CHAPTER I*

GROWTH AND PHYSIOLOGICAL RESPONSES OF TALL FESCUE TO SURFACE SOIL DRYING

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ABSTRACT

Drought stress often occurs in soil surface although water may be adequate deeper in the soil profile. The objective of this study was to investigate physiological responses of tall fescue (*Festuca arundinaceae* Schreb.) to surface soil drying. Such information is important for further understanding of drought resistance mechanisms in turfgrasses. Plants were grown in a greenhouse in split polyvinyl chloride tubes consisting of two sections (each 10 cm in dia., 20 cm long). Plants were subjected to three soil moisture treatments: a) well watered control: the whole soil profile (40 cm) was well watered; b) surface soil drying: the surface 20 cm of soil was allowed to dry down by withholding irrigation and the lower 20 cm was watered; c) full drying: the whole soil profile (40 cm) was allowed to dry down. Surface soil drying generally had no effects on turf quality and leaf relative water content (RWC), except at 15 d for turf quality and 17 d for RWC. Canopy net photosynthetic rate (Pn) of surface–dried plants increased to the maximum level at 11:00 h and decreased at 15:00 h, following the same diurnal pattern as well-watered plants. Also, the absolute levels of Pn were not significantly different between surface drying and control treatment during the day. Leaf growth rate (LGR) of surface-dried plants decreased to below the control level, beginning at 8 d of treatment. Canopy respiration rate (R_{canopy}) and root respiration rate (R_{root}) of surface-dried plants were lower than those of the control. Root to shoot ratio (R/S) and the proportion of roots in the deeper soil layer increased with surface drying. These results suggest that when water was sufficient for plant uptake in the deeper soil profile, tall fescue could adapt to surface soil drying gradually by developing deeper roots and lowering canopy and root respiration. Full drying, however, had adverse effects on all the physiological parameters.

ABBREVIATIONS:

LGR, leaf growth rate; LSD, least significance difference; Pn, canopy photosynthetic rate; R_{canopy}, canopy respiration rate; R_{root}, root respiration rate; R/S, root to shoot dry weight ratio; RWC, relative water content.

INTRODUCTION

Surface soil is often dry, although water may be sufficient for plant uptake deeper in the soil profile in natural environments. Drying of the upper portion of the soil profile has a profound impact on root functionality and growth in some plant species (Henson et al., 1989; Jensen et al., 1989; Smucker et al., 1991). In contrast, other species can maintain favorable water status and growth despite large portions of the root system being in dry soil (Sadras et al., 1993; Gallardo et al., 1994; Melkonian and Wolfe, 1995; Zhang and Kirkham, 1995; Huang et al.,1997). Huang et al. (1997) examined responses of several warm-season turfgrasses to surface soil drying and found that shoot growth and leaf water status were not affected for relatively drought-tolerant, deep-rooting species such as buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.], centipedegrass [*Eremochloa ophiuroides* (Munro) Hack.], and seashore paspalum (*Paspalum vaginatum* Swartz.), but were reduced for relatively drought-sensitive, shallow-rooting zoysiagrass (*Zoysia japonica* Steud.) and bermudagrass (*Cynodon dactylon* L.).

Previous studies have shown that plant adaptability to surface soil drying could be partially attributed to maintenance of water status by utilizing available water deeper in the soil profile via deep roots (Caldwell and Richards, 1987; Huang, 1998b). Blum and Johnson (1992) found that water absorbed by roots of wheat [*Triticum aestivum* L.] in deeper moist soil could be transported to the upper drying soil at night to maintain viable roots and nutrient uptake, suggesting that growth can be maintained by efficient water use when water availability is limited in surface soil.

Tall fescue has an extensive, deep root system and has been considered as a good drought avoider (Carrow, 1996). Extensive root development is beneficial for water uptake, but requires a large amount of carbon investment. Under drought stress conditions, the rate of photosynthesis often is limited (Stoneman et al., 1994). Therefore, efficient carbon expenditure and water use would prolong plant survivability in drying soil (Sisson, 1989). Bryla et al. (1997) reported that citrus, a drought-tolerant, tropical evergreen, down-regulates root respiration rates when grown in drying soil. Physiological mechanisms of tall fescue adaptation to surface soil drying are not well documented. Understanding growth and physiological responses of tall fescue to surface soil drought stress is important for developing drought-resistant turfgrass species or cultivars.

The present study was designed to investigate how tall fescue responds to surface soil drying when a small proportion of the root system is exposed to moist soil deeper in the profile.

MATERIALS AND METHODS

Plant Materials and Growth Conditions

Sod pieces of 'Falcon II' tall fescue were collected from field plots and transplanted into split polyvinyl chloride tubes consisting of two sections (each 20 cm long, 10 cm in diameter) filled with autoclaved fritted clay (Profile, ALMCOR, Deerfield, IL) and kept in a greenhouse. Fritted clay is a granular material made of firing coarsely milled, dry clay in a rotary kiln. It was used as a growing medium for the following reasons (van Bavel et al., 1978): it has a relatively low dry-bulk density; drains very rapidly; retains a large quantity of plant-available water; can be easily washed off the roots; and contains no organic matter, which minimizes the confounding effects on root respiration by soil microbial respiration.

The split PVC tubes consisted of two sections, each 20 cm in length. The two sections of the PVC tubes were taped externally with duct tape to hold the columns in place. Four drainage holes (5 mm in diameter) were drilled on the side wall at the bottom of each section to allow drainage of excess water and soil aeration. The holes were plugged during root respiration measurements. Soil layers in all three treatments were separated hydraulically with waxed paper and a sheet of nylon screen coated with Vaseline, which allowed root penetration but minimized water and gas exchanges between the top and bottom soil layers. This technique also provided a suitable system for simulating the field situation in which only the surface soil layers dry down, while enabling plant response to soil drying to be examined under controlled conditions. Drip irrigation tubes were positioned about 2 cm beneath the soil surface in each layer to allow separate irrigations, which were automated with a pressure and flow controller. Water content and temperature in each soil layer were monitored hourly using the dual-probe, heat-pulse technique (Tarara and Ham, 1997). Two probes (28 mm long) were buried horizontally at 10 and 30 cm soil depths in each split PVC tube.

Plants were grown in the PVC tubes for about 60 d, allowing roots to penetrate and establish in the bottom section before treatments were imposed. During this period, tubes with plants and with soil only were watered on alternate days until water drained freely from the holes on the side walls at the bottom of each section and were fertilized weekly with full-strength Hoagland's solution (Hoagland and Arnon, 1950). Turf was hand clipped weekly at about 4 cm height. Plants were maintained in a greenhouse, with daily maximum/minimum temperatures of 24°C/18°C and a 16-h photoperiod. The light regime in the greenhouse was supplemented with 1 kw metal halide lamps. Photosynthetically active radiation on a horizontal plane just above the canopy at 12:00 h averaged 900 μmol m^{-2} s^{-1}.

Treatments

The experiment consisted of three soil moisture treatments. A) Control: water content in the entire soil profile was maintained at field capacity (25%, v/v) by watering every other day. During the experimental period, soil water content ranged from 80 to 100% of field capacity. B) Upper drying: the surface 20 cm of soil was allowed to dry down by withholding irrigation, while the lower 20 cm of soil was maintained at field capacity by drip irrigation. At the end of the treatment, the surface soil was very dry, with a water content of only about 5% (v/v), whereas water content was about 80% of field capacity in the bottom 20 cm of soil. C) Full drying: the whole soil profile (40 cm) was allowed to dry down by withholding irrigation. At the end of this treatment, soil water contents in both layers were only 5% (v/v). The configuration of split PVC tubes and treatment set-up have been presented in Huang and Fu (2000).

Measurements

Turf quality was rated visually based on color, density, and uniformity using a scale of 0 (brown, dry turf) to 9 (green, turgid turf), with a rating of 6.0 or higher indicating acceptable quality.

Leaf relative water content (RWC) was calculated based on leaf fresh weight, dry weight, and weight of leaves at full turgor after soaking in water for 24 h at room temperature (22 °C).

Leaf growth rate (LGR) was estimated by the difference in turf canopy height before and after cutting in two-day intervals. A sheet of paper was rested on the canopy surface to measure canopy height as the distance from the paper to plant base. Canopy height was measured in four positions in each tube.

Canopy photosynthetic rate (Pn), canopy respiration rate (R_{canopy}), and root respiration rate (R_{root}) in the top 20 cm soil were measured from 7:00 to 21:00 h at 17 and 28 d of treatment with a LI-6400 portable gas exchange system (LICOR Inc., Lincoln, NE) following the method described in Huang and Fu (2000). Pn and R_{canopy} were measured by enclosing the whole canopy in a transparent plexiglass chamber (15×10×10 cm). The chamber was covered by an opaque box to exclude light exposure of the canopy during respiration measurement. The canopy chamber was attached to the CO_2 analyzer of the LI-6400 gas exchange system. Pn and R_{canopy} were expressed as CO_2 uptake and evolution per unit canopy area, respectively.

Root respiration rate in the upper 20 cm soil layers was measured by monitoring changes in the concentration of CO_2 in the air stream pumped out from this soil layer with the LI-6400 gas exchange system using the method of Bouma et al. (1997) with modification (Huang and Fu, 2000). Prior to R_{root} measurements, the gas in the soil was mixed and circulated inside for about an hour using a circulating pump. During the measurement, soil gas was diverted into LI-6400 CO_2 analyzer to determine changes in CO_2 concentration.

At the end of the experimental period (42 d), shoots and roots were harvested. Roots in each soil layer were washed free of soil. Both shoots and roots were dried in an oven at 85 °C. Root and shoot dry weights were determined, and root to shoot biomass ratio (R/S) was calculated.

Experimental Design and Statistical Analysis

Soil moisture treatments each with four replications were arranged in a completely randomized design. Treatment effects were determined by analysis of variance according to the general linear model procedure of the Statistical Analysis System (SAS Institute In., Cary, NC). Differences among treatment means were separated by least significant difference (LSD) at the 0.05 level of probability.

RESULTS

Turf quality in the surface-drying treatment was maintained at the same level as that in the well-watered control during most of the experimental period, except at 15 d of treatment (Fig. 1). When the soil profile was fully dried, turf quality decreased below the control level, beginning at 14 d.

Leaf RWC of surface-dried plants was not different from that of control plants at 7 d, decreased to below the control level at 17 d, and recovered at 28 d (Table 1). Full drying reduced RWC at 17 and 28 d. By 28 d of full drying, the majority of leaves became permanently wilted and brown, whereas surface-dried plants maintained green and turgid leaves, similar to control plants.

Leaf growth rate decreased with surface and full drying, starting at 9 d (Fig. 2). The LGR of surface-dried plants recovered to about 50% of the control level by 30 d of drying. The LGR of fully dried plants continued to decline to near zero at 16 d. LGR of surface-dried was significantly higher after 16 d.

Figures 3, 4, and 5 shows diurnal changes in Pn, R_{canopy}, and R_{root} at 17 d of treatment which followed the same pattern as at 28 d (data not shown). No significant difference in canopy Pn was observed between control and surface-dried plants during the day. Canopy photosynthesis rates of control and surface-dried plants increased to the maximum level at 13:00 h and declined thereafter (Fig. 3). Canopy Pn of fully dried plants remained at a constant level lower than that of surface-dried and well-watered plants during most time of the day, except at 7:00 and after 19:00 h.

R_{canopy} of control plants peaked at 17:00 h and then declined (Fig. 4). R_{canopy} values of surface-dried and fully dried plants remained relatively constant during the day, but were lower than that of control plants. Fully dried plants had lower R_{canopy} than surface-dried plants.

Root respiration rates of surface-dried and c ontrol plants did not exhibit apparent diurnal patterns in any treatment (Fig. 5). However, R_{root} for fully dried plants increased to the highest level at 13:00 h and then decreased rapidly in the afternoon. The R_{root} values of surface and fully- dried plants were lower than that of well-watered controls during the day.

Shoot dry weight decreased with surface and full drying, but to a greater extent with full drying (Fig. 6). However, plants in surface-dried soil had significantly higher root dry weight than control plants in both soil layers. With surface soil drying, the proportion of roots dry weight decreased in the top 20 cm soil, but increased in the lower 20 cm. With full drying, root dry weight in the top 20 cm of soil was not affected, but decreased in the lower 20 cm soil. Both surface soil drying and full drying significantly increased the R/S ratio, compared to the well-watered control (Fig. 7). No difference in the R/S ratio was detected between the two drying treatments.

DISCUSSION

Turf quality and leaf water content declined only during the initial period of surface drying. With prolonged surface drying, turf quality and leaf water status recovered to the same levels as control plants, despite half of the soil volume or the majority of roots (80%) being exposed to drying conditions. However, when the entire root systems were exposed to drying soil, turf quality, water status, and photosynthetic rate declined dramatically, although tall fescue is considered as a good drought-resistant species (Beard, 1973). These results suggest that watering is required to maintain quality turf, but frequent wetting of surface soil may not be necessary for tall fescue as long as water is available deeper in the soil profile.

The lack of effects of surface drying on turf quality, water relations and photosynthesis may have been due to the development of a relatively large root system following a prolonged period of surface drying. Root to shoot biomass ratio increased under drying conditions. This suggested that a relatively larger root system provided water and nutrients to support a relatively smaller canopy, which is conductive to plant adaptation to drought stress (Chartzoulakis et al., 1993; Xu and Bland, 1993; Carrow, 1996; Huang, 1998a). Furthermore, the absolute amount of roots in the deeper moist soil increased with surface soil drying, which could facilitate water uptake and contribute to the maintenance of turf quality, leaf water status, and canopy Pn.

Huang and Fu (2000) reported that canopy and root respiration rates of tall fescue decreased after about 8 d of surface and full drying. In the present study, canopy and root respiration rates remained at lower levels during the day under surface and full drying than under well-watered conditions. Because respiratory costs represent a major carbon expenditure of plants (Lambers et al., 1982; Lambers 1987), maintaining low respiration rate when water and nutrient uptakes are minimum in drying soil also may increase the possibility of plant survival during extended drought periods (Sisson, 1989; Dhopte and Ramteke, 1991).

Leaf growth rate and shoot dry weight, unlike turf quality, water status, and photosynthesis, decreased with surface soil drying. Although LGR recovered somewhat after a prolonged period of surface soil drying, it was still lower than the control levels. Several other split-root studies also found that leaf growth rates were reduced even though leaf water potential and turgor of the half-watered plants were no lower than those of well-watered plants (Zhang and Davies, 1987, 1989; Blum and Johnson, 1992; Zhang and Kirkham, 1995). These results suggest that soil drying influences plant growth not only by supplying water, but possibly by nonhydraulic signals transmitted to leaves from roots. Abscisic acid (ABA) in roots has been found to be the chemical messenger that mediates plant responses to drought (Zhang and Davies, 1987, 1989). Water-stressed roots accumulate ABA and transport it to leaves quickly, which inhibits leaf growth (Creelman et al., 1987; Zhang and Davies, 1989).

In summary, the results demonstrated that tall fescue was able to adjust root to shoot relations, root distribution patterns, and carbon expenditure to sustain water status, photosynthesis, and acceptable turf quality in soils with heterogeneous moisture. Leaf growth and shoot dry matter production decreased with surface drying, which actually could be desirable in terms of reducing mowing. However, drying of the entire soil profile should be prevented to maintain vigorous turf of tall fescue.

REFERENCES

Beard, J.B. 1973. Turfgrass: science and culture. Prentice Hall, Inc., Englewood Cliffs, NJ.

Blum, A, and J.W. Johnson. 1992. Transfer of water from roots into dry soil and the effect on water relation and growth. Plant and Soil 145:141-149.

Bouma, T.J., K.L. Nielsen, D.M. Eissenstat, and J.P. Lynch. 1997. Estimating respiration of roots in soil: interactions with soil CO_2, soil temperature and soil water content. Plant and Soil 195: 221-232.

Bryla, D.R., T.J. Bouma, and D.M. Eissenstat. 1997. Root respiration rate in citrus acclimates to temperature and slows during drought. Plant Cell and Envir. 20:1411-1420.

Carrow, R.N. 1996. Drought avoidance characteristics of diverse tall fescue cultivars. Crop Sci. 36 (2): 371-377.

Chartzoulakis, K., B. Noitsakis, and I. Therios. 1993. Photosynthesis, plant growth and dry matter distribution in kiwifruit as influenced by water deficits. Irrigation Sci. 14:1-5.

Creelman, R.A., D.A. Gage, J.T. Stults, and J.A.D Zeevaart. 1987. Abscisic acid biosynthesis in leaves and roots of sunflower. Plant Physiol. 85:726-732.

Dhopte **A.**M. and S.D. Ramteke. 1991. Relative changes in root growth and root respiration in drought tolerant and susceptible genotypes of peanut under field conditions. Ann. Plant Physiol. 5:213-217.

Gallardo,M., N.C. Turner, and C. Ludwig. 1994. Water relations, gas exchange and abscisic acid content of *Lupinus cosentinii* leaves in response to drying different proportions of the root system. J. Exp. Bot. 45:909-918.

Henson, I.E., C.R.Jensen, and N.C. Turner. 1989. Leaf gas exchange and water relations of lupins and wheat. I. Shoot responses to soil water deficits. Aust. J. Plant Physiol. 16 (5):401-413.

Huang, B., R.R. Duncan, and R.N. Carrow. 1997. Drought-resistance mechanisms of seven warm-season turfgrasses under surface soil drying. II. Root aspects. Crop Sci. 37(6): 1863-1869.

Huang, B., J. D. Fry, and B. Wang. 1998a. Water relations and canopy characteristics of tall fescue cultivars during and after drought stress. HortScience 33 (5): 837-840.

Huang, B., and J.D. Fry. 1998b. Root anatomical, physiological, and morphological responses to drought stress for tall fescue cultivars. Crop Sci. 38 (4): 1017-1022.

Huang, B.R., and J. Fu. 2000. Photosynthesis, respiration, and carbon allocation of two cool-season perennial grasses in response to surface soil drying. Plant and Soil. 227:17-26

Jensen, C.R., I.E.Henson, and N.C.Turner.1989. Leaf gas exchange and water relations of lupins and wheat. II. Root and shoot water relations of lupin during drought-induced stomatal closure. Aust. J. Plant Physiol. 16 (5): 415-428.

Lambers, H. 1987. Growth, respiration, exudation and symbiotic associations: the fate of carbon translocated to the roots. Semin. Ser. Soc. Exp. Biol. (30): 125-145.

Lambers, H.; R.J. Simpson, V.C. Beilharz, and M.J. Dalling. 1982. Growth and translocation of C carbon and N nitrogen in wheat (Triticum aestivum) grown with a split root system. Physiol-Plant. 1982. 56 (4): 421-429.

Melkonian, J., and D.W. Wolfe. 1995. Relative sensitivity of leaf elongation and stomatal conductance of cucumber plants to changes in leaf and soil water potentials. Can. J. Plant Sci. 75 (4): 909-915.

Sadras, V.O., F.J. Villalobos, and E. Fereres, 1993. Lead expansion in field-grown sunflower in response to soil and leaf water status. Agron. J. 85 (3): 564-570.

Sisson W.B. 1989 Carbon balance of *Panicum coloratum* during drought and non-drought in the northern Chihuahuan Desert. J. Ecol. 77:799-819.

Smucker, S.J.M., A. Nunez-Barrios, and J.T.Ritchie. 1991. Root dynamics in drying soil environment. Belowground Ecol. 1:1-5.

Stoneman, G.L., N.C. Turner, and B. Dell. 1994. Leaf growth, photosynthesis and tissue water relations of greenhouse-grown *Eucalyptus marginata* seedlings in response to water deficits. Tree Physiol. 14: 633-646.

Tarara, J.M., and J.M. Ham. 1997. Measuring soil water content in the laboratory and field with dual-probe heat-capacity sensors.Agron J. 89 (4): 535-542..

Xu, X., and W.L. Bland. 1993. Resumption of water uptake by sorghum after water stress. Agron. J. 85:697-702.

Zhang, J., and W.J. Davies. 1987. Increased synthesis of ABA in partially dehydrated root tips and ABA transport from roots to leaves. J. Exp. Bot. 38:2015-2023.

Zhang, J., and W.J. Davies. 1989. Abscisic acid produced in dehydrating roots may enable the plant to measure the water stress status of the soil. Plant Cell and Envir. 12: 73-81.

Zhang, J., and M.B. Kirkham. 1995. Water relations of water-stressed, split-root C_4 (*Sorghum bicolor,* Poaceae) and C_3 (*Helianthus annuus*, Asteraceae) plants. Am. J. Bot. 82:1220-122.

Table 1. Leaf relative water content (RWC) response to drought stress.

Treatments	Days of treatment		
	7	17	28
Control	97.8 a*	98.3 a	97.4a
Surface drying	94.9 a	86.2 b	92.1 a
Full drying	95.4 a	66.03 c	52.87b

*Means within a column followed by the same letters are not significantly different based on LSD (P=0.05) test.

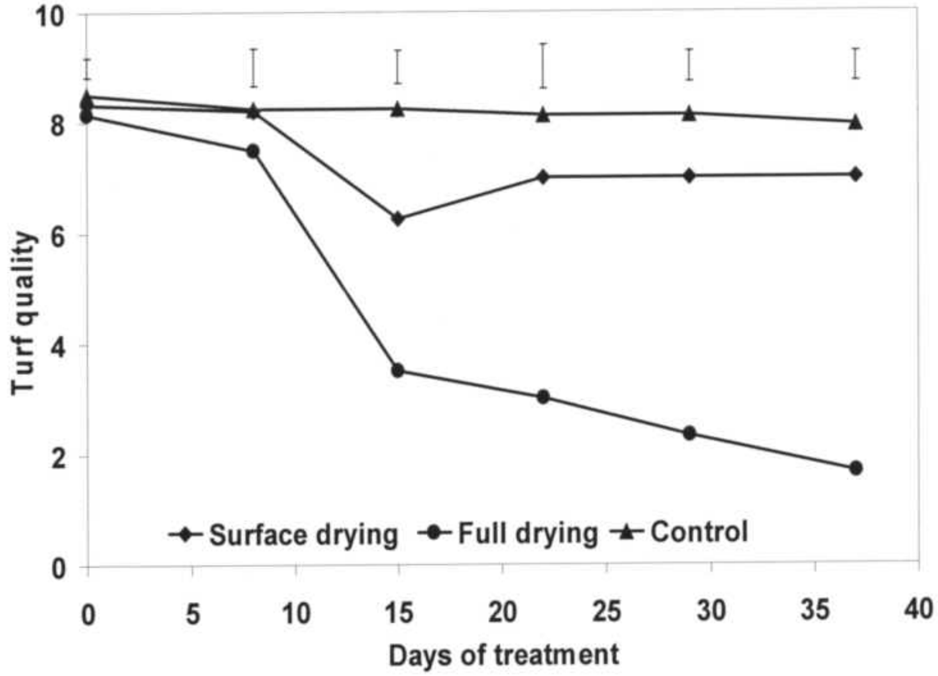

Fig. 1. Turf quality of tall fescue in response to soil drying. Vertical bars are LSD values (P=0.05) for treatment comparisons at a given day of treatment

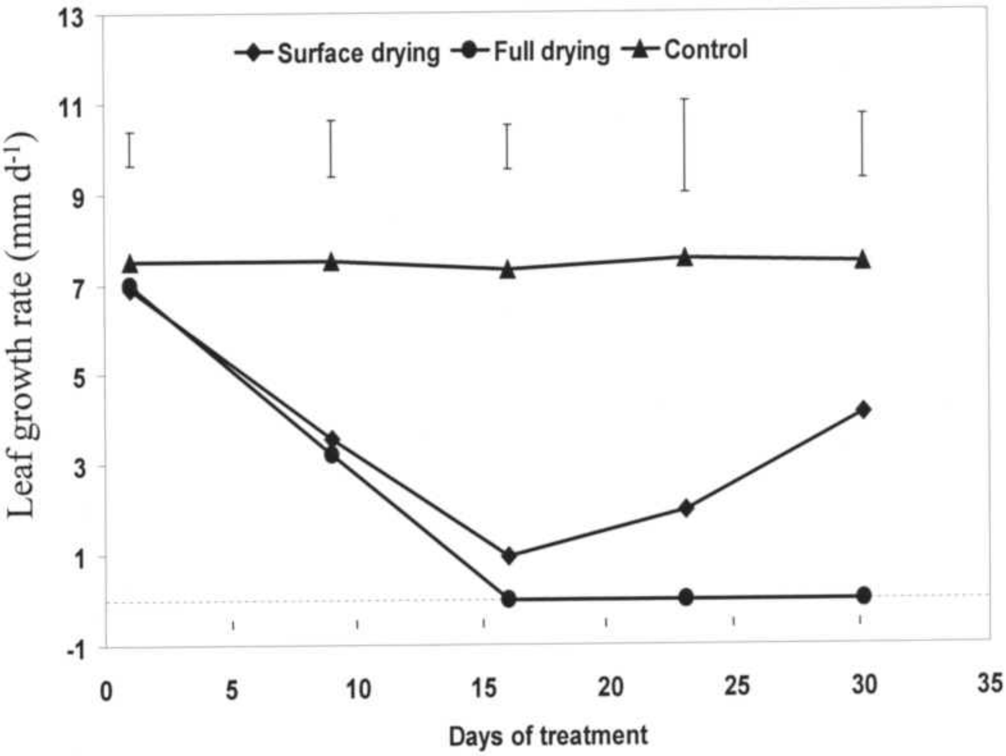

Figure 2. Leaf growth rate of tall fescue in response to soil drying. Vertical bars are LSD values (P=0.05) for treatment comparisons at a given day of treatment

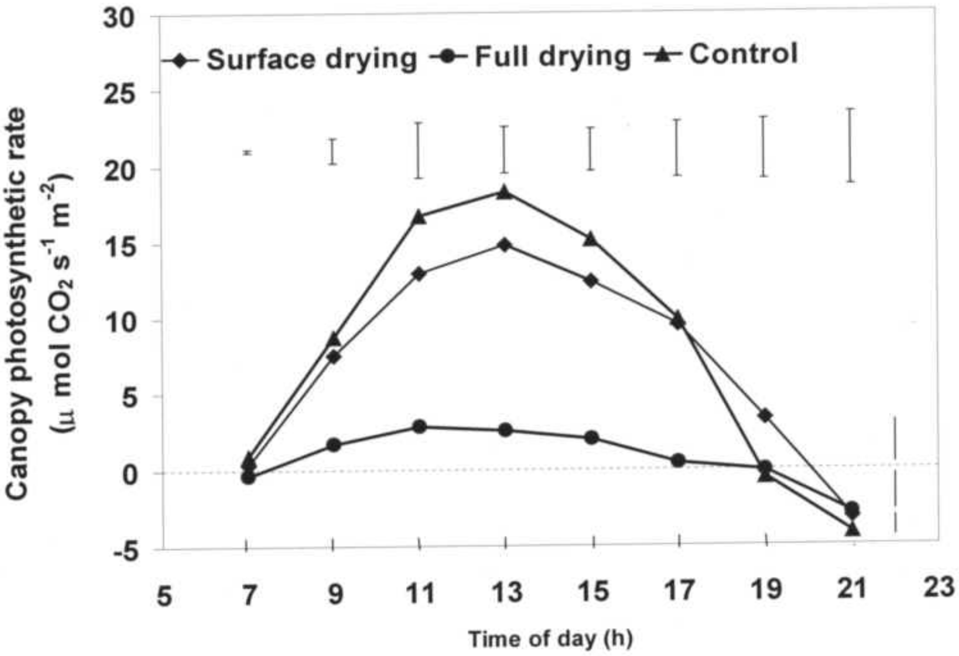

Figure 3. Diurnal changes in canopy net photosynthetic rate (Pn) of tall fescue in response to soil drying at 17 DOT. Vertical bars are LSD values (*P*=0.05) for treatment comparisons at a given time of the days, and those on the right are for comparisons between time of the day for a given treatment

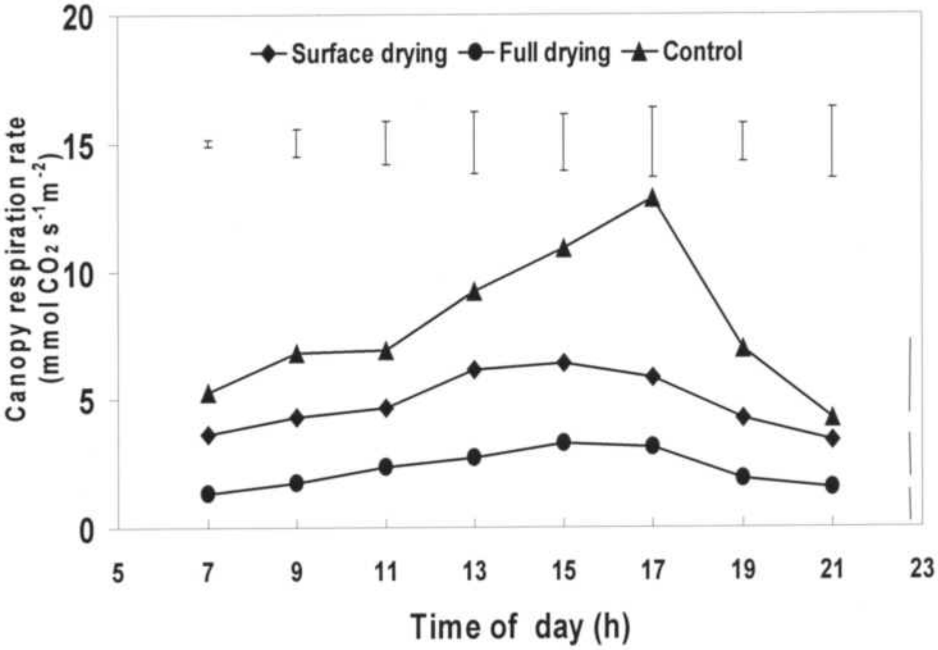

Figure 4. Diurnal changes in canopy dark respiration rate (R_{canopy}) of tall fescue in response to soil drying at 17 DOT. Vertical bars are LSD values (*P*=0.05) for treatment comparisons at a given time of the days, and those on the right are for comparisons between time of the day for a given treatment

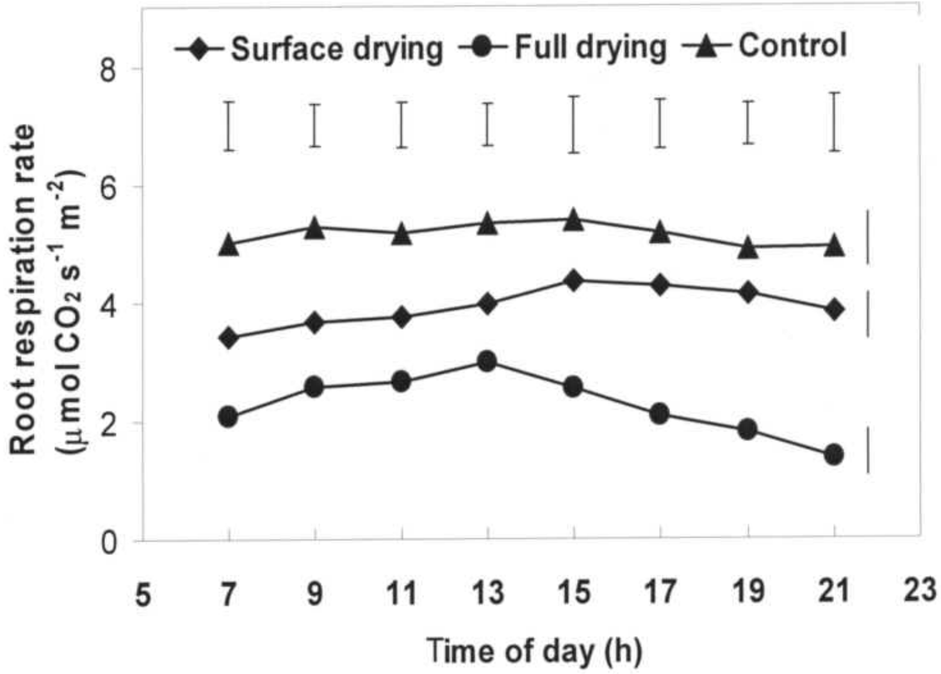

Figure 5. Diurnal changes in root respiration rate (R_{root}) of tall fescue in the surface 20-cm soil in response to soil drying at 18 DOT. Vertical bars are LSD values (*P*=0.05) for treatment comparisons at a given time of the days, and those on the right are for comparisons between time of the day for a given treatment

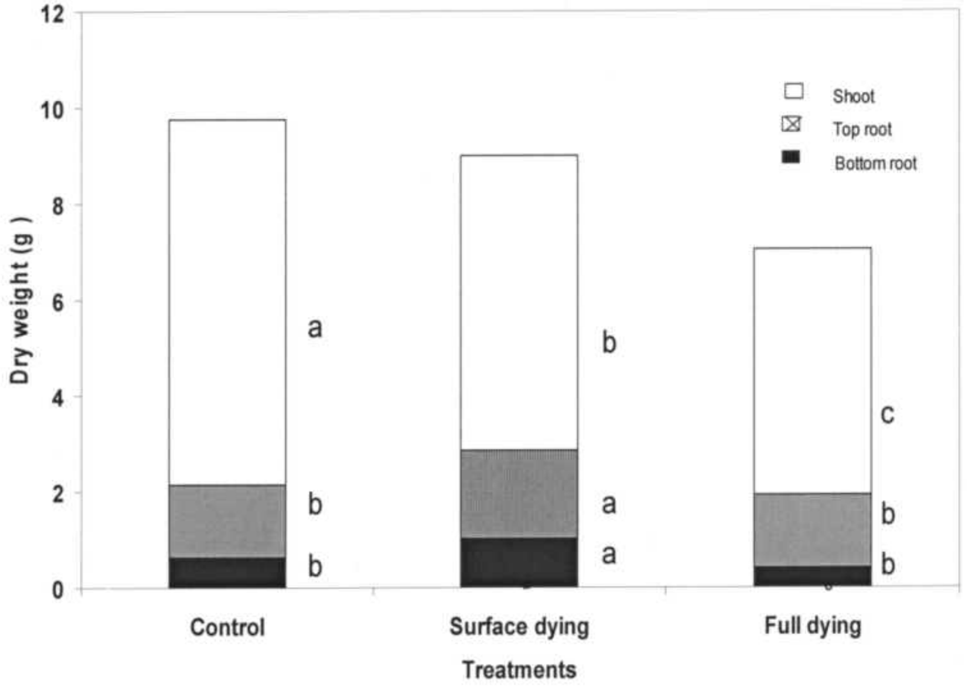

Figure 6. Shoot dry weight and weight of roots in the top 20 cm and lower 20 cm of soil and shoot dry weight of tall fescue at 42 d of soil drying. The letters on the right of the columns are for treatment comparisons of dry weight of shoots, top roots and bottom roots. Columns labeled with the same letters were not significantly different based on an LSD test (*P*=0.05).

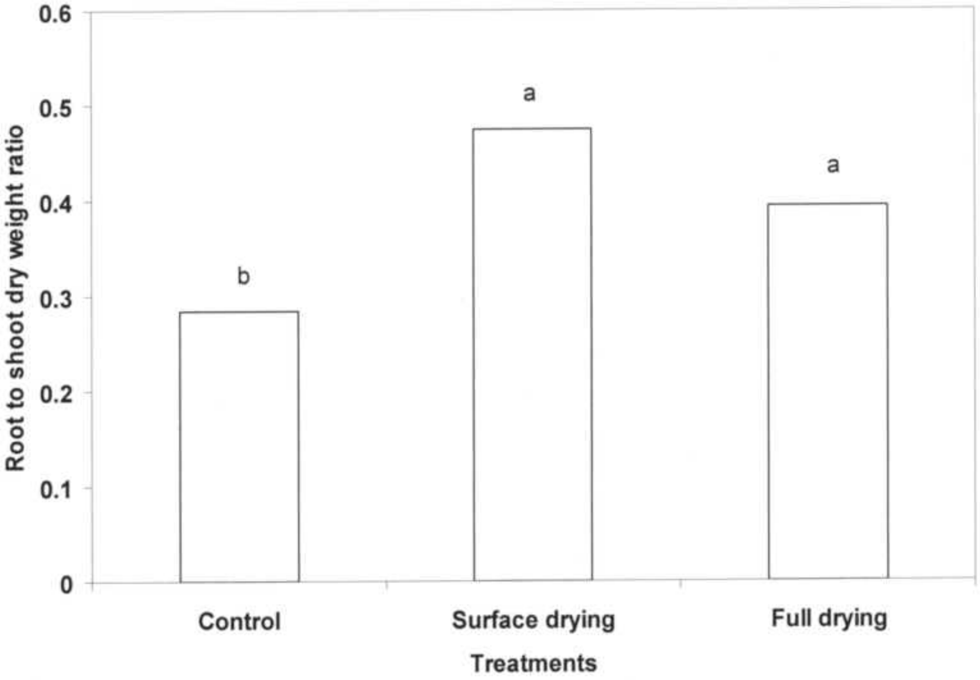

Fig.7. Root to shoot ratio in dry weight for tall fescue at 42 d of soil drying. The letters on the columns are for treatment comparison. Columns labeled with the same letters were not significantly different based on an LSD test (P=0.05)