CHAPTER II*

PHOTOSYNTHESIS, RESPIRATION, AND CARBON ALLOCATION OF TWO COOL-SEASON PERENNIAL GRASSES IN RESPONSE TO SURFACE SOIL DRYIHNG

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ABSTRACT

The study was conducted to investigate carbon metabolic responses to surface soil drying for two cool-season grasses. Kentucky bluegrass (*Poa pratensis* L.) and tall fescue (*Festuca arundinaceae* Schreb.) were grown in a greenhouse in split tubes consisting of two sections. Plants were subjected to three soil moisture regimes: (1) well-watered control; (2) drying of upper 20-cm soil (upper drying); and (3) drying of whole 40-cm soil profile (full drying). Upper drying for 30 d had no dramatic effects on leaf water potential (Ψ_{leaf}) and canopy photosynthetic rate (P_n) in either grass species compared to the well-watered control, but it reduced canopy respiration rate (R_{canopy}) and root respiration rate in the top 20 cm of soil (R_{top}). For both species in the lower 20 cm of wet soil, root respiration rates (R_{bottom}) were similar to the control levels, and carbon allocation to roots increased with the upper soil drying, particularly for tall fescue. The proportion of roots decreased in the 0-20 cm drying soil, but increased in the lower 20 cm wet soil for both grass species; the increase was greater for tall fescue. The Ψ_{leaf}, P_n, R_{canopy}, R_{top}, R_{bottom}, and carbon allocation to roots in both soil layers were all significantly higher for upper dried plants than for fully dried plants of both grass species. The reductions in R_{canopy} and R_{top} in surface drying soil and increases in root respiration and carbon allocation to roots in lower wet soil could help these grasses cope with surface-soil drought stress.

ABBREVIATIONS:

Ψ_{leaf}, leaf water potential; P_n, net canopy photosynthetic rate; R_{canopy}, canopy respiration rate; R_{top}, respiration rate of roots in the top 20-cm soil; R_{bottom}, respiration rate of roots in the bottom 20 - cm soil; TNC, total nonstructural carbohydrate.

INTRODUCTION

Drought stress near the soil surface is extremely common in the field, whereas water in the deeper soil profile may be sufficient for plant uptake. Soil drying in the upper profile may have a profound impact on plant growth. This is especially true if the majority of the root system is confined to the surface soil horizon (Smucker et al., 1991). In fact, more than 70% of the total root length of grasses often occurs in the top 20 cm of the soil profile (Carrow, 1996; Hays et al., 1991; Huang et al., 1997; Huang and Fry, 1998; Marcum et al., 1995 a, b).

Plants with a well-established root systems can utilize localized supplies of available soil water to maintain stomatal conductance and leaf water status, despite large portions of the root system being in dry soil (Erichson and Kirkham, 1979; Gallardo et al., 1994; Kirkham, 1980; Zhang and Kirkham, 1995). Huang et al. (1997) and Huang (1998) examined responses of several warm-season turfgrasses to surface soil drying and found that shoot growth and leaf water status were not affected by surface soil drying for relatively drought-tolerant, deep-rooted 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-rooted zoysiagrass (*Zoysia japonica* Steud.) and bermudagrass (*Cynodon dactylon* L.). Huang (1998) found that water absorbed by roots in deeper moist soil in buffalograss could be transported to drying surface 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.

The rate of photosynthesis often limits plant growth when availability of water in the

soil is limited. A negative whole-plant carbon balance could occur as a result of reduced photosynthetic capacity during drought, unless simultaneous and proportionate reductions in growth and carbon consumption take place. Roots are major consumers of the carbon produced through photosynthesis, and use it mainly for respiration and tissue construction (Lambers, 1987; Lambers et al., 1996). Lambers et al. (1982) reported that about 30% of the carbon allocated from shoots to roots of wheat (*Triticum aestivum* L.) was incorporated in dry matter and 30% was respired. Therefore, efficient carbon expenditure in root respiration and allocation to roots may increase the probability of plant survival during drought stress (Sisson, 1989). However, how carbon metabolism is involved in plant adaptation to localized soil drought is not well understood. More knowledge of these responses might provide insights into plant drought resistance mechanisms.

The objectives of this study was to investigate the response of photosynthesis, respiration, carbon allocation, and carbohydrate accumulation to surface soil drying for two cool-season grass species, Kentucky bluegrass (*Poa pratensis* L.) and tall fescue (*Festuca arundinaceae* Schreb.). The later is relatively more drought resistant than the former species (Beard, 1973). These two grass species are widely used as forage grasses and turfgrass in arid and semi-arid regions.

MATERIAL AND METHODS

Plant materials and growth conditions

Plants of 'Livingston' Kentucky bluegrass and 'Falcon II' tall fescue with five uniform tillers were collected from 3-year-old turfgrass plots at the Rocky Ford Turfgrass Research Center, Kansas State University, Manhattan, Kansas. Grasses were transplanted into split polyvinyl chloride (PVC) tubes (40 cm long, 10 cm in diameter) filled with autoclaved fritted clay (Profile, ALMCOR, Deefield, IL) (9:1, v/v) and kept in a greenhouse. Fritted clay is a granular material made by firing coarsely-milled, dry clay in a rotary kiln. It was used as the growing medium for the following reasons (van Bavel et al., 1978): this material 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 that minimize the confounding effects of root respiration by soil microbial respiration.

The split PVC tubes consisted of two sections, each 20 cm in length. The split segments 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 (i.e. 2 cm and 22 cm deep) to allow separate irrigation. Irrigation was automated using a pressure and flow controller. Soil water content and temperature in each soil layer were monitored hourly using the dual-probe heat –pulse technique (Tararra and Ham, 1997). Two probes (28 mm long) were buried horizontally in 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 20-40 cm 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 a 4-cm height. Plants were maintained in a greenhouse, with daily maximum/minimum temperatures of 24 ^{o}C/18 ^{o}C and a 16-h photoperiod. The light regime in the greenhouse was supplemented with 1 kw metal halide lamps. Light intensity on a horizontal plane just above the canopy at 12:00 h averaged 900 (mol-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 maintained at 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).

Measurements

Leaf water potential (ψ_{leaf}) was determined with a thermocouple psychrometer (Decagon Device, Pullman, Washington) on four young, fully expanded leaves from different plants in each of four split-tubes per treatment at various times during treatment. At each measurement time, 48 leaf samples were measured for each species. Measurements were made on leaves from one species each day.

Canopy net photosynthetic rate (P_n) and whole dark respiration rates (R_{plant}): Pn and R_{plant}, roots in the top 20-cm soil layer (R_{top}), and roots in the lower 20-cm layer (R_{bottom}) were measured with a LI-6400 portable gas exchange system (LICO Inc., Lincoln, NE). Canopy photosynthetic rate and dark respiration rate were measured from 10:00 to 14:00 h and 19:00 to 20:00 h, respectively, by enclosing the whole canopy in a transparent plexiglass chamber (15 x 10 x 10 cm). The canopy chamber was attached to the CO_2 analyzer of the LI-6400 gas exchange system. Canopy P_n and R_{canopy} were expressed as CO_2 uptake and evolution per unit canopy area, respectively.

Respiration rates of roots/soil in the upper and lower 20-cm soil layers were measured separately and nondestructively by monitoring changes in the concentration of CO_2 in the air stream pumped out from each soil layer with the LI-6400 gas exchange system using the method of Bouma et al. (1997) with modification. The top of the split tube was covered with a sliding plastic lid and sealed around the bases of shoots with parafilm and

Vaseline to minimize gas exchange between the ambient air and the soil. Gas exchange between the two soil layers was minimized by the barrier described above. A preliminary test, in which a known concentration of CO2 (1000 ppm) was blown into one layer and CO_2 concentration was measured in another layer, found no gas exchange between the two layers. Prior to root/soil respiration measurements, the gas in the soil was mixed and circulated inside each section of the split tube 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 in each soil layer. The growing medium (fritted clay) contained no organic matter and was autoclaved before being placed in the tubes to minimize soil microbial respiration. Bare soil respiration was measured. Root respiration rate in each soil layer was estimated by subtracting the bare soil respiration from the root/soil respiration. At the end of respiration measurements, roots in each soil column in each pot were washed free of soil. Root dry weight was then determined and used to calculate specific respiration rate expressed as μmol CO_2 g^{-1} s^{-1}.

Carbon allocation to roots was examined using radioactive labeling technique (Huang and Gao, 2000). At the end of the experimental period (39 d), plants in four containers were labeled with $^{14}CO_2$ at 10:00 h in the morning when some leaves in a plant remained turgid. Shoots were enclosed in a transparent plexiglass chamber (15 cm tall and 10 cm in diameter) fitted tightly to the PVC plant container and exposed for 40 min to 40 (Ci $^{14}CO_2$ that was released from $Na^{14}CO_3$ (6.8 (Ci mol-1) by reacting with 1 N HCl. After the 40-min labeling, excessive $^{14}CO_2$ was absorbed by bubbling the gas through a saturated NaOH solution for 20 min. Three days after labeling, 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 for 48 h. Root dry weight was determined and the percent roots in each layer of total root dry weight was calculated. Tissues were then ground with a tissue grinder, and stored separately in sealed vials for analyses of ^{14}C activity and carbohydrates. The ^{14}C activities in shoots and roots in each soil layer were measured with a liquid scintillation analyzer (Packard, Deers Grove, IL). Total nonstructural carbohydrate (TNC) concentrations of shoots and roots were measured using the method described by Chatterton et al. (1987).

Experimental design and statistical analysis

The experiment consisted of two factors (two grasses and three soil-moisture treatments) with four replications arranged in a completely randomized design with repeated measurements. Treatment effects were determined by analysis of variance according to the general linear model procedure of the Statistical Analysis System (SAS Institute Inc., 1988). Variation was partitioned into grass species, soil moisture and treatment duration (sampling time) as main effects and corresponding interactions. The comparison of moisture treatments within a grass clearly showed performance of each grass under stress conditions. Thus, the emphasis was on comparing responses to soil moisture treatment within a grass. Differences among treatment means within a grass were separated by least significant difference at the 0.05 level of probability.

RESULTS

Leaf water status

Leaf water potential (ψ_{leaf}) in the upper-drying treatment was maintained at the same level as that in the well-watered control during most of the experimental period for both grass species; however, it was lower at 22 d for tall fescue and at 15, 18, and 22 d of treatment for Kentucky bluegrass (Figure 2). When the soil profile was fully dried, ψ_{leaf} decreased below the control level beginning 4 d in both grasses. Fully dried plants also had a lower ψ_{leaf} than upper-dried plants beginning at 8 for both grasses. By 29 d of full drying, majority of leaves for both grasses became permanently wilted and brown, whereas upper-dried plants maintained green and turgid leaves, similar to control plants.

Canopy net photosynthetic rate

Canopy net photosynthetic rate (Pn) of upper-dried plants was not significantly different from that of well-watered plants for both grasses during most of the experimental period, except at 16 d of treatment when the reduction in Pn was more for Kentucky bluegrass than for tall fescue (Figure 3). However, Pn of fully dried plants was significantly lower than rates of well-watered and upper-dried plants beginning at 9 d for both grasses, to a greater extent for Kentucky bluegrass than fescue.

Canopy respiration rate

Canopy respiration rate (R_{canopy}) decreased significantly to below the control level beginning at 9 d of treatment for both grass species grown under upper drying and full

drying conditions (Figure 4). Fully dried plants had significantly lower R_{canopy} than upper dried plants after 6 d for both species. The reduction in R_{canopy} was greater for tall fescue than for Kentucky bluegrass under either upper or full drying conditions.

Root respiration rate

Full drying reduced total root respiration rates in both the top 20 cm (R_{top}) and lower 20 cm of soil (R_{bottom}) for both grasses beginning at 8 d of treatment (Figures 5A, B and 6A, B). Under upper-drying conditions, R_{top} decreased to below the control level and similar to that of fully dried plants beginning at 15 d for Kentucky bluegrass (Figure 5A) and 8 d for tall fescue (Figure 6A). Respiration rate of roots in the lower 20 cm of wet soil remained at levels similar to those of the control plants at 1, 8, and 28 d, and a lower level at 15 and 22 d for Kentucky bluegrass (Figure 5 B). For tall fescue, R_{bottom} in the lower wet soil was less in upper dried plants at 8 and 15 d, but higher than the control plants at 22 and 28 d (Figure 6 B). Root respiration rates in both layers were significantly higher than those of fully dried plants.

Specific respiration rate of roots in 0-20 and 20-0 cm soil was reduced by either upper or full drying for both grasses (Table 1). Upper-dried plants had higher specific respiration rate in both soil layers than fully dried plants for tall fescue. For Kentucky bluegrass, specific respiration rates were not significantly different between upper and full drying in either 0-20 or 20-cm soil.

Root distribution

Upper or full drying had no effect on root dry weight in the top 20 cm soil for Kentucky bluegrass. Upper drying increased root dry weight in the lower 20- cm wet soil for Kentucky bluegrass and that in both soil layers for tall fescue.

With upper drying, the proportion of roots in dry weight decreased in the top 20 cm drying soil, but increased in the lower 20-cm soil for both grasses (Figure 7); however, the increases in roots in the lower wet soil layer was more pronounced in tall fescue than Kentucky bluegrass. With full drying, the proportion of roots in the top 20 cm soil was not affected for both grasses, but decreased in the lower 20 cm soil for tall fescue.

Carbon allocation to shoots and roots

The proportion of newly fixed ^{14}C allocated to shoots was reduced for tall fescue but was not affected for Kentucky bluegrass under upper-drying conditions (Figure 8A). Full drying had no effects on carbon allocation to shoots for tall fescue, but increased it for Kentucky bluegrass.

Under upper-drying conditions, the amount of carbon allocated to roots in proportion to the total newly fixed ^{14}C increased in both the top 20 cm of drying soil and lower 20 cm of wet soil for tall fescue but decreased in the top 20 cm and increased in the lower 20 cm for Kentucky bluegrass (Figure 8B, C). Full drying reduced carbon allocation to roots in the top 20 cm of drying soil for Kentucky bluegrass but had no effects in the lower 20 cm. For tall fescue, full drying did not affect carbon allocation to roots in the top 20 cm soil but reduced it in the lower 20 cm soil.

Carbohydrate availability

The TNC concentration of shoots increased compared to the well-watered control for both grasses under either upper-drying or full-drying conditions (Figure 9). The TNC concentration of roots in the top 20 cm of drying soil also increased in the upper-dried treatment for both grasses (Figure 9) but decreased in fully dried tall fescue and was unaffected for fully dried Kentucky bluegrass. Root TNC in the lower 20 cm of soil was not affected by either upper or full drying.

DISCUSSION

Leaf water potential (Ψleaf) and canopy net photosynthesis rate (Pn) were basically unaffected during most of the experimental period, despite half of the soil volume or the majority of roots (80%) of both grass species being exposed to drying conditions. This lack of effects by surface soil drying suggested that both cool-season grasses were capable of utilizing water deeper in the soil profile with a limited number of deep roots to maintain physiological activities. However, drying of the entire soil profile was detrimental to growth, leaf water relations, and photosynthesis in both grass species, to a greater extent for Kentucky bluegrass than tall fescue.

For plants adapted to conditions with limited water availability, survival of drought periods may require a considerable amount of carbon investment belowground. Drought stress generally increases the root-to-shoot ratio (Hamblin et al., 1990). Sharp and Davies (1979) reported an absolute increase in root biomass in maize (*Zea mays* L.) seedlings subjected to water stress. Nicolas et al. (1985) found that biomass allocation to roots of drought-stressed plants was maintained in a drought-intolerant genotype but increased in a drought-tolerant genotype of wheat (*Triticum aestivum* L.). The present study showed that, in response to upper-dried soil, the amount of carbon allocated to roots in proportion to the total newly fixed carbon increased in both the top drying soil layer and the lower wet soil layer for tall fescue and increased only in the lower wet soil for Kentucky Bluegrass. Huang and Gao (2000) also reported that soil drying reduced the proportion of newly photosynthesized 14C allocated to leaves but increased the proportion allocated to roots for three tall fescue cultivars and to a greater extent for relatively drought-tolerant cultivars. When water is limited in the surface soil, increases in carbon investment in

roots, particularly to those in deeper soils where water is available for uptake, may enhance survival of plants during prolonged periods of drought stress. Several studies have reported that water absorbed by deep roots in moist soil can move through the roots and leak into the dry surface soil at night, which can sustain growth and nutrient uptake in localized dry soil (Blum and Johnson, 1992; Caldwell and Richards, 1989; Huang, 1998; Richards and Caldwell, 1987;Wraith and Baker, 1991).

Because root respiration represents a major carbon cost (Lambers, 1987; Lambers et al., 1982), maintaining low root respiration rate when water and nutrient uptakes are minimum in drying soil also may increase the possibility of plant survival during extended drought periods (Dhopte and Ramteke, 1991; Sisson, 1989). Hall et al. (1990) and Nicolas et. al. (1985) have shown that low soil water potential causes a rapid decrease in root respiration. Drought-tolerant cultivars of wheat (Nicolas et al., 1985) and peanut (*Arachis hypogaea* L.) (Dhopte and Ramteke, 1991) exhibited lower root respiration rate than sensitive cultivars during drought stress. Reduced respiration of roots exposed to dry soil also has been reported in citrus (Bryla et al., 1997), desert succulents (Palta and Nobel, 1989), and other desert perennial species (Holthausen and Caldwell, 1980; Sisson, 1989). In the present study, both shoots and roots in the top drying soil maintained low total respiration rates when water was limited. The reduction in total root respiration rate generally can be due to reduction in specific respiratory activity of roots or/and total root biomass. In our study, the reduction of total respiration rate in drying soil was related to the decreases in specific respiration rate, but not reduced root biomass, because only specific respiration rates in the top drying soil decreased for both grasses while root dry weight in this layer generally was either not affected or increased. During

exposure to dry soil, surface roots are essentially unable to provide appreciable benefit in terms of water and nutrient uptakes, so the decrease of carbon expenditure by reducing respiration rate is of great significance for plants coping with drought (Eissenstat, 1998). Our results also showed that roots of both grass species in the lower wet soil maintained relatively high respiration rates when the surface soil was drying, especially for tall fescue. The maintenance of respiration rates of roots in the lower wet soil layer could be mainly related to increased root growth in the lower wet soil in response to surface soil drying, because specific respiration rate of roots in the lower wet soil decreased with upper drying for both grasses. The maintenance of respiration of roots in deeper soil where water was available could support growth by providing water and nutrient uptakes. These results indicated that these two cool-season grasses were able to adjust their carbon expenditures and allocation pattern to sustain growth in environments with surface soil drying.

In general, total nonstructural carbohydrate concentrations in both shoots and roots of Kentucky bluegrass and tall fescue increased or were unaffected under either upper-drying or full-drying conditions. Huang and Gao (2000) also reported that for three other tall fescue cultivars, concentrations of TNC were higher in leaves of drought-stressed plants than in leaves of well-watered plants. Carbon accumulation during drying could be related to the reduction in consumption because of lower canopy and root respiration rates as discussed above. The results suggested that carbohydrate availability was not a limiting factor for shoot and root growth in tall fescue and Kentucky bluegrass during drought stress.

In summary, in response to surface soil drying, both grass species exhibited reduced respiration rates of canopy and roots in surface drying soil and increased root respiration rate and carbon allocation to roots in the deeper soil profile where water was available for uptake, to a larger extent for tall fescue than Kentucky bluegrass. The capability of perennial grasses of surviving surface drying soil is not only facilitated by efficient water use, as previously reported, but also could be related to the efficient carbon expenditure, as demonstrated in the present study.

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Table 1. Effects of soil drying on root dry weight and specific respiration rate on 0-20 and 20-40 cm soil layers. Values followed by the same letters within a column are not significantly different (P=0.05) based on a LSD test.

Grasses	Treatment	Root dry weight (g)		Specific respiration rate (μmol CO_2 g^{-1} s^{-1})	
		0-20 cm	20-40 cm	0-20 cm	20-40 cm
Kentucky bluegrass	Well watered	1.90 a	0.38 b	4.15 a	16.7 a
	Upper drying	2.38 a	0.75 a	1.71 b	8.51 b
	Full drying	2.18 a	0.43 b	1.30 b	7.71 b
Tall fescue	Well watered	1.52 b	0.64 b	4.78 a	9.02 a
	Upper drying	1.84 a	1.03 b	1.46 b	6.85 b
	Full drying	1.51 b	0.41 b	0.38 c	1.32 c

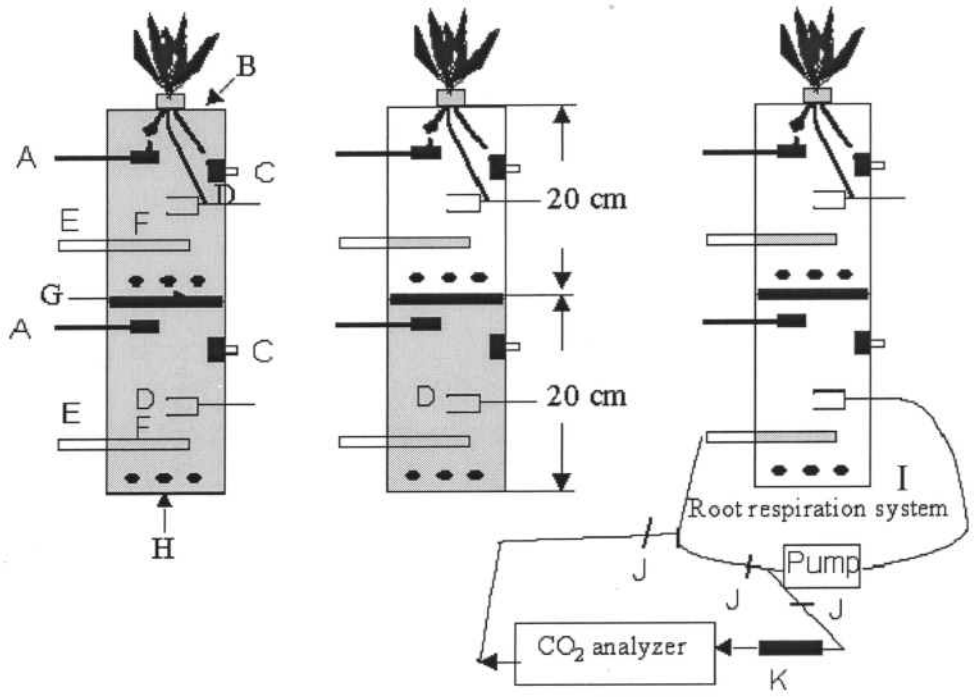

Fig. 1 Schematic of split-tube technique, depicting experiment set-up, three soil moisture treatment, and root-respiration measurement system. A, drip irrigation tubes; B, sealed plastic lid covering soil surface; C, gas outlet port for root respiration measurement; D, dual probes for monitoring soil moisture and temperature; E, gas inlet port for root respiration measurement; F, manifold; G, a sheet of wax paper and nylon screen coated with Vaseline which prevents gas and water exchange between soil layers; H, drainage holes (plugged during root respiration measurement); I, a circulating pump and LI-6400 gas exchange system for nondestructive measurement of root respiration in individual soil layer; J, flow control valves; K, desiccant tube.

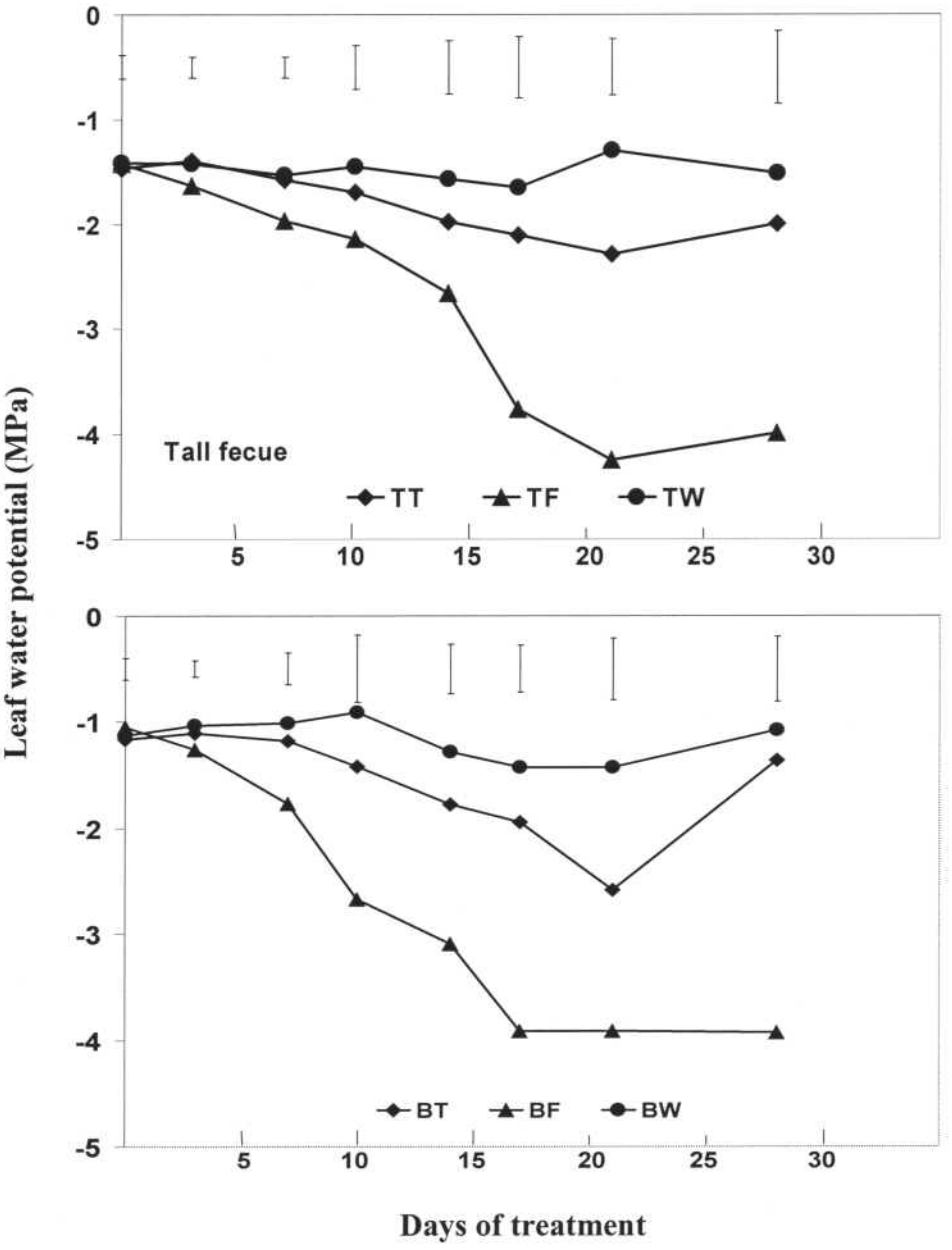

Fig. 2 Leaf water potential (ψ_{leaf}) of tall fescue and Kentucky bluegrass in response to drought stress. Vertical bars are LSD values (p=0.05) for treatment comparison within a grass species and at a given day of treatment

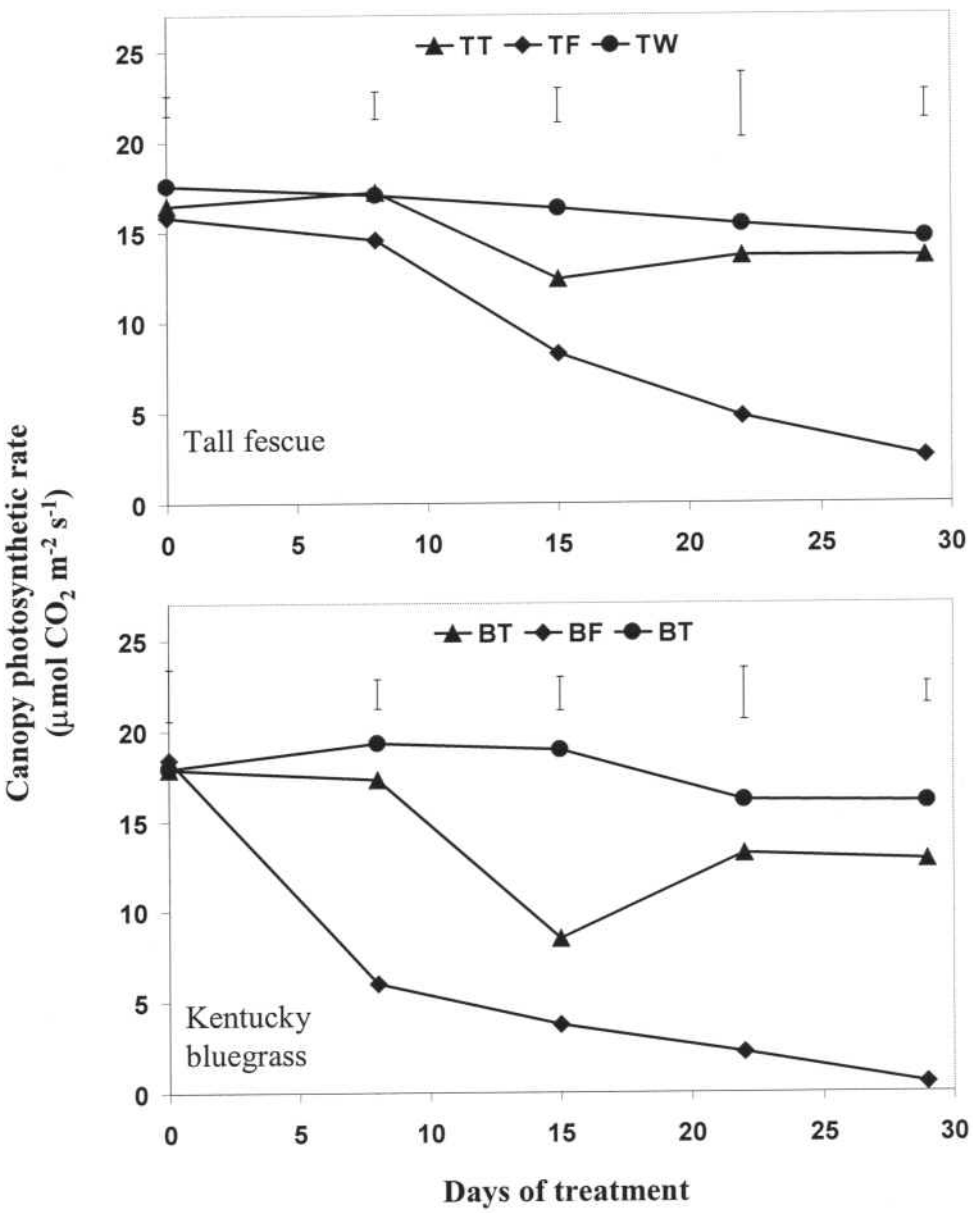

Fig. 3 Canopy net photosynthetic rate (Pn) of tall fescue and Kentucky bluegrass in response to drought stress. Vertical bars are LSD values (p=0.05) for treatment comparison within a grass species and at a given day of treatment

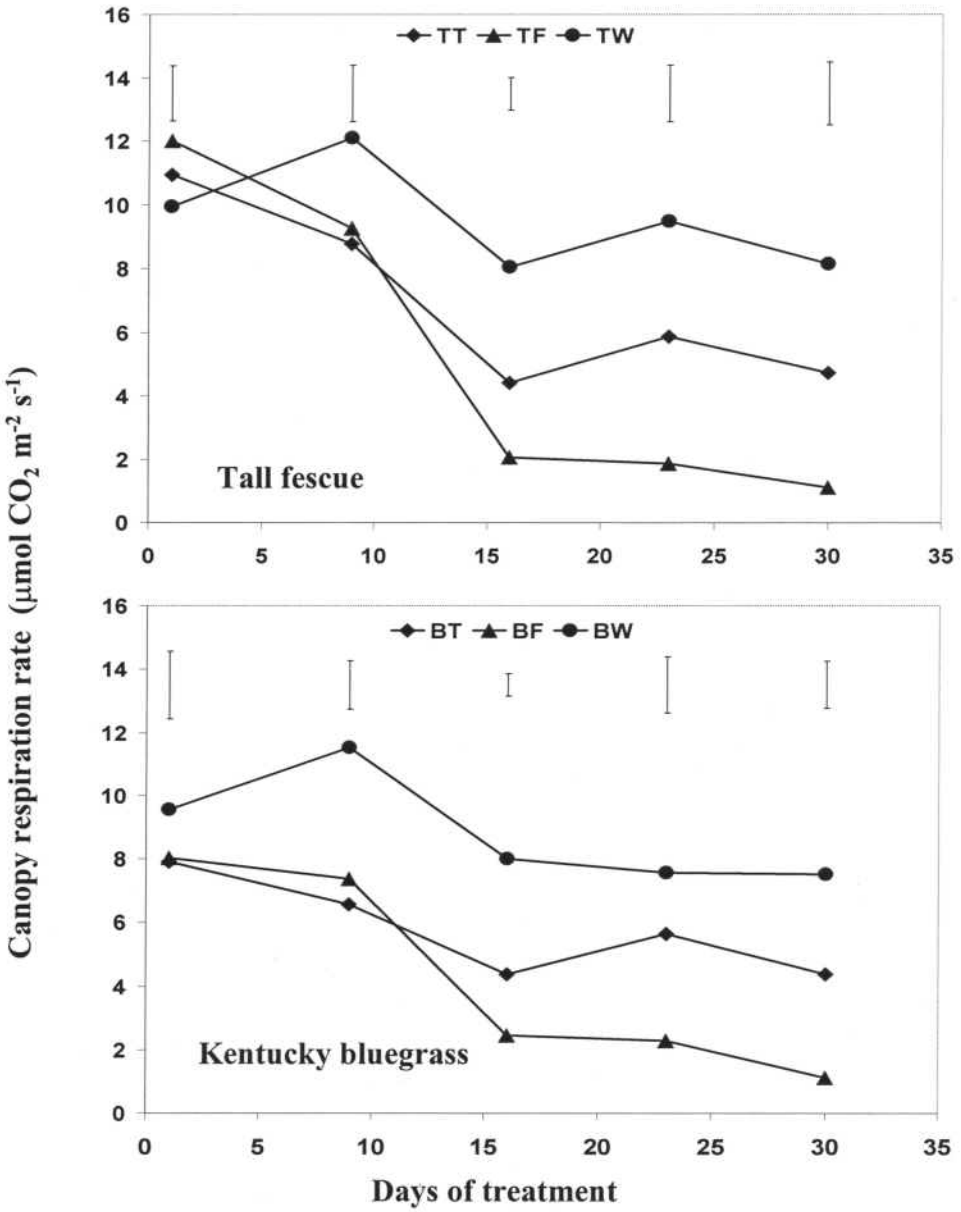

Fig. 4 Canopy respiration rate (Pn) of tall fescue and Kentucky bluegrass in response to drought stress. Vertical bars are LSD values (p=0.05) for treatment comparison within a grass species and at a given day of treatment

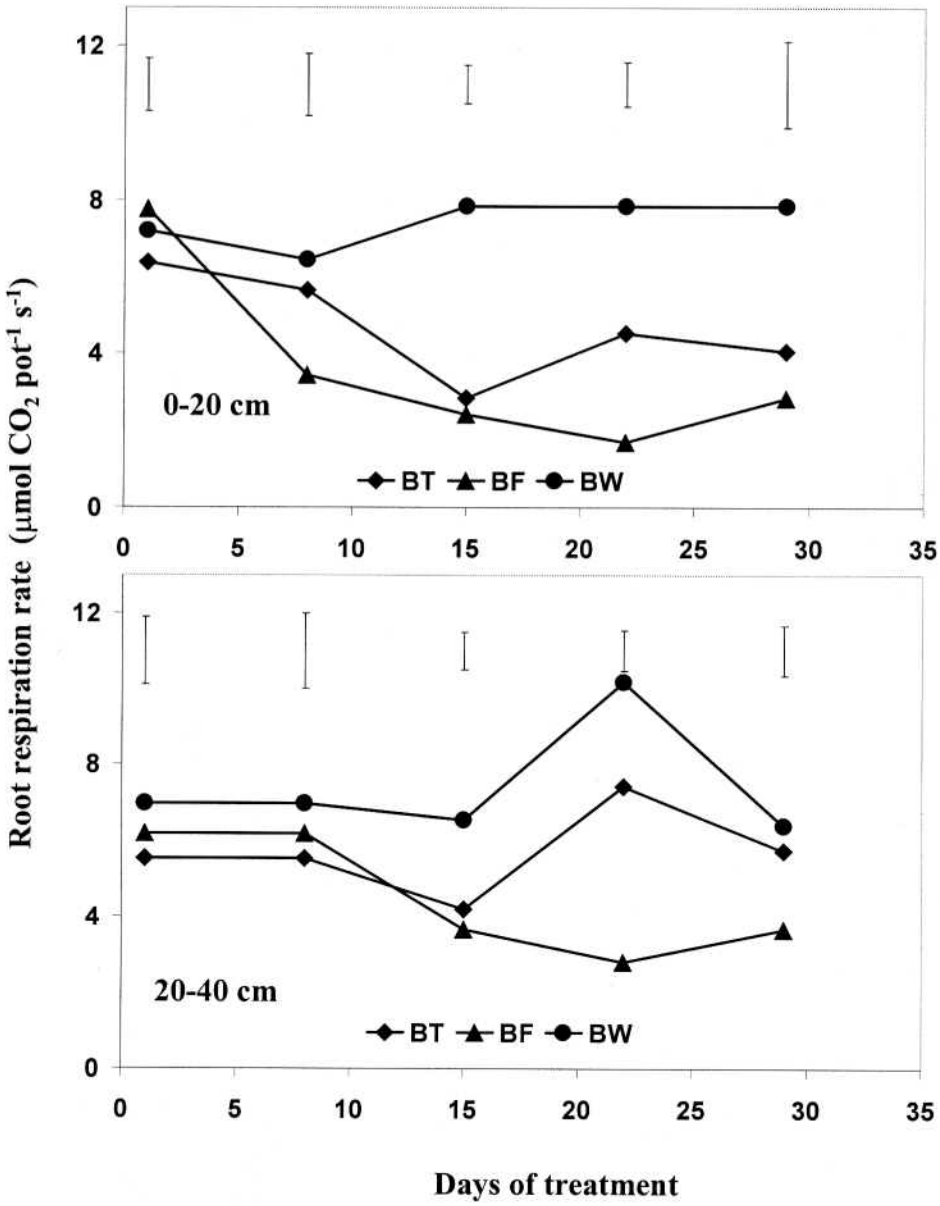

Fig. 5 Respiration rate of roots in the upper 20-cm (R_{top}) and lower 20-cm soil (R_{bottom}) of Kentucky bluegrass in response to drought stress. Vertical bars are LSD values (p=0.05) for treatment comparison within a grass species and at a given day of treatment

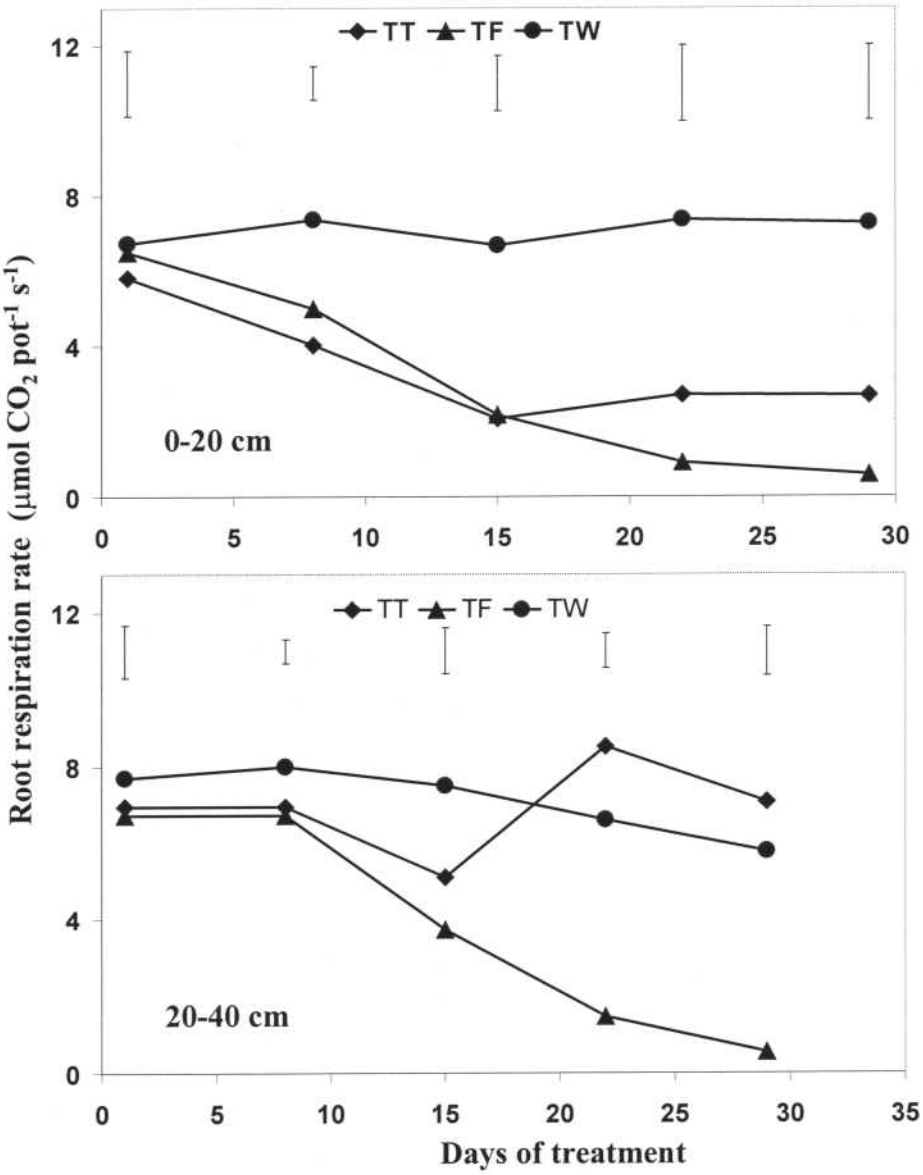

Fig. 6 Respiration rate of roots in the upper 20-cm (R_{top}) and lower 20-cm soil (R_{bottom}) of tall fescue in response to drought stress. Vertical bars are LSD values (p=0.05) for treatment comparison within a grass species and at a given day of treatment

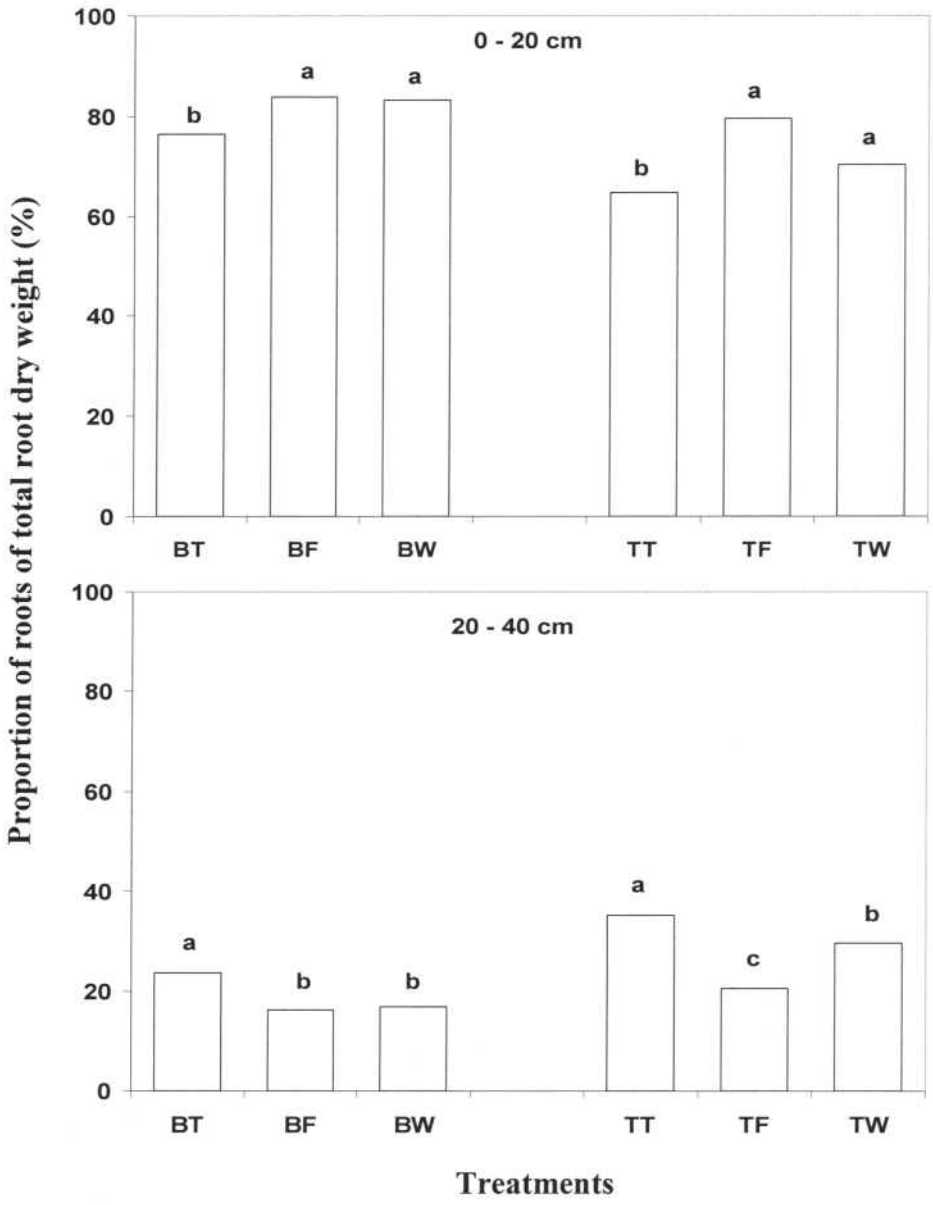

Fig. 7. Proportion of roots in dry weight in each soil layer in response to soil drying for tall fescue and Kentucky bluegrass. BT - Kentucky bluegrass, upper drying; BF - Kentucky bluegrass, fully drying; BW - Kentucky bluegrass, well watered; TT - tall fescue, upper drying; TF - tall fescue, fully drying; TW - tall fescue, well watered. Columns marked with the same letters within a grass species and not significantly different based on an LSD test (p=0.05).

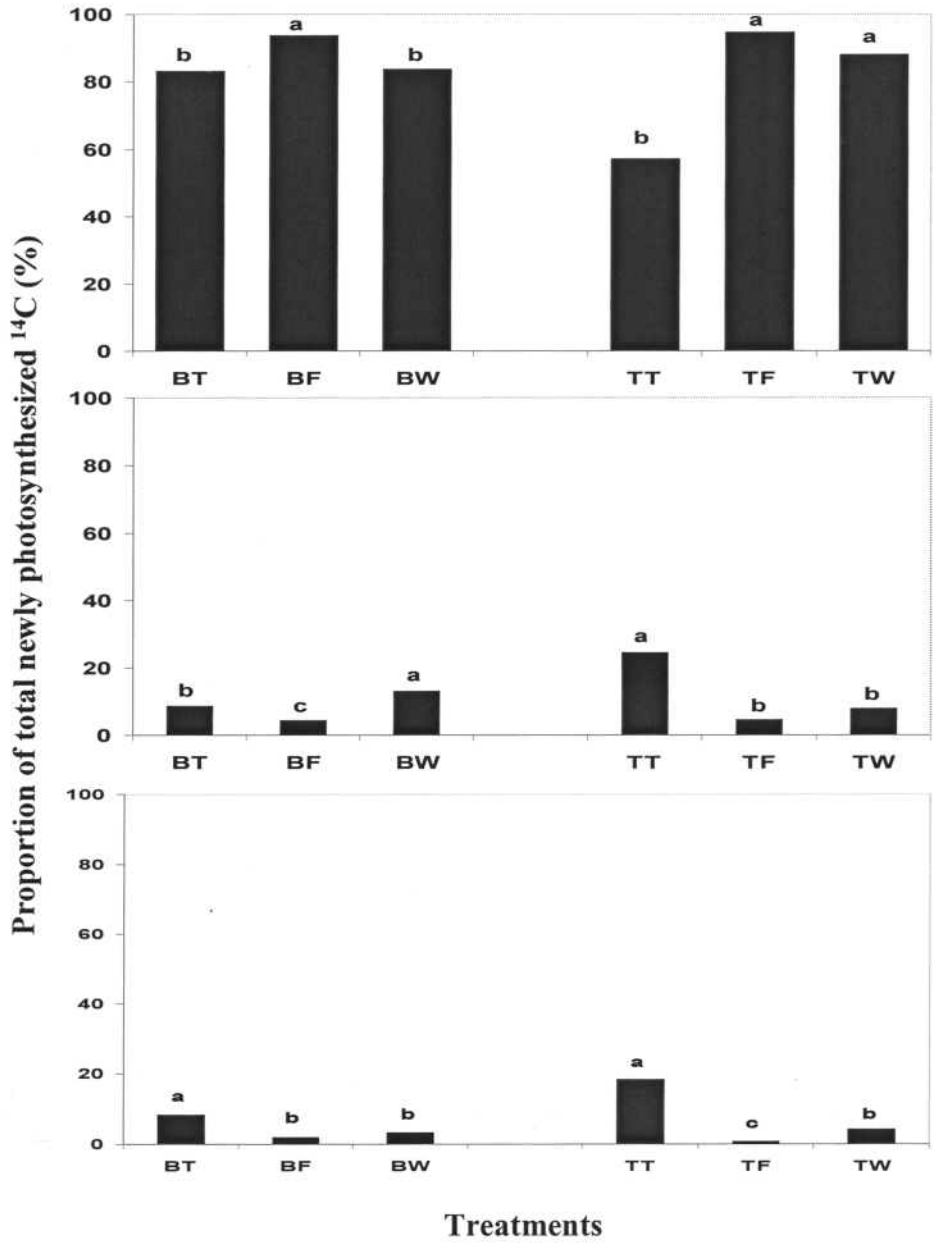

Fig. 8. Allocation of newly photosynthesized 14C carbon to shoots and roots in the upper 20 cm of soil and the lower 20 cm of soil as affected by drought stress for tall fescue and Kentucky bluegrass. BT - Kentucky bluegrass, upper drying; BF - Kentucky bluegrass, fully drying; BW - Kentucky bluegrass, well watered; TT - tall fescue, upper drying; TF - tall fescue, fully drying; TW - tall fescue, well watered. Columns marked with the same letters within a grass species and not significantly different based on an LSD test (p=0.05).

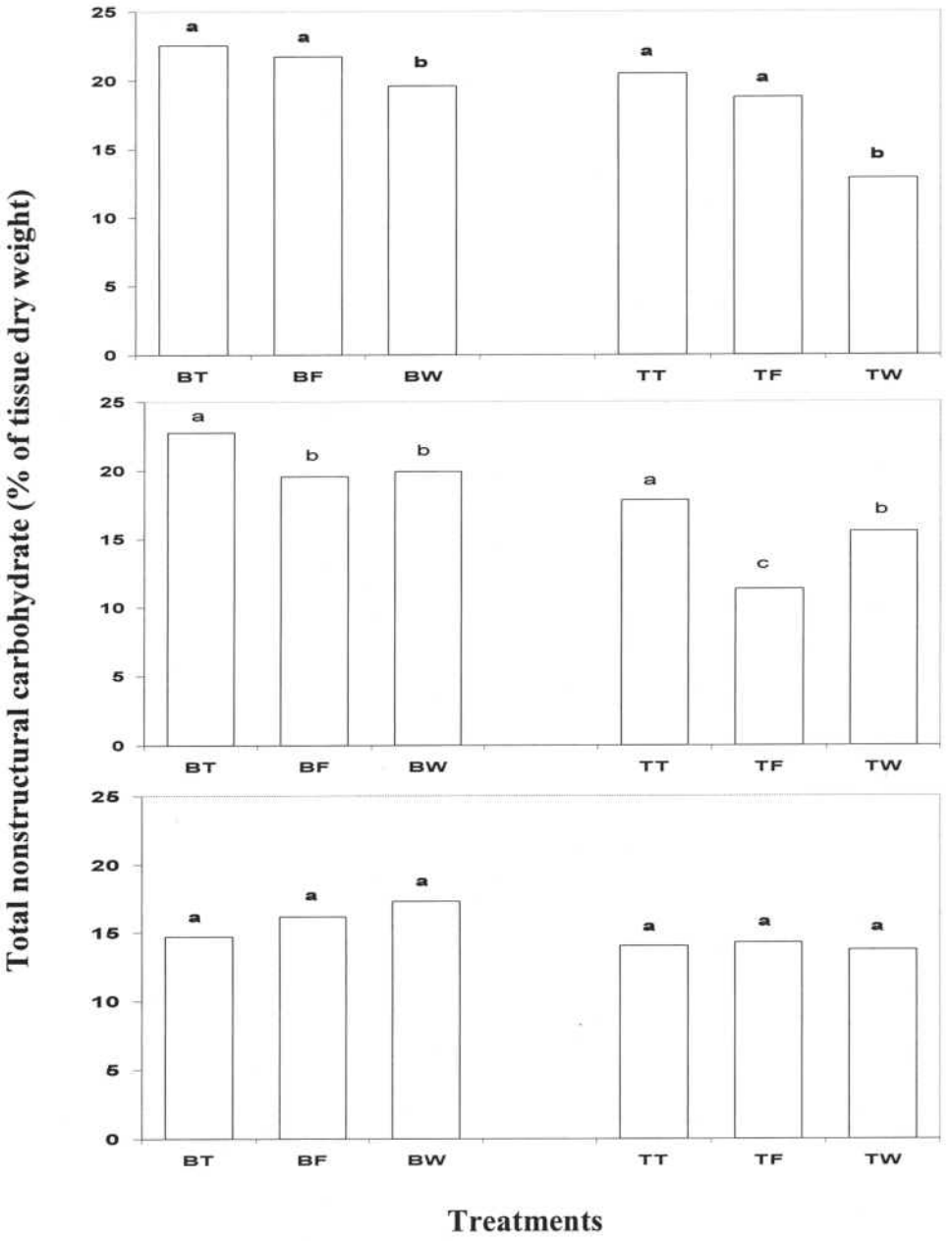

Fig. 9. Total nonstructural carbohydrate in shoots, roots in the upper 20 cm of soil and the lower 20 cm of soil as affected by drought stress for tall fescue and Kentucky bluegrass. BT - Kentucky bluegrass, upper drying; BF - Kentucky bluegrass, fully drying; BW - Kentucky bluegrass, well watered; TT - tall fescue, upper drying; TF -tall fescue, fully drying; TW - tall fescue, well watered. Columns marked with the same letters within a grass species and not significantly different based on an LSD test (p=0.05).