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Photosynthesis, root respiration, and grain yield of spring wheat in response to surface soil drying

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Abstract

The aims of this research were to test the influence of surface soil drying on photosynthesis, root respiration and grain yield of spring wheat (*Triticum aestivum*), and to evaluate the relationship between root respiration and grain yield. Wheat plants were grown in PVC tubes 120 cm in length and 10 cm in diameter. Three water regimes were employed: (a) all soil layers were irrigated close to field water capacity (CK); (b) upper soil layers (0–40 cm from top) drying (UD); (c) lower soil layer (80–120 cm from top) wet (LW). The results showed that although upper drying treatment maintained the highest root biomass, root respiration and photosynthesis rates at anthesis, the root respiration of the former was significantly ($P < 0.05$) lower than the latter at the jointing stage. There were no differences in water use efficiency or harvest index between plants from the upper drying and well-watered treatment. However, the grain weight for plants in the upper drying treatment was significantly ($P < 0.05$) higher than that of in well-watered control. The results suggest that reduced root respiration rate and the amount of photosynthates utilized by root respiration in early season growth may also have contributed to improve crop production under soil drying. Reduced root activity and root respiration rate, in the early growth stage, not only increased the photosynthate use efficiency (root respiration rate: photosynthesis ratio), but also grain yield. Rooting into a deeper wet soil profile before grain filling was crucial for spring wheat to achieve a successful seedling establishment and high grain yield.

Introduction

Drought stress near the soil surface is common in the field, whereas water availability deeper in the soil profile may be adequate for plant uptake; this is particularly true in Mediterranean-type environments. Soil drying in the upper profile may have a profound impact on plant growth and seed yield (Mwabanwebge et al. 1998). This is especially true if the majority of the root system is confined to the surface soil layer (Smucker et al. 1991; Nagarajan et al. 1999). For spring wheat, more than 70% of the total root length has been shown to be distributed in the top 40 cm of the soil profile (Sharm et al. 1983; Li et al. 2001).

Drought stress may results in a larger root system, which increases absorption of water from soil (Sharm and Chaudhary 1983; Blum and Johnson

1992). However, the rate of photosynthesis often restricts plant growth when soil water availability is limited (Amede et al. 1999; Huang and Fu 2000). A negative whole-plant carbon balance may occur as a result of reduced photosynthetic capacity during drought, unless simultaneous and proportionate reductions in growth and carbon consumption take place. Using partial root drying (PRD) and/or regulated deficit irrigation (RDI) methods, Davies et al. (1994, 2000) and Johnson et al. (1992) found that both crop production and water use efficiency could be enhanced by drying soil due to changes induced by the plants' chemical signaling system (ABA) and hydraulic architecture. Passioura (1982) considered that decreasing root biomass might be an effective way to increase crop production under drought stress.

Roots are major consumers of photosynthetic carbon and use it primarily for respiration, tissue growth and exudation, which is especially apparent during soil drying (Passioura et al. 1982; Lambers l987; Lambers et al. 1996). About 30% of the carbon allocated to roots of wheat was incorporated in dry matter and 50% was respired, depending on relative growth rate and nutritional status of the plants (Lambers et al. 1996). Thus, quantitative information on root respiration in response to surface soil drying is important in understanding plant growth as is photosynthesis (Bouma et al. 1997; Lohila et al. 2003). However, the responses of root respiration to surface soil drying and its influence on grain yield of crops are still not well understood. More knowledge of these responses might provide insights into plant drought-resistance mechanisms.

The aim of this study was to investigate the responses of photosynthesis, respiration and grain yield to surface soil drying for spring wheat (Longchun 8139-2), which is widely used as a main crop in arid and semi-arid regions.

Materials and methods

Plant materials and growth conditions

This study was conducted at Lanzhou University, P.R. China. Spring wheat (*Triticum aestivum*) cv. 'Longchun 8139-2' seeds were pre-soaked at 4 °C for vernalization and then transplanted into polyvinyl chloride (PVC) tubes (120 cm long, 10 cm in diameter). After emergence, the seedlings were thinned twice to 5 plants per tube, equivalent to 640 plants m^{-2}. The tubes were filled with a mixture of vermiculite and loess (5.2: 1, w/w). The field capacity of the mixture was 88% (gravimetric) and soil bulk density was 0.27 g cm^{-3}. Vermiculite was used as a growing medium for the following reasons: this material can be easily washed off the roots and contains no organic matter, which minimizes the confounding effects of soil microbial respiration on root respiration (van Bavel et al. 1978).

Treatments

The experiment consisted of three soil moisture treatments with three replicates arranged in a completely randomized design with repeated measurements. Water content in the well-watered treatment was maintained at field capacity (88% g/g) by drip irrigation (CK). The upper drying treatment allowed the surface (0–40 cm) soil to dry down by withholding irrigation, while the lower 80 cm of soil was maintained at field capacity by drip irrigation (UD). Lower wet treatment allowed the upper and middle soil profile (0–80 cm) to dry down by withholding irrigation, while water content was maintained at field capacity in the bottom 40 cm of soil (80–120 cm, LW). In the experiment, a well-watered treatment acted as the control. During the experimental period, tubes were watered every five days. Destructive sampling was carried out at jointing, anthesis, and grain filling stage, respectively.

Measurements

Two fully-expanded leaves from each tube were sampled from main stems and the first tiller between 9:00 and 11:00 at jointing, anthesis and grain filling stage, respectively, to measure leaf water potential (Ψ_{leaf}) using the liquid drip method (Zhang 1990). Briefly, all leaves were sampled with a cork borer (Φ = 1 cm). Three leaf pieces were immersed in sucrose solutions of different concentrations ranging from 0.05 to 0.3 M. After 30 min, the solution was extracted and injected into a graduated flask, with a sucrose solution gradient ranging from 0.01 M (top) to 0.5 M (bottom). Leaf water potential was recorded as the concentration of the sucrose solution where the drop was suspended.

Canopy net photosynthesis rates and root respiration rate were measured using an infra gas analysis system (CIRAS-1, PP-Systems, UK). Canopy net photosynthesis rates were measured under natural conditions from 8:00 to 18:00 at 2 h intervals.

Root respiration was measured as described by Kelting et al. (1998) and Larionova et al. (1998). Briefly, shoots were removed by clipping to soil level before measuring root respiration. After shoot excision, the roots were excavated and hand-washed, blotted dry to remove surface water and placed into a cuvette in a temperature-controlled room to equilibrate.

Equilibration was necessary because root tissue accumulates higher internal CO_2 concentrations in the soil environment. Upon removal from the soil, a rapid diffusion of this CO_2 occurs and initial respiration rates are generally overestimated until surplus CO_2 has dissipated from the roots. The time period required for respiration to reach equilibrium was around 30 min after extraction from the soil. This equilibrium period was determined after several sets of respiration measurements were taken at set time-intervals until a point of stabilization was reached (data not shown). Our results fall in the ranges (from 30 min to 1 h) reported (Carpenter and Mitchell 1980; Johnson and Owens 1986; Cropper and Gholz 1991). Respiration rate was measured with an open chamber infrared gas analysis system (CIRAS-1, PP-Systems, UK). The root tissues were placed into a cuvette (10 in diameter and 15 cm in height). The edge of cuvette was sealed by Vaseline. The reference air CO_2 concentration was controlled around at 370 μmol mol^{-1}. Once roots reached a cuvette equilibrium, respiration rate remained constant for at least 15 min, during which measurements were taken. Both canopy net photosynthetic rate and root respiration rate were expressed as μmol CO_2 m^{-2} s^{-1}. After respiration measurements, shoot and root tissues were dried (24 h at 105 °C) to measure above and below ground biomass.

Water use efficiency based on grain yield (WUE) was calculated as the ratio of grain yield per plant relative to the total amount of water used during the entire growth period. Three plants from each tube were harvested inn December for measurement of grain weight, spike length, fertile spikelet number, number of spikelets, grain number per spike and harvest index.

Results

Leaf potential

Although leaf water potentials in UD and LW were lower than in CK at the jointing stage, leaf water content did not differ significant between CK and UD at anthesis or between CK and LW treatments at grain filling, respectively (Table 1). Notably, there was a significant difference in leaf water potential ($P < 0.05$) between UD and LW at anthesis. This suggests that roots metabolic activity cannot be reestablished after dormancy, and therefore, the roots cannot absorb sufficient water from deeper in the soil, when the stress occurred after anthesis.

Root biomass and root/shoot ratio

The time when roots grew into the lower wet soil profile had a significant effects on root biomass and the root/ shoot ratio (Table 2). At the jointing stage, root dry weight in the upper drying and well-watered control were significantly ($P < 0.05$) higher than in the lower wet treatment, resulting in lower root/shoot ratio. At anthesis, although there was no difference in root/shoot ratio among treatments, the root dry weight of plants in upper drying and lower well-watered treatment (LW) were significantly ($P < 0.05$) higher and lower, respectively, than that of well-watered control. Root dry weight in CK and UD treatments reached a maximum at anthesis and decreased slightly at grain filling stage. However, it was at the

Table 1. Predawn leaf water potential (MPa) of spring wheat in three soil water regimes at different growth stage.

	Well water (CK)	Up drying (UD)	Lower wet (LW)
Jointing (DAE 33)	−0.43 a	−0.66 b	−0.66 b
Anthesis (DAE 61)	−0.39 a	−0.37 a	−0.50 b
Grain filling (DAE 88)	−0.50 a	−0.53 a	−0.56 b

DAE means days after emergence.
Values followed by the same letter within a row are not significantly different ($p < 0.05$).

Table 2. The root dry weight (g $plant^{-1}$) and root/shoot ratio for spring wheat of three soil water regimes at different growth stage.

		Well watered (CK)	Upper drying (UD)	Lower wet (LW)
Jointing	Root	0.74 a	0.73 a	0.54 b
(DAE 33)	R/S	0.85 a	0.83 a	0.99 b
Anthesis	Root	0.69 a	0.76 b	0.50 c
(DAE 61)	R/S	0.46 a	0.43 a	0.46 a
Grain filling	Root	0.66 a	0.61 a	0.53 b
(DAE 88)	R/S	0.39 a	0.35 a	0.36 a

Values followed by the same letter within a row are not significantly different ($p < 0.05$).

grain filling stage that root dry weight of LW plants reached a maximum. This suggests that root biomass may increase when roots reached the wetter soil profile at grain filling.

Gas exchange

Surface drying reduced root respiration rate and photosynthesis rate when compared with the well-watered treatment (Table 3). However, the influence of surface drying on photosynthesis rate was smaller than that on root respiration, resulting in a smaller respiration/photosynthesis rate. At anthesis photosynthesis and root respiration in UD treatment increased dramatically and was significantly ($P < 0.05$) higher than CK. Unlike root biomass, photosynthesis and root respiration of LW plants did not increase and was significantly ($P < 0.05$) lower than that of CK. This suggests that root growth into a lower wetter soil profile, before grain filling, was very important for plants' during the resumption of metabolic activity after drought stress.

Grain yield and water use efficiency

Although water use efficiency and harvest index of plants in UD treatment were similar to those of CK, the grain weight of the former was significantly ($P < 0.05$) higher than latter (Table 4). There were no significant differences in grain number per spike among the three soil water treatments, but the spikelet number of the UD and LW treatments was significantly ($P < 0.05$) higher and lower than CK, respectively. Plants in the LW treatment showed the highest water use efficiency and harvest index, but the grain yield was significantly ($P < 0.05$) lower than that of in CK and UD treatments.

Discussion

A large body of work describes effects of soil surface drying on shoot and root growth, photosynthesis and grain yield (Davies et al. 1994; Leport et al. 1998; Huang and Gao 2000; Bryla et al. 2001). Few of these reports focus on the influence of surface soil drying on root respiration rate and its potential effects on grain yield. Some data does however show that surface soil drying can enhance crop productivity, which is ascribed to the development of deeper root system, the use of water at greater soil depths, and the regulation of the plants' chemical signaling system (ABA) and hydraulic architecture (Johnson et al. 1992; Davies et al. 1994; Loss and Siddique 1997; Li et al. 1999; Davies et al. 2000; Huang and Fu 2000).

Table 3. Daily mean photosynthesis rate (μmol CO_2 m^{-2} s^{-1}), root respiration rate (μmol CO_2 m^{-2} s^{-1}) and the ratio between root respiration and photosynthesis (%) of three soil water regimes at different growth stage.

	Jointing (DAE 33)			Anthesis (DAE 61)			Grain filling (DAE 88)		
	Pn	Rr	R/P	Pn	Rr	R/P	Pn	Rr	R/P
Well water (CK)	8.06 a	1.73 a	0.21 a	10.72 a	2.38 a	0.22 a	14.84 a	1.34 a	0.09 a
Upper drying (UD)	7.09 b	1.04 b	0.15 b	13.61 b	3.75 b	0.28 b	8.01 b	1.47 a	0.18 b
Lower wet (LW)	7.06 b	1.11 b	0.16 b	9.63 c	1.89 c	0.20 c	6.82 c	0.98 b	0.14 c

Pn means daily mean photosynthesis rate; Rr means root respiration rate; and R/P means the ratio of root respiration rate to leaf photosynthesis rate. Values followed by the same letter within a row are not significantly different ($p < 0.05$).

Table 4. 4 Yield components and water use efficiency of spring wheat in three soil water treatments.

Treatments	Grain weight (g plant^{-1})	Spike length (cm)	Number of spikelet	Grain number per spike	Harvest index	WUE (mg ml^{-1})
Well water (CK)	0.53 a	6.16 a	6.89 a	18.64 a	0.32 a	0.14 a
Upper drying (UD)	0.56 b	6.69 a	8.44 b	17.92 a	0.32 a	0.14 a
Lower wet (LW)	0.52 a	5.85 b	5.35 c	17.86 a	0.35 b	0.17 b

Values followed by the same letters within a column are not significantly difference ($p < 0.05$).

However, our results show that reduced root respiration rate and the amount of photosynthates utilized by root respiration in the early growing season may also have contributed to improved crop production under soil drying. Root respiration is a major consumer of photosynthetic carbon and thus has an impact on whole plant carbon balance (Waisle et al. 1996; Huang and Fu 2000). Lambers et al. (1996) found that more than 50% of the daily accumulated photosynthate was respired by the root, with the overall fraction determined by metabolic efficiency and plant growth conditions (Bouma et al. 1997). It is generally believed, for spring wheat, that photosynthate is mainly allocated belowground to construct the root system before the anthesis stage. Prior to anthesis, root growth is rapid and metabolic activity is high, utilizing a large proportion of available photosynthates. Considering that root respiration uses a high proportion of photosynthates (Weiner 1990), any decrease in carbon consumption by the root system would potentially, if reallocated to grain filling, improve yield. Here the carbon consumed in root respiration accounted for 21% of total photosynthates for well watered plants, while it was only 15 and 16%, respectively, for plants in UD and LW treatments. Although water use efficiency and harvest index of well-watered treatment was slightly, but not significantly, lower than that of plants from the UD treatment, the grain yield of former was significantly ($P < 0.05$) lower than the latter. This result suggests that reduced root respiration rate, along with less photosynthates utilized by root respiration, in the early growth season, may have improved crop production under soil drying.

At anthesis in wheat, root biomass, root respiration rate and R/P ratio, for plants in upper drying treatment were all significantly ($P < 0.05$) higher compared with control and the LW treatment. These results indicate that root activity, as expressed by root respiration rate, can recover quickly from drought stress conditions by growing into the wetter soil profile. However, if the demand for increased root growth, into a deeper soil profile, occurred at grain filling, the contribution of root system to grain yield was limited, because the most active metabolic organ or carbon allocation pattern has shifted from root to shoot growth shortly after anthesis. That may reduce grain yield and root biomass as apparent with plants in LW treatment, despite having the highest water use efficiency and harvest index.

Although, there were no difference in water use efficiency and harvest index between UD and CK treatment, the grain yield of UD treatment was significantly ($P < 0.05$) higher than that of CK. This suggests that under soil surface drying, plants can enhance their grain yield through effectively allocation and utilization of carbohydrates.

Conclusion

Spring wheat grain yield was increased by upper drying treatment, but decreased by lower wet treatment, although the water use efficiency and harvest index of latter was significantly ($p < 0.05$) higher than the former. Upper drying decrease the photosynthates utilized by root respiration in early growth season, which make it possible for root to attract and utilize more allocated assimilates as respiratory substrate to provide energy for water uptake in later growth season. However, rooting into deeper soil profile before grain filling was crucial for spring wheat to achieve a successful seed establishment and high grain yield.

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