stem quality, radiation use efficiency.

INTRODUCTION

Photoperiodic induction of flowering was first shown by Tournois (1912) in hemp (*Cannabis sativa* L.) and Japanese hop (*Humulus japonicus* L.). Tournois demonstrated that flowering in hemp was hastened by short days and delayed by long days : thus hemp is a short-day plant.

Hemp is dioecious, but monoecious cultivars have been bred. The two sexes are morphologically indistinguishable before flowering. The first sign of a transition to flowering is the formation of undifferentiated flower primordia, which is accelerated by decreasing photoperiod, but occurs even under continuous illumination (Borthwick and Scully, 1954 ; Heslop-Harrison and Heslop-Harrison, 1969). In this respect hemp is a quantitative short-day plant. To produce open fertile flowers some cultivars require short days ; in other cultivars flowering occurs in continuous light, but only after a protracted period of growth (Schaffner, 1926 ; Borthwick and Scully, 1954 ; Heslop-Harrison and Heslop-Harrison, 1969). According to Borthwick and Scully (1954) the critical daylength may be longer for male plants than for female plants of the same cultivar.

In young hemp plants phyllotaxis is opposite, but as flowering begins phyllotaxis changes from opposite to alternate (Heslop-Harrison and Heslop-Harrison, 1958). This change is considered to be the result of flower primordia interacting with leaf primordia at the apex (Bernier, 1988).

ISSN 1161-0301/94/02/$ 4.00/ © *Gauthier-Villars - ESAg*