

The relations of stomatal conductance, water consumption, growth rate to leaf water potential during soil drying and rewatering cycle of wheat (*Triticum aestivum*)

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Abstract. The wheat, *Triticum aestivum*, was used to study the relationships among stomatal conductance, water consumption, and growth rate to leaf water potential during a soil drying and rewatering cycle. Stomatal conductance of wheat steadily decreased with decreases in the days of drying and leaf water potential. Upon rewatering, leaf water potential rapidly returned to the control levels, whereas the reopening of stomata showed an obvious lag time. The length of this lag time was highly dependent on times of the drying and rewatering cycle. The result proved that the drying-rewatering alternation had a significant aftereffect on wheat stomata that could reduce wheat transpiration. The results of the trial showed that the slowly intensified soil water deficiency and the following recovery of soil moisture could decrease the osmotic regulation of wheat, keep wheat leaves turgid and growing under water deficient conditions, and decrease the threshold of leaf water potential below which wheat growth would slow much more rapidly. The fact that, at the same leaf water potential, the wheat growth rate after the recovery of soil moisture was higher than before indicates that the osmotic regulation induced by the drying and rewatering alternation could keep wheat growing and wheat soil water use efficiency significantly increasing under drought conditions. The decreased wheat water consumption mainly resulted from the decreased stomata conductance and transpiration rate. During the recovery of soil moisture, the transpiration through stomata, although wheat growth rate was able to return to normal, did not completely recover. This showed that the drying and wetting alternation had after-effects on wheat growth. Meanwhile, the drying and rewatering alternation increased the ratio of root dry weight to shoot dry weight.

Keywords: Drying; Growth; Leaf water potential; Water consumption; Wheat.

Introduction

Plants usually experience a fluctuating water supply during their life cycle due to continuously changing climatic factors. Even in areas where annual rainfall is high, uneven distribution often exposes plants to periodic soil drying (Liang and Zhang, 1999). The alternate drying-rewatering of soil is the actual situation faced in both dryland and irrigation farming (Shao and Liang, 1999; Siddique et al., 2000). Plants will meet various soil-water deficiencies of varying severities, frequencies, and durations during their growth stages.

These deficiencies, if severe, can injure crops and induce them to adapt with certain physiological and morphological processes (Jones, 1980; Deng and Shan, 1995; Liang and Zhang, 1999; Shan et al., 2000). Understanding

these processes can help us regulate soil moisture through water-saving irrigation, allowing us to avoid the injurious influences of water deficiency, and promote initiation of physiological adaptations during crop growth. This initiation can improve the biological functions of crop roots and leaves during later growing stages, and these improved functions can increase crop yields, crop quality, and water use efficiency to make the dream of high quality, high-yield, and high-profit crop production come true (Liang et al., 2001a). However, little information about the physiological and biochemical mechanisms of recovery from water deficit has been published. Indeed, this area is almost entirely untouched (Boyer, 1995).

This study was designed to investigate the relationship between wheat growth rate, water consumption, and leaf water potential during the drying soil and rewatering cycles so as to understand the mechanisms of raising soil water use efficiency and preventing injurious influences on crops from drying.

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Materials and Methods

Plant Materials and Treatments

Seed of wheat (*Triticum aestivum*) was germinated in moist sand at 20–24°C. After 3 days, germinated seedlings were transplanted into plastic pots (24 cm in high, 18 cm in diameter), filled with John Innes No. 2 composted soil, and transferred to a greenhouse at the top of plants and temperatures of 28/23°C light/dark, a photosynthetic active radiation (PAR) flux density of 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (enhanced by high pressure sodium lamps) and a photoperiod of 16 h. Plants were irrigated with tap water daily and supplemented with Hoagland nutrient solution 1/2 strength weekly. The soil was composed of loam, peat and coarse sand in a 7:3:2 volume ratio, and NPK (15:15:15) fertilizer was added. Field capacity of the soil was measured at about 0.31 g water g⁻¹ dried soil, and permanent wilting point (at -1.5 MPa soil water potential) at -0.07 g water g⁻¹ dried soil.

The seedlings were well supplied with water until the drying-rewatering alternation began, at which time they had 3–4 leaves or growth were three weeks. 90 uniform-sized (6 plants per pot) and well-grown wheat plants were chosen for experiment. The drying and rewatering cycle began with the irrigation for the treated pots stopped. From then on, the soils of the treated pots were left to dry. When soil drying satisfied the requirement of the treatment of the drying-wetting alternation, 300 ml of water was added to each of the treated pots, and then the soil was left to dry again. This process was repeated twice in the treatment of the drying-wetting alternation. Meanwhile, 100 ml of water was added to each of the control pots every day from the beginning to the end of the treatment. The treatment lasted 22 days, and all the concerned items were determined on schedule everyday during the 22 days.

Determination of Wheat Water Parameters and Consumption

The leaf water potentials and osmotic potentials of wheat were measured with a Model 3005 pressure chamber and a Wescor 5500 vapor pressure meter, respectively. The leaf pressure potentials were equal to the leaf water potential minus the leaf osmotic potential, and the method of measuring the relative leaf water content was what appeared in references (Gao, 2000). For all these leaf measurements, five wheat leaves were chosen from both the control and the treated pots.

The procedure to determine wheat water consumption was as follows: After each addition of water to the pots, the soil surfaces of the pots were closely covered or sealed with aluminum foil. Twelve plants were taken from two control and treated pots, respectively, from 11:30 to 13:30 everyday, and their water consumptions (g plant⁻¹ h⁻¹) were measured by a balance with an accuracy of 1/1000 g. The stomata conductance and wheat transpiration rate were measured with a Licor-1600 steady state porometer, and five wheat leaves were chosen from each of the control and treated pots for the measurements.

Determination of Wheat Relative Growth Rate and Biomass

The relative leaf growth rate of wheat was calculated with wheat leaf lengths. For the calculation, the growing leaves of ten plants were chosen from the control and the treated pots, respectively, and their leaf lengths were measured on schedule with a ruler everyday. The formula to calculate the relative leaf growth rate of wheat was $\text{RGR} = 1/L_0 \cdot dL/dt$, in which L_0 stood for the leaf lengths of selected plants at the beginning of the treatment (or leaf length of before 24 h everyday) and dL/dt stood for the length increments of selected wheat leaves per day during the treatment. For the measurement mean of biomass of per plant, 12 wheat plants were taken from two control and the treated pots, respectively, and the plants were dried at 105°C. Next, the weights of the dried plants were measured and averaged as the biomass per wheat plant (g). The water consumption of wheat approximated the sum of the water amounts added to the pots each time seedlings growth period. So the total water use efficiency of wheat was equal to the biomass per wheat plant/ the water consumption per wheat plant.

Results and Discussion

Effects of the Drying-Wetting Alternation on Wheat Water Parameters and Growth Rate

The data determined showed that the plants of the control pots had a good water supply for their growth, and thus their leaf water potential (ψ_w) always fluctuated within -0.4~-0.5 MPa during the trial. The leaf water potential of the treated pots, however, changed rather sharply depending on their soil water content (Table 1). The leaf water potential of the treated pots declined to -1.3 MPa on the seventh day of the first drying spell, recovered to -0.5 MPa 24 h after the second addition of water to the treated pots, and declined again to -1.5 MPa on the seventh day of the second drying spell. So the leaf water potential of the treated pots varied significantly with the drying and wetting alternated. The leaf osmotic potential of the treated pots changed with drying and watering alternating in a manner similar to the leaf water potential of the treated pots and declined to a very low level of -1.8 MPa at the end of the third drying spell. The leaf osmotic potential of the treated pots did not differ much from the leaf water potential of the treated pots during the first two drying spells, but during the third drying spell the former declined significantly with the leaf relative water content of the treated pots keeping at a rather high level of 78%, indicating that the leaves of the treated pots experienced an osmotic regulation through the treatment. The leaf turgor of the treated pots remained high during the third drying spell, and the maintenance of this turgor was the prerequisite to a certain leaf growth rate. At the same drying temperature, the leaf growth rate of the treated pots remained obviously higher during the third drying spell than during the first two drying spells. The comparison of the relative leaf water contents and the leaf osmotic potentials indicated that

Table 1. Effects of the drying-rewatering alternation on wheat (*Triticum aestivum*) water parameters and growth rate.

Drying-wetting alternation	The first drying spell ^a					The second drying spell					The third drying spell				
	0	1	3	5	7	9	11	13	14	15	17	19	21		
Relative water content (%) ^b	91±2.1	90±2.5	87±2.0	83±2.1	73±1.9	90±2.2	83±1.8	73±2.0	72±2.6	90±3.1	89±1.9	85±2.0	78±1.7		
Leaf water potential (MPa)	-0.4	-0.5	-0.6	-0.9	-1.3	-0.6	-0.9	-1.2	-1.5	-0.6	-0.9	-1.0	-1.5		
Leaf osmotic potential (MPa)	-0.6	-0.7	-0.9	-1.0	-1.4	-0.8	-1.2	-1.3	-1.5	-0.9	-1.1	-1.5	-1.8		
Leaf turgor (MPa)	0.2	0.2	0.3	0.1	0.1	0.2	0.3	0.1	0.0	0.3	0.4	0.5	0.3		
Relative leaf growth rate (mm/cm·day)	-	0.33±0.03	0.26±0.02	0.20±0.01	0.05±0.01	0.35±0.01	0.22±0.02	0.11±0.01	0.07±0.00	0.36±0.04	0.31±0.02	0.25±0.02	0.10±0.01		

^aThe first, second and third spell is duration of drying 0-7, 8-14 and 15-21, rewatering in the morning of the 8th and 15th day, respectively.^bData in table are means±SE (n=5). Data of relative leaf growth rate are means±SE (n=10).**Table 2.** Effects of the drying-wetting alternation on the stomata conductivity and transpiration of wheat (*Triticum aestivum*).

Drying-wetting alternation	The first drying spell ^a					The second drying spell					The third drying spell				
	0	1	3	5	7	9	11	13	14	15	17	19	21		
Stomata conductance	Control	170±9	168±7	158±8	166±6	167±9	169±8	151±6	166±8	160±7	171±6	164±9	155±8	174±5	
(mmol/m ² ·s)	Treated	170±7	163±8	142±7	123±6	58±8	131±9	94±7	40±5	38±5	117±6	94±6	56±6	49±5	
Transpiration rate	Control	3.40±0.45	3.07±0.34	2.90±0.31	2.69±0.28	3.05±0.33	2.89±0.40	2.98±0.25	3.16±0.44	2.67±0.24	2.96±0.41	3.05±0.3	3.17±0.33	3.20±0.31	
(mmol/m ² ·s)	Treated	3.40±0.45	3.12±0.32	2.54±0.28	2.01±0.21	1.32±0.22	2.55±0.31	2.07±0.26	1.08±0.18	0.82±0.16	1.11±0.15	0.92±0.1	0.75±0.10	0.45±0.11	

^aThe first, second and third spell is duration of drying 0-7, 8-14 and 15-21, rewatering in the morning of the 8th and 15th day, respectively.^bData in table are means±SE (n=10).

the leaf growth rate of the treated pots decreased as the leaf water potential of the treated pots decreased. When the growth rates started to decrease sharply during the three drying spells, the leaf water potentials were -0.9 MPa, -1.2 MPa and -1.5 MPa, respectively. The leaf water potential at which the leaf growth rate started to decline sharply had a tendency to decrease as the drying and wetting alternation went on. This proved that a leaf osmotic regulation existed. At the same leaf water potentials, the leaf growth rate during one drying spell was obviously higher than that during the one before the drying spell. This proved that the osmotic regulation induced by the drying-wetting alternation could make wheat continue to grow under water-deficit conditions.

Effects of the Drying-Wetting Alternation on the Stomata Conductance and Transpiration of Wheat

Data in Table 2 show that the stomata conductance of the control pots always varied between 150 mmol m⁻²·s⁻¹ and 170 mmol m⁻²·s⁻¹ and the transpiration rate of the control pots always changed within about 3.0 mmol m⁻²·s⁻¹. The stomata conductance of the treated pots varied significantly with drying and wetting alternated. While the leaf potential of the treated pots declined, the stomata conductance and transpiration rate of the treated pots significantly decreased (Table 2). At the end of the first drying spell, the stomata conductivity and transpiration rate of the treated pots decreased to 58 mmol m⁻²·s⁻¹ and 1.12 mmol m⁻²·s⁻¹, respectively. They did not recover as high as those of the leaves of the control pots 24 h after the second addition of water to the treated pots, but recovered, respectively, to 120 mmol m⁻²·s⁻¹ and 2.33 mmol m⁻²·s⁻¹ 48 h after the second addition of water to the treated pots. The stomata conductance of the treated pots gradually decreased to 38 mmol m⁻²·s⁻¹ until the seventh day of the second drying spell and rose to 108 mmol m⁻²·s⁻¹ and 117 mmol m⁻²·s⁻¹ 24 h and 48 h, respectively, after the third addition of water to the treated pots. All of this proves that the drying-wetting alternation had a significant aftereffect on wheat stomata that could reduce the wheat transpiration rate (Fischer et al., 1970).

Effects of the Drying-Rewatering Alternation on Wheat Water Consumption

According to the data in Table 3, the water amount of wheat transpiration of the treated pots decreased as the drying was intensified (the first, third and fifth days of a drying spell). The wheat water consumption of the treated pots during the first drying spell was higher than that of the treated pots during the second drying spell, which was in turn higher than that during the third drying spell. The wheat water consumption of the treated pots per day differed sig-

Table 3. Effects of the drying and rewatering cycle on wheat (*Triticum aestivum*) water consumption^a.

	Day after drying treatment 1st	Day after drying treatment 3rd	Day after drying treatment 5th
Control	1.980	2.021	2.173
The first spell	1.910a	0.942a	0.445a
The second spell	1.512b	0.862b	0.323b
The third spell	1.336c	0.776c	0.218c

^aValues are means of two pots of 12 plants for control and treatment.

^bLetter following numbers indicate statistical significance within the same day of drying at $P_{0.05}$ level using Duncan's multiple range test.

nificantly among the three drying spells. The wheat consumption of the control pots highly surpassed that of the treated pots because the plants of the control pots had a sufficient water supply. As the drying and wetting alternation went on, the water consumption per plant of the treated pots had a decreasing tendency that might be correlated with decreased stomata conductance and transpiration rate (Liang et al., 2001a,b).

Effects of the Drying-Rewatering Alternation on Wheat Biomass and Total Water Use Efficiency

It can be clearly seen from the data in Table 4 that the wheat water consumption of the control pots was higher than that of the treated pots; the wheat biomass of the control pots was slightly lower than that of the treated pots, the amount of wheat dry matter of the treated pots formed with 1 kg of water significantly increased compared with that of the control pots, and the ratio of dry root weight to the dry weight of the former markedly increased compared with that of the latter. So the drying-wetting alternation not only favored the raising of wheat water use efficiency, it helped wheat to form a well-developed root system for kernel formation during its later growing stage (Zhang et al., 1998; Zhang et al., 2001)

Conclusions

Our results showed that the slowly intensified soil water deficiency during the time when wheat had 3-4 leaves and the following recovery of soil moisture was able to decrease the osmotic regulation of wheat, keep wheat leaves turgid and growing under water deficient conditions, and decrease the threshold of leaf water potential below which wheat growth would slow much more rapidly. The fact that at the same leaf water potentials, the wheat growth rate after the recovery of soil moisture was higher than before the recovery of soil moisture indicated that the osmotic regulation induced by the drying and wetting alternation could keep wheat growing under drought conditions.

Stomatal conductance of wheat steadily decreased with decreases in days of drying and leaf water potential. Upon rewatering, leaf water potential rapidly returned to the control levels, whereas the reopening of stomata showed an obvious lag time. The length of this lag time was highly dependent on times of drying and the rewatering cycle.

Table 4. Effects of the drying-wetting alternation on wheat biomass and total water use efficiency (g/plant).

Items ^a	Control	Treatment ^d
All water consumption per plant ^b	756a	487b
Biomass		
Shoot weight	2.830a	2.181b
Root weight	0.368	0.338
Total biomass	3.198a	2.519b
Ratio of Root weight to shoot weight	0.130	0.155
Water use efficiency (g/kg) ^c	4.23a	5.17b

^aValues are means of two pots of 12 plants for control and treatment.

^bLetter following numbers indicate statistical significance within the same day of drying at $P_{0.05}$ level using Duncan's multiple range test (n=12, 2 pots of 12 plants).

^cData of water use efficiency in table are from total biomass / all water consumption per plant.

^dData were determined in 3rd drying spell and all test finished.

The result proved that the drying-rewatering alternation had a significant aftereffect on wheat stomata that could reduce wheat transpiration. Although the drying and rewatering alternation decreased wheat biomass to some extent, wheat water consumption decreased rather sharply, and wheat soil-water use efficiency significantly increased. The decreased wheat water consumption mainly resulted from the decreased stomata conductance and transpiration rate. During the recovery of soil moisture, the transpiration rate through stomata, although wheat growth rate could return to normal, did not completely recover. This showed that the drying and wetting alternation had after-effects on wheat growth. Meanwhile, the drying and rewatering alternation increased the ratio of dry root weight to dry weight shoot. These effects of the drying and wetting alternation on wheat production could play an important role in kernel formation, drought tolerance, kernel-filling maintenance, and improvement of wheat.

Results of this research can be used as a guide to water-saving irrigation, to artificially regulating the supply of irrigation water and the time of irrigation, and to using a drying and rewatering alternation to enhance the osmotic regulation and compensative functions of crops. It is hoped our findings will finally allow us to realize the goal of high-yield, high-efficiency, high-quality crop production and saving water.

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土壤乾濕循環過程中小麥葉片氣孔導度、耗水量、生長速率 與葉水勢的關係

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在土壤乾濕循環過程中研究了小麥 (*Triticum aestivum*) 葉水勢與氣孔導度、生長速率和耗水量的變化，每次復水後葉水勢迅速恢復而氣孔導度表現出滯後現象，滯後時間隨乾濕交替次數增加而增加，氣孔的這種後效明顯的降低了小麥葉蒸散作用。實驗結果表明在緩慢乾旱後復水，小麥葉片的滲透勢明顯低於一直濕潤條件下，這有利於保持葉片膨壓而維持乾旱下小麥葉片的生長速率，使葉片生長速率快速下降的葉水勢閾值降低，在相同葉水勢下經乾濕交替的小麥葉片生長速率快於未經交替脅迫的葉片，證明乾濕交替能夠誘導小麥葉片的滲透調節能力，經 2-3 次乾濕循環後耗水量的下降，主要是由於氣孔導度的下降和蒸散速率的下降，並使水分利用效率提高，小麥生長速率恢復到了對照水平，但總的生長小於對照，這表明乾濕交替過程能夠對小麥生長、氣孔行為、耗水過程產生後效，同時能夠使根冠比增加。

關鍵詞：葉水勢；耗水量；生長；乾旱；小麥。