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Grain Yield and Ear Development of Spring Barley as Influenced by Environmental Conditions during Early Stages of Plant Development

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Abstract. Barley plants were grown until day 21 under conditions which were different in relation to photon flux density, carbon dioxide concentration and temperature. Dry weight and leaf area increase from day 7 until day 21, shoot apex development between day 15 and day 47, and yield of each treatment group were considered. Photon flux density was demonstrated to have a greater influence on net assimilation rate (NAR) of young plants than has carbon dioxide enrichment. High temperature treatment seems to influence NAR less than growth and developmental processes. Grain yield of high temperature treated plants was significantly lower than that of the other treatment groups. Significant correlations have been found between growth analysis values of young plants and some yield components of each treatment.

Yield physiological studies have shown that photosynthesis is essential not only for biomass production of the plant but plays an important role in formation of the economic yield (BASSHAM 1977). The influence of exogenous factors on plant growth and yield formation has been investigated by several authors (KRENZER and MOSS 1975, GIFFORD 1977, CHABOT 1978, KENDALL *et al.* 1978, WARRINGTON *et al.* 1978). APEL (1976) reported that in growth chamber experiments an increased CO_2 concentration of the ambient air during the whole growing period of spring wheat plants led to a significantly higher grain yield, whereas the same treatment during the grain filling period only increased the carbohydrate content of culms and leaves but not the economically important grain yield. The influence of photosynthesis on yield formation should not be simplified as a source-sink relation between production of assimilates and their storage in mostly non photosynthesizing tissues (GIFFORD *et al.* 1973, HICKLENTON and JOLLIFFE 1978). The grain yield of cereals is formed by interrelationships between assimilate producing and assimilate consuming processes during the whole ontogenesis of the plant (NEALES and NICHOLLS 1978). According to KUPERMAN (1977) the effect of an environmental influence on the further vegetative and generative development of the plant depends on the developmental stage of the plant during that influence. The growth conditions during the second stage of organ development, according to the KUPERMAN scale of organogenesis, determine the vegetative habit, *e.g.* the number of nodes and internodes and the

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number of tillers formed by a cereal plant. The third stage is the beginning of ear differentiation and thus influences yield formation considerably. The aim of this work was to inquire into the effect of environmental influences during these stages of development on further growth, ear formation, and grain yield of barley plants.

MATERIAL AND METHODS

Spring barley plants (*Hordeum vulgare* L. cv. Frigga) were grown in controlled environment growth chambers KTLK 1250, KTLK 20000 (VEB NEMA, Netzschkau, GDR) and VKPM 1500 (E. Vötsch, Frommern, FRG) under different environmental conditions (Table 1) until day 21 after sowing. From day 21 until ripeness all plants grew up in a growth chamber KTLK 20000 under conditions corresponding to those of the HL treatment.

Growth Analysis of Young Plants

Samples containing eight plants of each treatment group were harvested six times between day 7 and day 21 after sowing when plants were undergoing stages 1 to 4 of their morphological development according to the FEEKES scale (LARGE 1954). Leaf area was estimated using a Lambda Instruments LI 3000 area meter and LI 3050 conveyor belt accessory. Dry weights of the plants were determined after drying at 70 °C for 24 hours.

The following growth characteristics were calculated from the primary values (KVĚT *et al.* 1971):

1. Biomass duration between two successive harvests equals

$$\mathrm{BMD}_{12} = \frac{W_2 - W_1}{\ln W_2 - \ln W_1} (t_2 - t_1) .$$

The biomass duration over the whole period under consideration (BMD) s obtained as the sum of the single values.

2. Leaf area duration is obtained analogously from

$$\mathrm{LAD}_{12} = \frac{A_2 - A_1}{\ln A_2 - \ln A_1} (t_2 - t_1)$$

and over the whole period as the sum of values (LAD). Both BMD and LAD were only used as auxiliary values for calculating the remaining growth characteristics.

3. Mean relative growth rate (RGR) in the time interval $t_e - t_i$ was calculated as

$$\mathrm{RGR} = \frac{W_e - W_i}{\mathrm{BMD}}$$

where W_e and W_i are the dry weights at the end and at the beginning of the time interval from day 7 until day 21, respectively.

4. Mean net assimilation rate (NAR) in the time interval $t_e - t_i$ is a value for the efficiency of photosynthetic production during that interval. It is obtained from

$$\mathrm{NAR} = \frac{W_e - W_i}{\mathrm{LAD}}$$

TABLE 1
Growth conditions of young plants until day 21

Treatment*	HL(+)	HL(−)	CO_2(+)	CO_2(−)	LL	HT
Temperature [°C] day : night	20 : 15	20 : 15	19 : 15	19 : 15	20 : 15	27 : 21
Photon flux density [μeinstein m^{-2} s^{-1}]	500	500	330	330	130	330
CO_2 conc. [μl l^{-1}]	300	300	1500	1500	300	300

* Abbreviations: HL : High photon flux density
LL : Low photon flux density
CO_2 : High carbon dioxide concentration
HT : High temperature
\+ : First leaf remained at the plant
− : First leaf was detached when being fully expanded (day 9 after sowing)

presuming a linear relationship between dry weight and leaf area. Symbols are used correspondingly to the calculation of RGR.

5. Mean leaf area ratio (LAR) characterizes the relative size of the assimilatory apparatus. It is calculated for the time interval $t_e - t_i$ as

$$\mathrm{LAR} = \frac{\mathrm{LAD}}{\mathrm{BMD}}.$$

The weighted values of RGR and NAR obtained by the aid of BMD and LAD are used to smooth out differences of single interval values caused by random fluctuations of dry weight and leaf area.

Growth and Development of the Shoot Apex

Samples containing five plants of each treatment group were taken from day 15 to day 47 after sowing, corresponding to the second to seventh stage of organ development according to the KUPERMAN scale. The parts of the main culm containing the shoot apex were fixed with a mixture composed of formaldehyd, ethanol, acetic acid, and distilled water (2 : 10 : 1 : 7, v/v/v/v), and the shoot apex was prepared under a stereomicroscope. The length of the shoot apex and the number of spikelets and/or spikelet primordia were determined as quantitative values characterizing growth and development of the ear.

Single Plant Yield

The remaining plants (40 to 60 of each treatment group) were harvested at ripeness, and the yield components were estimated. Grain weight per plant, grain number per plant, number of ears per plant and straw weight per plant were determined directly after drying at 60 °C, grain weight and grain number per ear, mean grain weight (weight of a thousand grains) and harvest index (relation of grain weight to straw weight) were calculated from these values.

One way analysis of variance and SCHEFFÉ's test were applied for comparison of dry weight and leaf area of each treatment group at day 21 and for comparison of shoot apex length and primordia number of each treatment at

each harvest time from day 15 to 47. Because of the inhomogeneity of variances the comparison of yield components was performed with the aid of KRUSKAL-WALLIS' nonparametric test in addition to DUNN'S test (SACHS 1969).

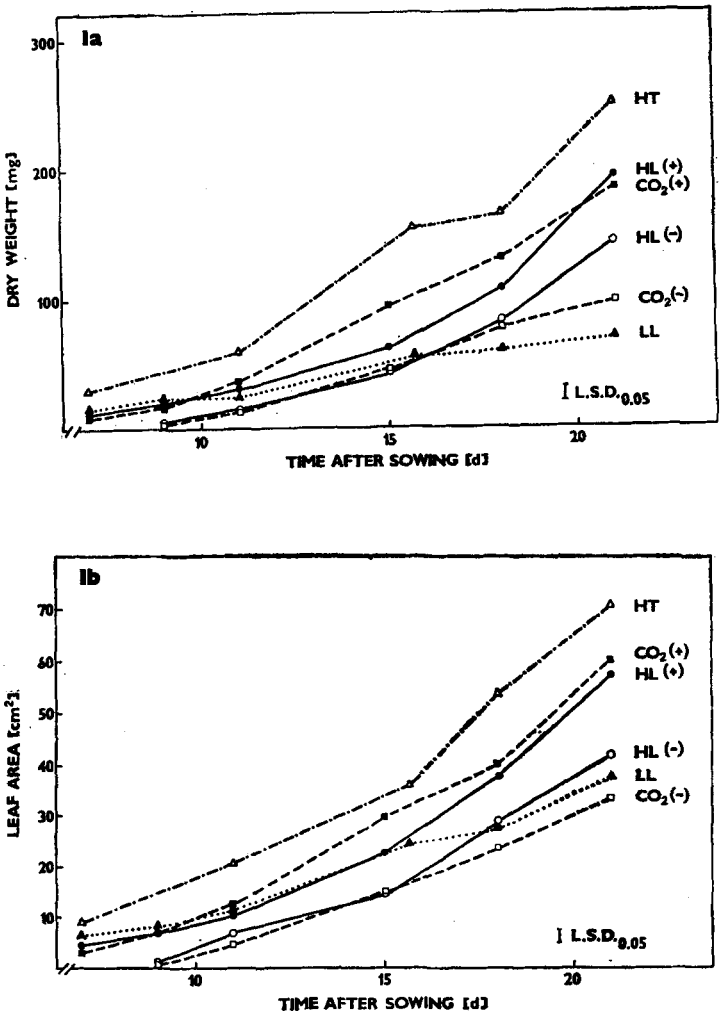

Fig. 1. Dry weight increase (a) and leaf area increase (b) of each treatment group. Abbreviations are used correspondingly to Table 1.

RESULTS

Different cultivation conditions until day 21 caused different responses in dry weight and leaf area increase of the plants (Fig. 1a, b). There are significant differences between the values at day 21 except those of HL(+) and CO_2(+) treatments. The higher mean NAR in HL treatment compared with CO_2 treatment suggests that high photon flux density caused a higher rate of photosynthesis than carbon dioxide enrichment (Table 2). Obviously

this is due to a light-limitation of the rate of photosynthesis under the given conditions (Table 1). LL treatment results in low RGR and NAR but high LAR (Table 2). This indicates that a great specific surface of the leaves could compensate the light-limited rate of photosynthesis per unit leaf area.

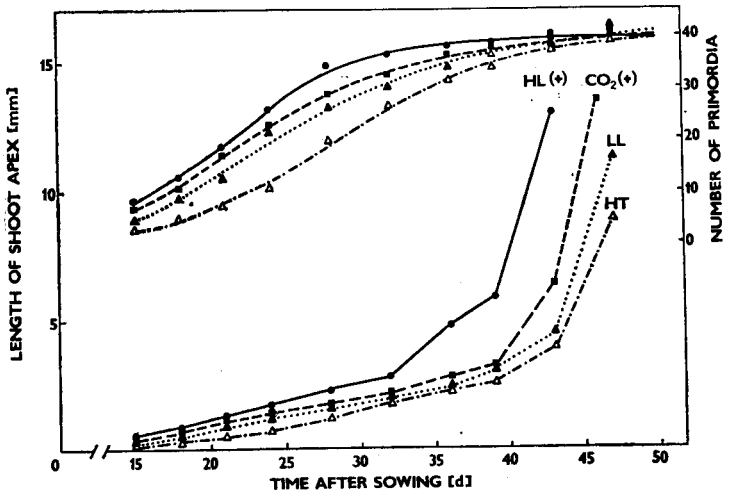

Fig. 2. Length increase of shoot apex (lower part) and initiation of spikelet primordia (upper part) in different environments. Abbreviations are used correspondingly to Table 1.

Loss of photosynthesizing tissue by detaching the first leaf was not compensated during the considered growth period as is indicated by the significantly lower dry weight of these plants compared with the other treatment groups.

The differences of the treatment groups in shoot apex and ear development are represented in Fig. 2. The final spikelet number does not depend on environmental conditions and seems to be genetically determined with a magnitude of about 40, *i.e.* twice more than the grain number of the ripe ear whereas one caryopsis is formed per spikelet. However the time course of primordia initiation is apparently affected by the growth conditions (RAHMAN and WILSON 1978). Table 3 demonstrates the time at which 50% and 90% of the maximal primordia number are achieved. The values are calculated with the aid of Richards' logistic growth equation (APEL *et al.* 1975). It is obvious from Fig. 2 that the exponential length growth of the ear begins only after achieving the maximal primordia number, *i.e.* after com-

TABLE 2
Growth analysis mean values between day 7 and day 21

Treatment	HL(+)	HL(−)	CO_2(+)	CO_2(−)	LL	HT
RGR	0.192	0.197	0.155	0.150	0.097	0.136
NAR [mg d^{-1} cm^{-2}]	0.560	0.585	0.486	0.467	0.210	0.467
LAR [cm^2 mg^{-1}]	0.343	0.337	0.319	0.320	0.461	0.292

TABLE 3
Achieving time of 50% and 90% of the maximum primordia number [days after sowing]. (Values are calculated by the aid of an adapted logistic growth equation)

Treatment	HL(+)	HL(−)	CO_2(+)	CO_2(−)	LL	HT
50% of maximum	21.3	21.7	23.1	25.7	25.3	28.7
90% of maximum	35.9	31.9	38.6	39.8	42.3	41.1

pletion of ear differentiation. Analogous results were obtained from comparisons of ear development of different barley genotypes (APEL, unpublished).

The values of yield components represented in Table 4 demonstrate the influence of the different cultivation conditions until day 21. The values of each yield component except mean grain weight and ear number per plant of the LL and HT treatments are significantly lower than those of all others. The differences between the HL and CO_2 treatments are significant in relation to grain weight per ear and mean grain weight only, although greater values of the other components are obtained for the HL treatment, too. No significant differences could be stated between the groups with and without the first leaf.

The correlation coefficients represented in Table 5 indicate positive correlations between RGR and NAR and the yield components. LAR correlates with yield negatively but not significantly in most cases. Obviously the influence of the environmental factors considered on yield is realized mainly through ear number per plant as is indicated by the close correlation of RGR and NAR with this yield component.

DISCUSSION

The influence of environmental conditions affecting the rate of photosynthesis during the early developmental stages of a plant can be followed throughout growth of the shoot apex and ear differentiation up to single plant yield. Photon flux density and carbon dioxide concentration are known to influence production of assimilate by photosynthesis that can be assessed by NAR. High NAR and consequently an increased assimilate supply during the second stage of organogenesis gives rise to favourable

TABLE 4
Yield components

Treatment	HL(+)	HL(−)	CO_2(+)	CO_2(−)	LL	HT
Grain number per plant	87.36	92.38	89.50	85.19	62.15	54.25
Grain weight per plant [g]	3.294	3.238	2.834	2.416	1.878	1.564
Grain number per ear	20.17	22.33	19.64	20.38	18.74	14.73
Grain weight per ear [g]	0.822	0.733	0.670	0.590	0.542	0.424
Ears per plant	4.360	4.390	4.150	4.000	3.330	3.410
Harvest index	0.500	0.519	0.507	0.416	0.295	0.237
Mean grain weight (weight of 1000 grains [g])	36.75	37.33	29.49	27.95	29.06	29.87

TABLE 5
Correlation coefficients between growth analysis mean values and yield components

	RGR	NAR	LAR
Grain number per plant	0.896*	0.969**	−0.949*
Grain weight per plant	0.975**	0.942*	−0.699 n.s.
Grain number per ear	0.805 n.s.	0.799 n.s.	−0.568 n.s.
Grain weight per ear	0.540 n.s.	0.819 n.s.	−0.516 n.s.
Ears per plant	0.978**	0.996***	−0.856 n.s.
Harvest index	0.918*	0.953*	−0.849 n.s.
Mean grain weight	0.807 n.s.	0.659 n.s.	−0.215 n.s.

Level of significance: * 0.95
** 0.99
*** 0.999
n.s. not significant

conditions for the start of the third stage because the great leaf area represents a high photosynthetic potential in terms of LAD, and the plant disposes of a greater carbohydrate pool as a reserve of energy and matter for growth under unfavourable conditions for photosynthesis (APEL and NÁTR 1976). As a consequence the number of spikelet primordia increases rapidly, and after achieving its maximum, quantitative growth of the ear begins. The high photosynthetic potential positively influences quantitative ear growth and consequently increases grain weight per ear, grain weight per plant and mean grain weight. Because the number of initiated spikelet primordia does not depend on the environmental conditions the number of caryopses formed per ear is determined later. It is reasonable to assume that under the same conditions the number of primordia developing into functionable generative organs depends on the amount of supplied assimilates which can either be produced by photosynthesis or be mobilized from stored carbohydrates, or can come from both these sources. In every case the vegetative development of the plant until that time is of decisive importance.

By an increased temperature growth and development as well as respiration are influenced because of the higher Q_{10} values of these processes whereas the rate of photosynthesis changes little over the considered range of temperature (HOFFMANN 1975). If this occurs during the second stage of organogenesis a remarkable vegetative growth resulting in high dry weight and great leaf area will be the consequence. Ear differentiation, however, will be delayed as is shown by the curve of primordia number increase of the HT treatment in Fig. 2. Consequently, the exponential length growth of the ear will begin later. Obviously the time for spikelet differentiation is short, and a small number of caryopses per ear and per plant will be formed (WARRINGTON *et al.* 1977). The fact that mean grain weight is not affected by high temperature treatment suggests a sufficient assimilate supply during the grain filling period. The low harvest index of the HT treatment represents an extremely unfavourable relation of grain weight to weight of vegetative organs which could be referred to delayed differentiation processes and coincident increased vegetative growth.

The spring barley cultivar which was taken as the object of the present investigations is characterized by its genetic homogeneity. An analogous

experiment was performed with a modern high yielding but genetically inhomogeneous cultivar, however the dispersion of yield component values was extremely high so that no correlations with growth analysis values were found. Although it would be desirable for practical purposes to examine modern cultivars, for physiological investigations genetically homogeneous ones should be preferred.

In agricultural practice the rate of photosynthesis of plants cannot be influenced by exogene factors except in glasshouse crops. Therefore search for genotypes which are characterized by a high rate of photosynthesis could be a suitable way for increasing cereal crop productivity. It, thus, seems to be reasonable to apply features which are sufficiently closely correlated with the rate of photosynthesis as a criterion for early selection of cereal crops.

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