Effects of Water Supply and Light Intensity on the Growth of Spring Wheat

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The effects of water supply and light intensity on the growth of spring wheat (*Triticum aestivum* L.) was studied under carefully controlled conditions. The leaf water potential (LWP) was measured from 5 to 40 d after the initiation of water supply treatments (DAIT). The LWP decreased as DAIT progressed. At higher photosynthetic photon flux densities (PPFDs), the LWP decreased as the water supply decreased. The water supply rate had little impact on tiller initiation and survival under low PPFD. As the PPFD increased, however, tillering responded sharply to water supply. Differences in tiller numbers were mainly due to differences in the number of subtillers from T0, T1 and T2 primary tillers. The water supply rate did not affect plant growth significantly under low PPFD. Increased PPFD resulted in increased plant growth, except for leaf numbers per main stem, as water supply rate increased. Thus, there was a highly significant interaction of water supply and light intensity on the growth of spring wheat.

Keywords : growth, leaf water potential, light intensity, wheat, water supply

INTRODUCTION

While responses of plants to either water or light stress have been extensively investigated, the interactions of these two environmental factors on the growth of wheat are unclear. Both water and light stresses impact growth of wheat adversely. In general, leaves which developed in shade are longer, thinner and lower in specific leaf weight than those developed at high PPFD (Allard et al., 1991). Friend et al. (1962) found that, below $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, increasing light intensity resulted in faster rates of leaf emergence and increased leaf thickness, but decreased leaf length. Rahman and Wilson (1977) and Rickman et al. (1985) reported a slowing of vegetative development of wheat at reduced light intensity.

Tiller initiation and survival are affected by water or light stress. Klepper et al. (1982) and Rickman et al. (1985) reported that wheat plants responded to low PPFD by failing to produce tillers at specific nodes. The appearance of particular tillers was delayed and in some cases, the coleoptilar, secondary and tertiary tillers did not develop at all in a water-stressed environment. Stark and Longley (1986) found that soil water deficits delayed the growth of main stem tillers. Roy and Gallagher (1985) and Davidson and Chevalier (1987) observed that drought delayed tiller emergence. Krenzer et al. (1991) and Tamaki et al. (1999) also found lower leaf emergence rates at low water supply. All of above reports showed that both

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water and light stresses caused decreased plant growth.

The objective of this experiment was to study the interaction of water supply and light intensity on the growth of spring wheat under carefully controlled water conditions. To accurately and reproducibly control the water supply to individual plants, we used a water control system (Tamaki et al., 1999) suggested by Wookey et al. (1991) of originally described by Snow and Tingey (1985).

MATERIALS AND METHODS

The water control system (Tamaki et al., 1999) consists of a sleeve in which plants are grown in a rooting medium which fits into a device containing a column of floral foam through which the water flow passes toward the rooting medium. The height differential between the rooting medium and the water table, and the hydraulic conductivity of the pathway through the floral foam are controlled. The roots are prevented from growing into the floral foam column by a nylon screen.

Four seeds of spring wheat (*Triticum aestivum* L. cv. Penawawa) were sown in each plant sleeve, using a rooting medium of a 2 : 1 : 1 : 1 mixture (by volume) of pumice, sand, peat moss, and sandy loam soil. The plant assemblies were placed in a controlled environment chamber (Controlled Environments Inc., ND, USA) at 25/15°C day/night temperature, and PPFDs of 100, 200, 300 and 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (I_{100} , I_{200} , I_{300} , I_{400}), with a 14-h photoperiod. Plants were illuminated under VHO 'cool white' 110-W fluorescent lamps and 60-W tungsten-filament lamps at different bench heights. The PPFD was measured 4 cm above the top of the canopy using LI-188B quantum sensor (LI-COR, Lincoln, NB, USA). As we did not measure the plant temperature, we did not take into account it in the analysis of this study.

After germination, the plants were thinned to one per sleeve to eliminate population density effect. The plants were irrigated as needed with a modified Long Ashton complete nutrient solution (Hewitt, 1966) until the second leaf was mature. Thereafter, the water supply treatments were imposed. We used three rates of water supply as follows:

W_H (high water supply): The water table was set at 12 cm below the root screen, with no ceramic disc in the floral foam column.

W_M (medium water supply): The water table was set at 12 cm below the root screen, and a ceramic disc of flow rate of 50 $\text{mL h}^{-1} \text{cm}^{-2} \text{atm}^{-1}$ (Soil Moisture Equipment, Santa Barbara, CA, USA) was installed in the floral foam column.

W_L (low water supply): The water table was set at 12 cm below the root screen, and a ceramic disc of flow rate of 1 $\text{mL h}^{-1} \text{cm}^{-2} \text{atm}^{-1}$ was installed in the floral foam column.

The LWP was measured every 7 d on the second youngest main stem leaf on each plant, using SC10A multiple chamber thermocouple psychrometer (Decagon Devices, Pullman, WA, USA), from 5 until 40 d after the initiation of water supply treatments (DAIT). We did not obtain the water potential of rooting medium but the levels of LWP must reflect the status of rooting medium.

Individual tillers were tagged and labeled as they emerged from the leaf sheaths, using the nomenclature suggested by Klepper et al. (1982). At anthesis, all plants were harvested, and fertile tillers and plant height were recorded. Leaf area was measured using LI-3100 leaf area meter (LI-COR). The plants were then separated into shoots and roots, and oven-dried for 48 h at 75°C and weighed.

Two identical experiments were conducted with four single plant replications per treatment in each experiment, for a total of eight single plants per treatment. Data from the two experiments were not significantly different and were combined for statistical analysis.

Fig. 1 Changes in leaf water potential with days after the initiation of treatments (DAIT) under different water supply rates and PPFDs.

Treatments for water levels W_H , W_M and W_L are high, medium and low supply rates, and for PPFD levels I_{100} , I_{200} , I_{300} and I_{400} are 100, 200, 300 and 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD with a 14-h photoperiod, respectively. Vertical bars indicate $\pm$ SD.

Fig. 2 Changes in tiller numbers with days after the initiation of treatments (DAIT) under different water supply rates and PPFDs.

Abbreviations of treatments are the same as in Fig. 1. Vertical bars indicate $\pm$ SD.

RESULTS AND DISCUSSION

Leaf water potential decreased as DAIT progressed in all treatments and increased PPFD decreased LWP, because transpiration increased as plants grew (Fig. 1). At I_{100} , the LWP was not affected by water supply rate and was higher than that at higher PPFDs, probably because of the stomatal closure at I_{100} . At higher PPFDs, the LWP decreased as the water supply decreased. In the I_{300} and I_{400} , the LWP of W_L at 40 DAIT was significantly lower. The PPFD effects on LWP were accelerated under severe water stress and water supply effects on them were also accelerated under higher PPFDs. Tamaki et al. (1999) also showed that water deficiency lowered LWP in the other study.

Tiller initiation and survival were affected by both water supply and PPFD (Fig. 2). Increased PPFD resulted in an increased number of tillers. Tillers appeared earlier and grew more vigorously with the increase in PPFD. Evans (1975) and Barnes and Bugbee (1991) also found that tiller number increased linearly with increasing solar radiation.

At I_{100} , there were no effects of water supply rate on tiller emergence and survival. Maximum tiller numbers were 3.9, 3.6 and 3.8 at W_H , W_M and W_L , respectively. From 28 DAIT until anthesis, no changes in tiller numbers were observed at I_{100} . At I_{200} , there were fewer tillers, but not significantly, at W_L compared to W_H and W_M . Maximum tiller numbers were 8.8, 8.6 and 7.1 at W_H , W_M and W_L , respectively. From 24 until 46 DAIT, tiller numbers did not change. After 46 DAIT tiller numbers decreased slightly. At I_{300} and I_{400} , the water supply rate affected the tiller initiation and survival significantly. Tiller initiation increased as the water supply increased. However, tillering at W_L ceased earlier and fewer tillers were survived than at W_H and W_M . At I_{300} , maximum tiller numbers were 20.8, 16.0 and 13.3 at W_H , W_M and W_L , respectively. At I_{400} , those were 27.8, 24.4 and 14.5, respectively. Furthermore, there were only small effects of PPFD on tillering at W_L , and significant effects at W_H .

There was a highly significant interaction of water supply and light intensity on tiller initiation and survival (Fig. 2). Allard et al. (1991) reported that few tillers survived under low PPFD. Roy and Gallagher (1985) and Tamaki et al. (1999) reported that, under water stress, few tillers were initiated and survived. From this experiment, we found that the water supply rate affected the tiller initiation and survival significantly over I_{300} . The time to maximum tiller numbers was shorter as the water supply decreased at both I_{300} and I_{400} . The DAIT to maximum tiller numbers were 40, 33 and 31 at W_H , W_M and W_L at I_{300} , and 31, 28 and 26 at I_{400} (Fig. 2).

Fertile tiller numbers at anthesis are shown in Table 1. Total surviving tiller increased as light intensity and water supply increased. Differences in the total tiller numbers were mainly due to differences in the number of sub tillers from T0, T1 and T2 primary tillers. There were no significant effects of water supply rates on tillering at I_{100} . Tillers were initiated primarily from the main stem and there were no sub tillers except at W_H , where a sub tiller was produced at T2 on one of eight plants. At I_{200} , total tiller numbers were fewer at W_L . At W_L , primary tillers of T0 and after T5 were not produced (data not shown), and only primary and secondary tillers at nodes T1 and T2 were produced. The PPFDs at I_{300} and I_{400} had similar effects to water stress. Total tiller numbers decreased significantly at W_L . The W_L initiated significant low numbers of tillers from primary and secondary tillers, and no sub tillers from T3 and T4. Furthermore, the PPFDs had no significant effects on total tiller numbers at W_L . At W_H and W_M , however, higher PPFDs increased them.

Plants responded to I_{100} by failing to produce particular tillers. No T0 tillers were produced at I_{100} (data not shown). Sub tillers from T0 were not found in any treatments of I_{100} and I_{200} , and in W_L at I_{300} . The T0 tillers were produced on only 1 of 24 plants among all treatments at I_{200} , on only 2 of 24 plants in all treatments at I_{300} , and 8, 7 and 5 of 8 plants at W_H , W_M and W_L , respectively at I_{400} (data not shown). Peterson et al. (1982) pointed out that the initiation of a T0 tiller was very sensitive to environmental stress. All T1 tillers survived in all treatments at I_{300} and I_{400} (data not shown). However, T1 survived on only 7 of 24 plants in all treatments at I_{200} , and T1 was absent at I_{100} (data not shown). Klepper et al. (1982) and Rickman et al. (1985) found that plants responded to a low light by failing to produce T0 and T1 tillers. Such failure significantly influenced total tiller numbers, because

Table 1 Fertile tiller numbers of primary, secondary, tertiary and quaternary tillers, and of sub tillers from T0-T4 primary tillers.

Treatments ^z	Total	Primary	Secondary	Tertiary	Quaternary	Sub tillers from				
						T0	T1	T2	T3	T4
$W_H I_{100}$	3.5 e ^y	3.4 d	0.1 e	0.0 b	0.0	0.0 c	0.0 c	0.1 c	0.0 b	0.0
$W_M I_{100}$	3.4 e	3.4 d	0.0 e	0.0 b	0.0	0.0 c	0.0 c	0.0 c	0.0 b	0.0
$W_L I_{100}$	3.4 e	3.4 d	0.0 e	0.0 b	0.0	0.0 c	0.0 c	0.0 c	0.0 b	0.0
$W_H I_{200}$	7.0 d	4.9 bcd	2.0 d	0.1 b	0.0	0.0 c	0.6 c	1.1 bc	0.4 ab	0.0
$W_M I_{200}$	6.9 d	4.9 bcd	1.9 d	0.1 b	0.0	0.0 c	1.3 c	0.7 bc	0.0 b	0.0
$W_L I_{200}$	4.3 de	3.8 d	0.5 e	0.0 b	0.0	0.0 c	0.3 c	0.2 bc	0.0 b	0.0
$W_H I_{300}$	16.3 b	5.9 ab	7.4 b	2.9 a	0.1	1.4 b	4.6 ab	2.9 a	1.3 a	0.2
$W_M I_{300}$	12.0 c	5.4 abc	4.8 c	1.8 ab	0.0	0.6 bc	3.8 b	1.6 b	0.5 ab	0.1
$W_L I_{300}$	6.0 de	4.1 cd	1.8 de	0.1 b	0.0	0.0 c	1.4 c	0.5 bc	0.0 b	0.0
$W_H I_{400}$	21.4 a	7.0 a	9.8 a	4.5 a	0.1	4.0 a	5.8 a	3.0 a	1.5 a	0.1
$W_M I_{400}$	18.8 ab	6.6 ab	8.7 ab	3.4 a	0.1	3.0 a	5.0 ab	2.8 a	1.3 a	0.1
$W_L I_{400}$	6.3 de	4.1 cd	2.2 d	0.0 b	0.0	0.3 bc	1.3 c	0.6 bc	0.0 b	0.0

^z W_H , W_M and W_L represent high, medium and low water supplies, respectively. I_{100} , I_{200} , I_{300} and I_{400} represent 100, 200, 300 and 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD with a 14-h photoperiod, respectively.

^y Within columns, values followed by different letters are significantly different at $p < 0.05$.

T0 and T1 tillers produced many sub-tillers (Table 1).

Increasing PPFD and water supply resulted in an increase in the rate of leaf emergence on the main stem and, therefore, a decrease in phyllochron value (Table 2). Phyllochron was significantly higher in W_L at higher PPFDs. Krenzer et al. (1991) also found higher phyllochron values under low water supply. However, the water supply rate did not affect the phyllochron significantly at I_{100} and I_{200} . Leaf numbers were not affected significantly by water supply rate, but were affected significantly by PPFD (Table 2).

The water supply rate on plant growth responses has no effects under low PPFD (Table 3). Plant height was not significantly affected by water deficiency at I_{100} and I_{200} , but at I_{300} and I_{400} it was significantly shorter at W_L . Both increased water supply and PPFD resulted in increased shoot and root weights. At I_{100} and I_{200} , shoot and root weights were not affected by water supply, but at I_{300} and I_{400} , they were affected significantly. The W_L did not affect dry matter production significantly, but the W_H increased it significantly as PPFD increased. With the decrease in water supply, the shoot/root ratio decreased at I_{200} , I_{300} and I_{400} , but

Table 2 Phyllochron and leaf numbers on the main stem.

Treatments ^z	Phyllochron (degree-d leaf ⁻¹)	Leaf numbers
$W_H I_{100}$	133 a ^y	8.8 b
$W_M I_{100}$	133 a	8.5 b
$W_L I_{100}$	134 a	8.3 b
$W_H I_{200}$	127 bc	9.6 ab
$W_M I_{200}$	126 bc	9.6 ab
$W_L I_{200}$	128 b	9.3 b
$W_H I_{300}$	111 e	9.9 ab
$W_M I_{300}$	114 de	10.3 ab
$W_L I_{300}$	123 c	10.1 ab
$W_H I_{400}$	108 e	10.6 a
$W_M I_{400}$	111 e	10.4 a
$W_L I_{400}$	116 d	10.5 a

^z Symbols are the same as in Table 1.

^y Within columns, values followed by different letters are significantly different at $p < 0.05$.

Table 3 Plant growth responses under different water supply rates and PPFDs.

Treatments ^z	Plant height (cm)	Biomass (g plant ⁻¹)	Leaf area (cm ² leaf ⁻¹)	Specific leaf weight (mg cm ⁻²)	Shoot dry weight (g plant ⁻¹)	Root dry weight (g plant ⁻¹)	Shoot/root ratio
$W_H I_{100}$	71.6 c ^y	21.3 d	18.2 a	4.5 c	4.8 d	0.3 d	17.1
$W_M I_{100}$	73.6 c	20.3 d	17.4 a	4.7 c	4.6 d	0.2 d	20.0
$W_L I_{100}$	68.6 cd	17.3 d	16.1 a	4.6 c	4.2 d	0.2 d	26.3
$W_H I_{200}$	70.2 cd	36.7 d	10.0 bc	7.6 ab	8.2 d	0.8 bc	10.8
$W_M I_{200}$	72.8 c	36.1 d	9.4 bc	7.7 ab	7.8 d	0.8 bc	10.4
$W_L I_{200}$	68.7 cd	20.4 d	9.2 bc	7.8 bc	5.0 d	0.7 bc	7.1
$W_H I_{300}$	80.2 b	100.5 b	9.4 bc	9.3 a	21.5 bc	1.6 b	13.8
$W_M I_{300}$	81.8 ab	74.2 c	10.3 b	8.9 a	17.3 c	1.3 b	13.5
$W_L I_{300}$	63.7 d	28.7 d	9.0 bc	7.6 ab	7.2 d	0.7 bc	9.7
$W_H I_{400}$	86.0 a	152.3 a	9.6 bc	8.7 a	31.0 a	2.5 a	12.5
$W_M I_{400}$	82.4 ab	120.9 b	9.1 bc	8.0 ab	24.1 b	2.5 a	9.5
$W_L I_{400}$	71.3 c	23.0 d	7.4 c	6.5 b	6.7 d	1.2 b	5.8

^z Symbols are the same as in Table 1.

^y Within columns, values followed by different letters are significantly different at $p < 0.05$.

increased at I_{100} . Leaves grown at I_{100} had larger areas but lower specific leaf weights than leaves grown at higher PPFDs. Similar characteristics of plants grown at low PPFD were reported by Allard et al. (1991) and Barnes and Bugbee (1991). Wheat plants grown at I_{100} allocated relatively more dry weight to the production of leaf area and less to the roots than did plants grown at higher PPFDs. Although the plants grown at I_{100} had low dry matter production, they had a higher shoot/root ratio and higher leaf area than plants grown at higher PPFDs. This indicates a morphological adjustment to compensate for low PPFD and is similar to the results reported by Allard et al. (1991). The larger leaf size at I_{100} was reflected by increased duration of leaf elongation. However, the longer duration of leaf expansion occurred with a reduced number of leaves produced during the growth period and, consequently, reduced the number of available sites for tiller production (Hunt and Thomas, 1985).

Present experiment showed a significant interaction of water supply and PPFD on development, tillering and dry matter production of spring wheat. At low PPFD few tillers were produced, the dry matter production was small, and the water supply rate had little impact on plants. As the PPFD increased, the water supply rate affected the production of tiller and dry matter significantly. In other words, as the water supply increased, the growth was largely affected by PPFD. Since higher PPFDs increased transpiration, the plant growth was promoted under increased water supply. Further studies under much higher PPFDs would be worthy to suite the field conditions.

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<和文抄録>

春コムギの生育に及ぼす水分および光強度の影響

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水分供給量と光強度が春コムギの生育に及ぼす影響を, 人工光グロースチャンパー内に設置した水分供給制御装置を用いて検討した。葉の水ポテンシャルを処理開始後5日目から40日目までにわたって測定したところ, 処理日数の経過とともに低下した。光強度が葉の水ポテンシャルに及ぼす影響は, 水分供給量が少ない場合大きくなり, また, 水分供給量が葉の水ポテンシャルに及ぼす影響は, 光強度が高い場合大きくなった。弱光下では, 水分供給量が分げつの発生とその後の発育に及ぼす影響は小さかったが, 光強度が高くなると水分供給量に対する分げつの反応は大きくなった。さらに, 水分供給量により光に対する分げつの反応は有意に影響を受けた。分げつ発生数の差は主に T0, T1, T2 分げつから発生した分げつ数の差に基づくものであった。実験に用いた範囲の弱光 ($100\sim 200\ \mu\text{mol m}^{-2}\text{s}^{-1}$ PPFD) 下では, 水分供給量の差が有意に作物体の生育に影響を与えることはなかったが, 光強度の水準が高くなると, 主茎の葉数を除いて生育は水分供給量の増加に伴って旺盛になった。また, 水分供給量が多くなると生育は光強度の増加に伴って旺盛となった。このように, 春コムギの生育に対して, 水分供給量と光強度との間に強い交互作用がみられた。