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DROUGHT-INDUCED NITROGEN RETRANSLOCATION IN PERENNIAL C_4 GRASSES OF TALLGRASS PRAIRIE[1]

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Abstract. We determined if drought-induced nitrogen retranslocation occurs in perennial grasses of tallgrass prairie, as suggested from studies of annual changes in plant N content. To test this, we analyzed six C_4 grasses representing a wide range of drought tolerance for shoot, rhizome, and root N before and after controlled drought. Shoot N concentration decreased in all species during drought (31–41%), including in recently expanded leaves (23–38%). No consistent pattern with respect to drought tolerance was apparent in these decreases or in observed changes in distribution of whole-plant N, although there was some suggestion of a mesic-to-xeric gradient in the magnitude of retranslocation. For example, the proportion of total plant N allocated to shoots decreased during drought 20–29% in the most mesic species over three experiments, 2–12% in the three intermediate species, and 4–6% in the two most xeric species, for pre- vs. post-drought comparisons. However, when drought-stressed plants were compared to well-watered age controls, the respective values were 20–21%, 12–20%, and 0–19%, the apparent result of size-related changes in N allocation in control plants in one experiment. In most cases, shoot N was moved primarily into rhizomes, though in one species with intermediate drought tolerance, evidence suggested that much of the retranslocated shoot N was apparently lost through fine-root turnover. Retranslocation of shoot N to rhizomes and roots, confirmed by monitoring movement of ^{35}S-methionine, was in response to drought stress rather than phenology and involved the entire shoot (e.g., blades, culms, recently expanded leaves). Post-drought photosynthesis and leaf N concentration remained well below pre-drought levels 6 d following rewatering. Thus decreases in leaf N status during drought as a consequence of retranslocation likely result in lower photosynthetic capacity and decreased whole-plant carbon gain following relief of water stress after rain. Drought-induced retranslocation may serve to protect plant N from loss to herbivory, fire, and volatilization during periods when soil N uptake and carbon assimilation are limited by water availability.

Key words: drought stress; grasses; nitrogen; perennial; photosynthesis; prairie; reallocation; remobilization; retranslocation; tallgrass prairie; water stress.

INTRODUCTION

Drought-induced nitrogen retranslocation from shoots to belowground tissues in perennial C_4 grasses of tallgrass prairie is strongly suggested from studies documenting annual variation in plant N content (McKendrick et al. 1975, Risser and Parton 1982, Adams and Wallace 1985). Prior to flowering and subsequent senescence, decreases in total shoot N and concomitant increases in root or rhizome N appear to coincide with periods of drought in several species. The focus of these studies, however, was on annual patterns of N content, and data on plant water status were not collected; thus, a relationship between N retranslocation and water stress can only be inferred.

Water-stress-induced movement of N from shoot to roots or rhizomes in grasses may have important consequences for growth and survival during and after drought. Because of the strong relationship between photosynthetic capacity and leaf N status (Field and Mooney 1986), retranslocation of foliar N would probably decrease carbon gain during and after drought. Benefits of drought-induced retranslocation might include increased root growth, and thus better plant water status and post-drought nutrient acquisition, and improved photosynthetic nitrogen-use efficiency during drought. Additionally, movement of shoot N to belowground tissues may limit losses to fire and herbivory when soil N uptake and photosynthesis are limited by water availability.

Such a trade-off between photosynthesis and N conservation was proposed by del Arco et al. (1991), who found that the magnitude of seasonal N retranslocation was inversely related to leaf retention during summer drought in woody species of central Spain. They suggested that prolonged leaf retention and decreased retranslocation during the dry season in xeric species may increase photosynthesis while decreasing N recovery from abscissing leaves. Perhaps a similar situation ex-

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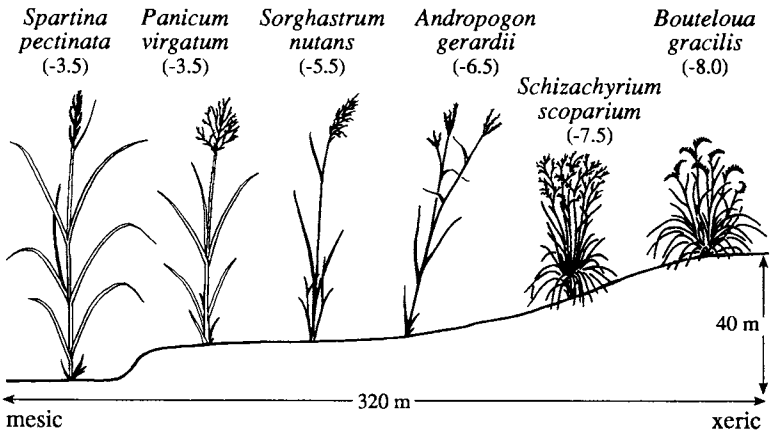

FIG. 1. Idealized distribution of *Spartina pectinata, Panicum virgatum, Sorghastrum nutans, Andropogon gerardii, Schizachyrium scoparium,* and *Bouteloua gracilis* along a typical mesotopographic moisture gradient at Konza Prairie Research Natural Area (Manhattan, Kansas). Leaf water potential (MPa) at which stomatal closure is complete and photosynthesis ceases is indicated for each species (see *Materials and methods: Nitrogen budget experiment*).

ists for xeric prairie species, which maintain photosynthetic activity during drought. Interestingly, Adams and Wallace (1985) observed that xeric prairie grasses retranslocated a similar proportion of N from foliage seasonally as mesic species. Whether this pattern extends to drought-induced N retranslocation remains unknown, as does the potential ecological significance of this phenomenon.

In contrast to seasonal retranslocation of N from senescing foliage to storage organs, which has been documented in a variety of species (Wetselaar and Farquhar 1980, Cole 1981, Vitousek 1982), including prairie grasses (McKendrick et al. 1975, Clark 1977, Risser and Parton 1982, Adams and Wallace 1985, Hayes 1985, Li and Redmann 1992), investigations of N retranslocation specifically in response to water stress are rare. Gates (1968), Dina and Klikoff (1973), Nicolas et al. (1985), and Lajtha (1987) observed drought-related N retranslocation in tomato (*Lycopersicon esculentum*), *Artemisia tridentata,* wheat (*Triticum aestivum*), and *Larrea tridentata,* respectively. However, Killingbeck (1992) and Hocking (1982) found that drought inhibited retranslocation in *Fouquieria splendens* and *Lupinus angustifolius.* These studies focused on single species; thus we know little about interspecific differences in retranslocation or the possible costs or benefits associated with drought-induced N retranslocation.

The objectives of this study were (1) to determine if retranslocation of N from shoots to roots or rhizomes occurs in response to water stress in perennial prairie grasses and (2) to identify differences among species with varying drought tolerance in the proportion or belowground destination of remobilized shoot N. Finally, because of the influence of foliar N concentration on photosynthetic capacity, we also examined the impact of shoot N retranslocation on photosynthesis during and after drought.

MATERIALS AND METHODS

Nitrogen budget experiment

We examined N allocation during drought in three rhizomatous perennial C_4 grasses native to tallgrass prairie. Based on their distribution and the maintenance of physiological activity at low water potential, these grasses represent a gradient of drought tolerance from mesic to xeric as follows: *Spartina pectinata* Link (prairie cordgrass), *Andropogon gerardii* Vitman (big bluestem), and *Schizachyrium scoparium* (Michx.) Nash (little bluestem) (Fig. 1; Weaver and Fitzpatrick 1932, Bazzaz and Parrish 1982, Knapp 1985, S. A. Heckathorn and E. H. DeLucia 1991 and *unpublished data*).

Plants were grown in a greenhouse from seed collected at the Konza Prairie Research Natural Area (Manhattan, Kansas, USA). Individual plants were grown in 18-L pots containing loam, calcite clay, and sand (1:1:1, on a volume basis) under ≈28°C days and 20° nights. Relative humidity was not controlled and ranged from 20 to 60%. Multivapor high-intensity-discharge lamps were used to extend the photoperiod to 15 h and to supplement natural lighting. Minimum irradiance at pot height at midday was 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux density (PPFD). Plants were watered daily and a commercial N:P:K (12:31:14) fertilizer was applied weekly.

A 14-d drydown was imposed after 10 wk of growth by withholding water. Droughts of this duration (or longer) are experienced by these species approximately once per growing season at Konza prairie (S. A. Heckathorn and E. H. DeLucia, *unpublished data*). The rate that leaf water potential decreased was controlled by weighing pots daily and partially replenishing water lost over the previous 24 h, so that ≈50% of the decrease in water potential during the drydown occurred in 7 d. Plants were watered at the soil surface (water only) to prevent leaching of foliar N. These plants re-

ceived no fertilizer during the drydown. Leaf water potential was monitored regularly as the drought progressed using a pressure chamber (Model 1000, PMS Instrument, Corvallis, Oregon, USA) or dew-point hygrometer (C-52, Wescor, Logan, Utah, USA). Individual plants were never sampled more than twice as they dried, and tissue removed for determination of water status, <1% of total plant biomass, was included in the final harvest.

During the drydown, each species was subjected to water stress similar in severity to that experienced in the field at Konza prairie during a prolonged drought (i.e., to the point of complete stomatal closure; Kemp and Williams 1980, Knapp 1985, S. A. Heckathorn and E. H. DeLucia 1991 and *unpublished data*). For example, *S. pectinata* was allowed to dry to leaf water potentials as low as −4 MPa (midday), *A. gerardii* to ≈−6.5 MPa, and *S. scoparium* to −7.5 MPa (Fig. 1). A subset of plants of each species continued to receive water and fertilizer during the drydown, to provide an age-control treatment.

Six to eight plants of each species were harvested prior to the drought and an additional set of plants was harvested following the drought, as were well-watered age controls. Soil was removed from roots by gentle washing. Dry mass, percent Kjeldahl N (tissue dry mass basis), and total Kjeldahl N were determined for shoots (recently expanded leaves were analyzed separately), roots, and rhizomes/crowns (hereafter referred to as rhizomes). Soil N content was also determined. Leaf senescence was minimal during the experiment, and dead leaves remained attached in all species and were included in shoot tissue analyses. Flowering did not occur.

Plant tissue and soil were oven dried at 65°C for 48 h and ground in a Wiley mill (tissue only) prior to acid digestion (Lowther 1980). Nitrogen concentration of plant material and soil was determined colorimetrically (nitroferricyanide reaction, Traacs 800, Bran-Luebbe, Buffalo Grove, Illinois, USA).

Radioisotope experiment

Radiolabelled methionine was used in a second experiment to indirectly monitor the movement of organic N during drought, and thus to confirm results of the N-budget experiment. *Spartina pectinata, A. gerardii,* and *S. scoparium* plants were grown for 8 wk as in the first experiment, but in 15-L pots. Prior to initiation of a drought, 1.85 MBq (in 50–65 μL of water) of ^{35}S-methionine (trans ^{35}S-label, ICN Biomedicals, Irvine, California, USA) was applied to one or two abraded, recently expanded leaves of 10–15 plants of each species (Martino-Catt et al. 1993). Preliminary experiments indicated that radioisotope applied in this manner was readily taken up and distributed throughout the plant within 24 h.

The distribution of radioisotope was determined for shoot, rhizome, root, and soil compartments of both drought-stressed plants and well-watered controls after a 14-d drydown (n = 5–7 for each treatment), imposed as described in the previous experiment. Plant tissues were prepared for digestion, also as above, and then plant and soil samples were mixed with and covered with $NaHCO_3$ (to prevent S volatilization; Steinbergs et al. 1962) and dry ashed at 500°C. Ashed soil samples were washed with acetic and orthophosphoric acid to remove all S (Butters and Chenery 1959) and plant samples were dissolved in 0.1 mol/L HCl. Radioactivity of the dissolved samples was measured with a liquid scintillation counter (LS 7500, Beckman Instrument, Irvine, California, USA).

Radiolabelling with ^{35}S-methionine was an inexpensive alternative to using ^{15}N and mass spectrometry. In using ^{35}S-met., we were actually monitoring movement of organic S. However, while N and S retranslocation patterns are not necessarily identical (Marschner 1986), we had reason to expect that eventual distribution of radioisotope would reflect N distribution within the plant. ^{35}S-met. applied to leaves in this manner is primarily incorporated into mesophyll chloroplast proteins (Dietz and Busch 1990, Martino-Catt et al. 1993); this is not true for S given as sulfate or cysteine (Rennenberg 1984, Marschner 1986). In contrast to inorganic forms, organic S, such as ^{35}S-met., is labile and circulates throughout the plant within the phloem (Cram 1990, Rennenberg and Lamoureux 1990, Martino-Catt et al. 1993, and see above). Furthermore, roots are dependent on organic S translocated from the shoot to meet their requirements for reduced S (Rennenburg 1984, Rennenburg and Lamoureux 1990). As with N, the majority of plant S (≈80%) is in organic form; consequently, the organic S : organic N ratio is largely constant for a species (Dijkshoorn and van Wijk 1967, Rennenburg 1984). Thus, in situations of adequate S supply, eventual distribution of ^{35}S (provided as met.) should reflect distribution of organic S, which should reflect organic N distribution (Rennenberg 1984). This is, in fact, what we observed.

Photosynthesis experiment

We conducted a third experiment to assess the potential impact of retranslocation on photosynthesis and to extend our examination of drought-induced N retranslocation to three additional species: *Panicum virgatum* L. (switchgrass); *Sorghastrum nutans* (L.) Nash (indiangrass); and *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths (blue grama) (Fig. 1).

Plants were grown as in the above experiments, but in 22-L pots containing loam, calcite clay, perlite, and peat moss (2:1.5:1:1, volume/volume). A 21-d drydown was imposed as described previously after 12 wk of growth. *Panicum virgatum* was allowed to dry to ≈−4 MPa, *S. nutans* to −5.5 MPa, and *B. gracilis* to −7.5 MPa (Fig. 1). Ten plants were harvested before and 10 plants after the drought and analyzed for N content using an ammonium analyzer (Model 360,

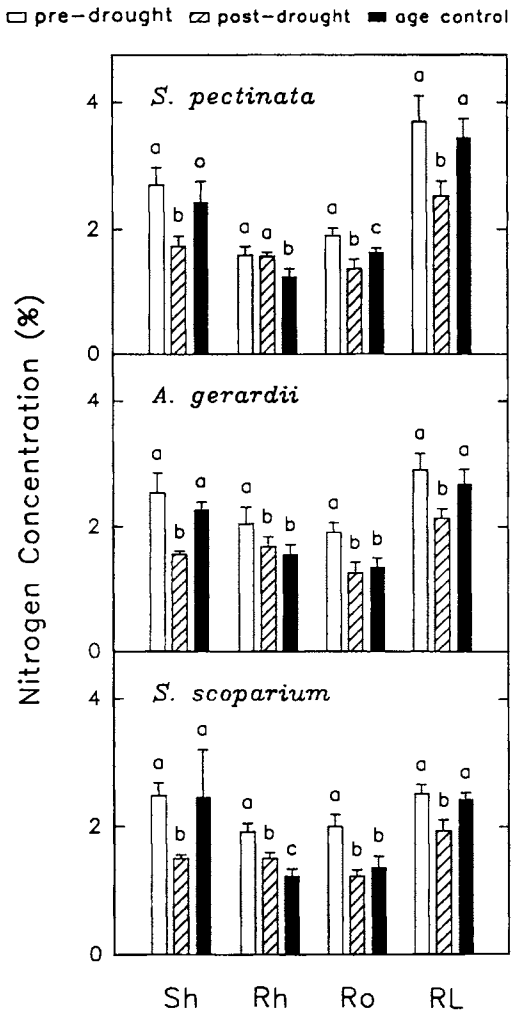

FIG. 2. Nitrogen concentration of shoots (Sh), rhizomes (Rh), roots (Ro), and recently expanded leaves (RL) of pre-drought (open bars), post-drought (shaded bars), and age-control plants (solid bars) of *Spartina pectinata, Andropogon gerardii,* and *Schizachyrium scoparium.* Significant differences ($P < 0.05$) among treatments are indicated by different letters above the bars. Error bars = 1 SD.

Wescan Instrument, Santa Clara, California, USA). Because the two most mesic species in this experiment, *S. pectinata* and *P. virgatum,* produce culms, we separated *S. pectinata* shoots into blades and culms to determine if N was retranslocated from both of these tissues.

Age controls in this experiment were not harvested because well-watered control plants of all species flowered during the drydown. Thus, estimates of retranslocation from pre- and post-drought comparisons may be conservative, relative to post-drought and age-control comparisons (see *Results,* Fig. 3).

Instantaneous net CO_2 assimilation was measured on recently expanded leaves at an irradiance of 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (PPFD) using a portable open-flow photosynthesis system (Parkinson leaf chamber and LCA-2 CO_2 analyzer, Analytical Development, England). Measurements were made during and after drought. Carbon dioxide concentration of air entering the cuvette was 350–365 cm^3/m^3. Air temperatures in the greenhouse, where measurements were made, were 27°–33°C, and leaf temperatures were within 1.5°C of air temperature. Photosynthesis over this temperature range changes little in these grasses (Kemp and Williams 1980, Knapp 1985). Leaf boundary layer conductances were estimated for each species using filter paper leaf replicates. Photosynthetic rates were calculated following von Caemmerer and Farquhar (1981).

Statistical analysis

Because of small sample sizes, statistical comparisons within and between species were conducted with parametric and nonparametric (Friedman) two-way analysis of variance (ANOVA). Student's *t* test or the least-significant-difference multiple-comparison test was then used to identify differences among treatments and species. Variances were tested for homogeneity using Bartlett's test. If parametric and nonparametric conclusions differed, the more conservative test result was accepted. Percentage data were arcsine transformed prior to parametric analyses following Zar (1974); however, means and error bars in figures are untransformed values. Statistical differences were accepted at the $P < 0.05$ level.

RESULTS

Shoot N concentration (%N) decreased during drought in all species in the N budget experiment (36–40%; Fig. 2). However, shoot %N of well-watered age controls was not significantly different from pre-drought plants. These same trends were observed for recently expanded leaves (23–32% decrease). In contrast, decreases in rhizome and root %N were of similar magnitude in drought-stressed and age-control plants, with three exceptions: rhizome %N of drought-stressed plants did not decline in *S. pectinata* and declined less than controls in *S. scoparium,* and root %N in *S. pectinata* decreased more in drought-stressed than control plants. Soil N concentration remained unchanged with drought in all species (data not shown).

The proportion of total plant N allocated to shoots decreased during drought in *S. pectinata* and *A. gerardii* (20 and 8%, respectively), but not in *S. scoparium* (Fig. 3). Shoot N remained unchanged or increased in age controls of all species. Nitrogen allocation to rhizomes increased in drought-stressed plants of all species, but not in controls, while allocation to roots decreased in age controls, but did not change in drought-stressed plants. Biomass allocation was largely reflective of N allocation in all three grasses (Fig. 3).

Results of the radioisotope experiment were consistent with the N-budget experiment (pre- vs. post-drought comparisons). The proportion of isotope in the shoot was 20% lower in drought-stressed *S. pec-*

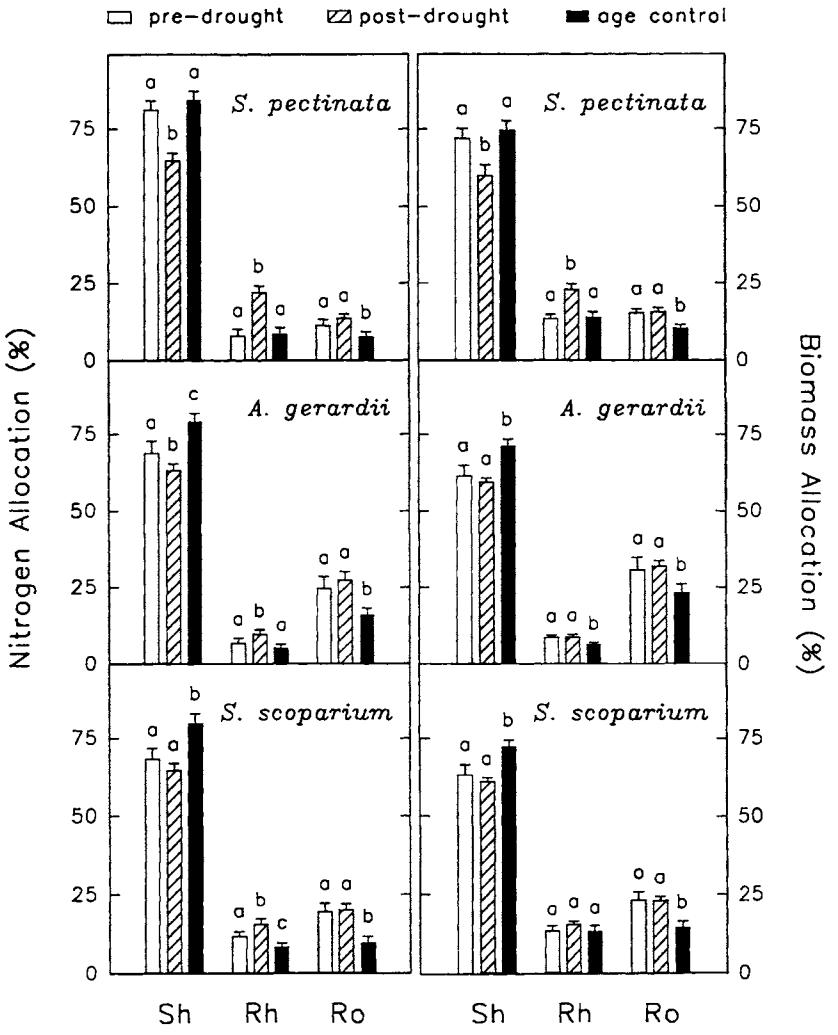

FIG. 3. Nitrogen and biomass allocation to shoots (Sh), rhizomes (Rh), and roots (Ro) of pre-drought (open bars), post-drought (shaded bars), and age-control plants (solid bars) of *Spartina pectinata, Andropogon gerardii,* and *Schizachyrium scoparium.* Significant differences ($P < 0.05$) among treatments are indicated by different superscripts. Error bars = 1 SD. Total plant N of pre-drought, post-drought, and age-control treatments, respectively, for each species are as follows: *S. pectinata* (115, 250, 523 mg); *A. gerardii* (89, 294, 541 mg); and *S. scoparium* (181, 339, 921 mg). Total plant dry mass for the same treatments are: *S. pectinata* (4.5, 14.8, 23.2 g); *A. gerardii* (3.9, 19.4, 26.5 g); and *S. scoparium* (8.0, 22.8, 42.6 g).

tinata plants relative to well-watered age controls, while the fraction found in rhizomes was higher (Fig. 4). Root radioactivity was lower in drought-stressed plants. The shoot isotope fraction also declined (12%) in *A. gerardii* during drought, but only soil radioactivity increased in this species. No changes in distribution of ^{35}S occurred with drought in *S. scoparium.*

Within each species and treatment, distribution of radioisotope among shoots, rhizomes, and roots was similar to biomass allocation to these tissues (Fig. 4). The only significant exception to this was seen in *S. pectinata,* where the fraction of total plant ^{35}S in shoots (drought-stressed plants) and roots (control and drought-stressed plants) was lower, and in rhizomes higher (both treatments), than the fraction of biomass allocated to these compartments.

Shoot %N decreased during drought in all six species in the photosynthesis experiment (31–41%; Fig. 5). Root and rhizome %N also decreased in each species, with the exception of root %N in *S. pectinata* and rhizome %N in *A. gerardii.* In only three species were appreciable changes in allocation of whole-plant N observed (Fig. 6). The proportion of total plant N found in shoots decreased in *S. pectinata, P. virgatum,* and *A. gerardii* (relative decreases of 29, 12, and 8%, respectively), while N allocation to rhizomes increased in all three species and root allocation increased in the two mesic species.

Photosynthesis, leaf N concentration, and midday water potential of drought-stressed plants 1 d after rewatering was lower than pre-drought plants of all species (Fig. 7). Six days after rewatering, leaf water po-

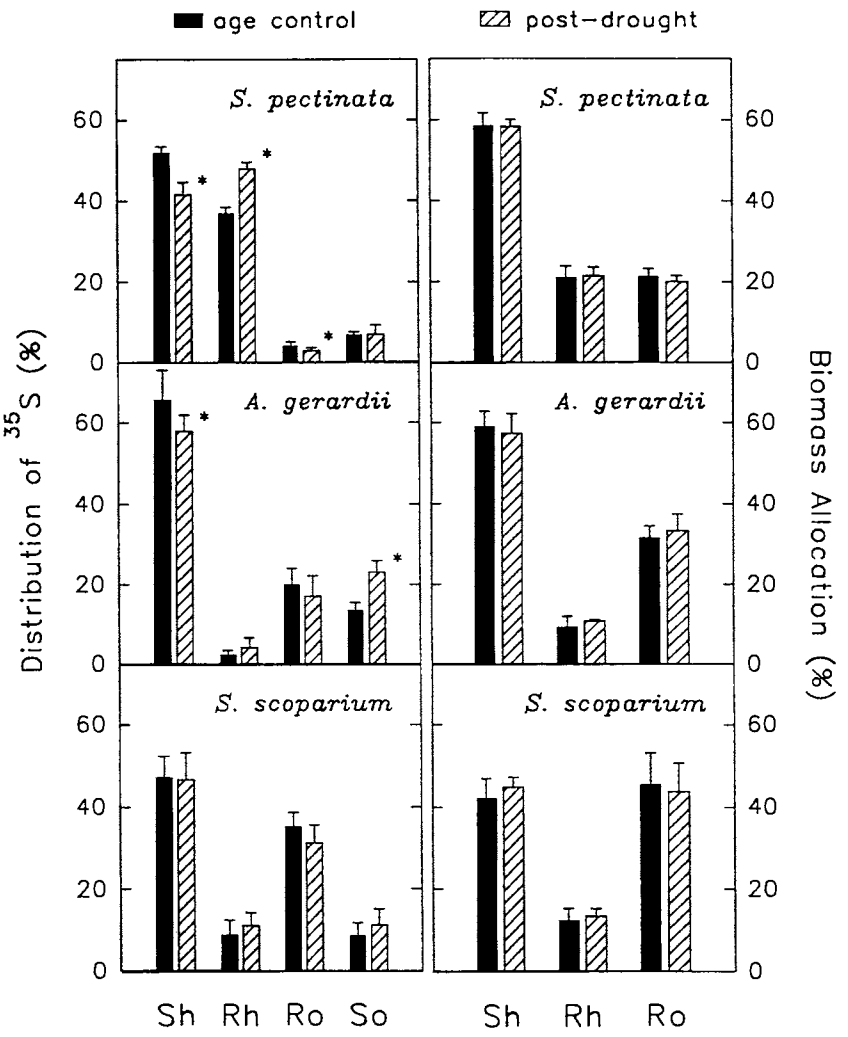

FIG. 4. Distribution of ^{35}S and biomass allocation to shoots (Sh), rhizomes (Rh), roots (Ro), and soil (So) of well-watered age controls (solid bars) and drought-stressed plants (shaded bars) of *Spartina pectinata, Andropogon gerardii,* and *Schizachyrium scoparium.* Significant differences ($P < 0.05$) between treatments are indicated with an asterisk. Error bars = 1 SD.

tentials had recovered to pre-drought levels, yet photosynthesis and leaf N had not recovered.

DISCUSSION

Drought-induced retranslocation of shoot N to rhizomes and roots in perennial C_4 prairie grasses was a whole-shoot phenomenon and was not associated simply with accelerated senescence of older foliage. Nitrogen content declined in culms and blades as well as in recently expanded leaves (Figs. 2, 6, and 7), and leaf death during the drought was negligible. In most species, shoot N was moved primarily to rhizomes with smaller changes in root N content (Figs. 3, 4, and 6). For *A. gerardii,* recovery of ^{35}S from the soil suggests that some of the shoot N was moved to roots and lost as fine-root turnover or exudation (Fig. 4). In contrast to autumnal retranslocation, drought-induced N movements are reversible. If adequate late season rains occur, resumption of N uptake can lead to total shoot N amounts in excess of early season levels in field-grown plants (McKendrick et al. 1975).

Continued uptake and sequestration of N in roots and rhizomes during drought could explain the observed changes in N reallocation (Figs. 3 and 6). However, results of the radio-labelling experiment (Fig. 4), coupled with the observation that shifts in N allocation generally exceeded shifts in biomass allocation (Fig. 3), indicate that net movement of shoot N to belowground tissues occurred during drought and was not associated strictly with biomass reallocation. We conclude that shoot N was actively retranslocated during drought in these experiments.

The magnitude of retranslocation varied with experiment and, in some cases, whether post-drought N allocation was compared to pre-drought or age-control allocation. For example, the proportion of total plant N found in shoots decreased 20–29% in *S. pectinata,*

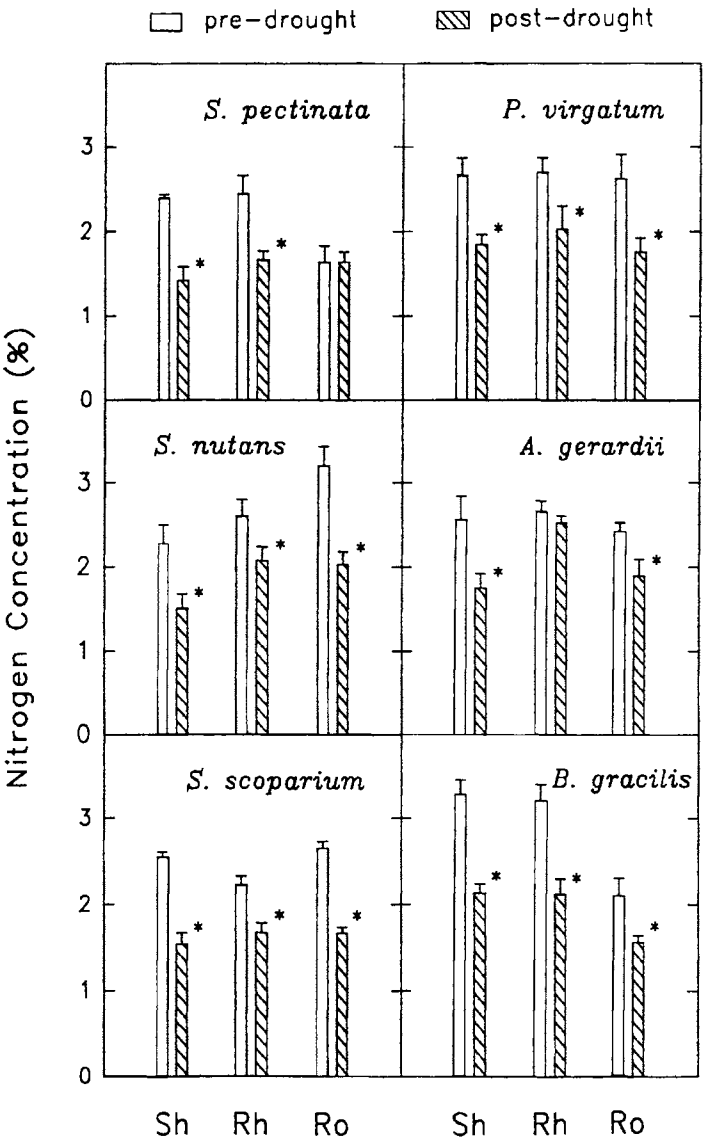

FIG. 5. Shoot (Sh), rhizome (Rh), and root (Ro) nitrogen concentration before (open bars) and after drought (shaded bars) for *Spartina pectinata, Panicum virgatum, Sorghastrum nutans, Andropogon gerardii, Schizachyrium scoparium,* and *Bouteloua gracilis.* Significant differences ($P < 0.05$) between harvests are indicated with an asterisk. Error bars = 1 SD.

8% in *A. gerardii,* and did not change significantly in *S. scoparium* for post- vs. pre-drought comparisons (Figs. 3 and 6). This same trend was observed for post-drought/age-control comparisons in the isotope experiment (allocation to shoots decreased 20% in *S. pectinata,* 12% in *A. gerardii,* and 0% in *S. scoparium*; Fig. 4), suggesting that mesic species may retranslocate more shoot N than xeric species. However, the apparent degree of retranslocation was similar among species in the N-budget experiment, when based on post-drought vs. age-control values (19–21%; Fig. 3). Plants were older (10 wk at the start of the drydown) and larger in this experiment than in the isotope experiment (8 wk), where we did not see shifts in biomass allocation in age controls, suggesting a possible interaction between size and retranslocation. Therefore, neither post-drought/pre-drought or post-drought/age-control comparisons may be perfectly valid when calculating the magnitude of retranslocation in older plants; the ideal comparison would be with plants of similar size. The use of similar-size plants when examining plant allocation responses has been suggested in the past by others (Evans 1972, Coleman et al. 1993).

The proportion of shoot N retranslocated during drought in these greenhouse experiments is probably similar to that remobilized in field-grown plants. Shoot N concentration of *A. gerardii* plants in these experiments was within the range of values reported for naturally occurring plants (McKendrick et al. 1975, Hayes 1985), indicating that soil N availability was compa-

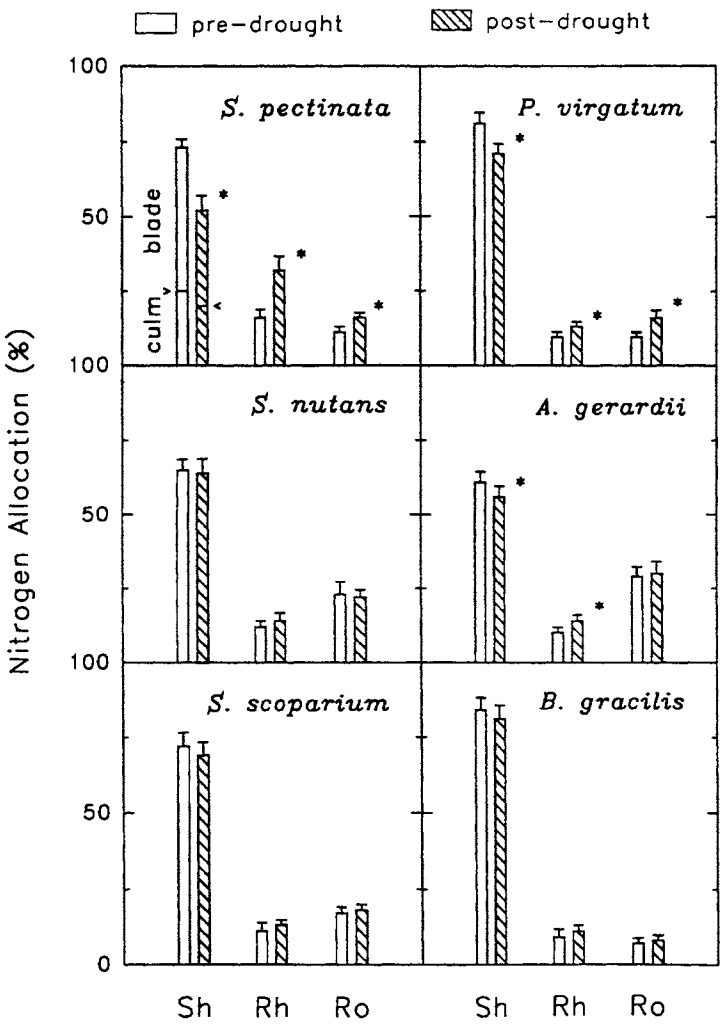

FIG. 6. Nitrogen allocation to shoots (Sh), rhizomes (Rh), and roots (Ro) before (open bars) and after drought (shaded bars) for *Spartina pectinata, Panicum virgatum, Sorghastrum nutans, Andropogon gerardii, Schizachyrium scoparium,* and *Bouteloua gracilis.* Significant differences between harvests are indicated with an asterisk ($P < 0.05$). Error bars = 1 SD.

rable to field situations. In addition, we subjected plants to droughts similar in severity and duration to those experienced by plants in the field.

Some of the shoot N retranslocated to belowground tissues during drought in these grasses was apparently derived from photosynthetic proteins, as suggested by incomplete recovery of photosynthesis and leaf %N following resumption of daily watering and recovery of leaf water potential (Fig. 7). In addition to retranslocation, volatilization (gaseous loss) of foliar N and dilution of existing leaf N (as growth continues while uptake of soil N declines) also contribute to decreases in leaf N concentration. The relative importance of these processes appears to be species dependent (S. A. Heckathorn and E. H. DeLucia, *unpublished data*). Given the strong relationship between leaf N content and maximum photosynthesis (Field and Mooney 1986), it was not surprising that photosynthetic capacity declined as %N decreased. Although photosynthesis would be limited by stomatal closure during drought, potential carbon fixation following precipitation may be limited by low foliage N concentration until leaf N returns to pre-drought levels. Thus, N retranslocation during drought probably reduces carbon gain during intermittent rainfall.

The ecological significance of drought-induced N retranslocation is unknown. Del Arco et al. (1991) suggested that seasonal retranslocation may represent a compromise between carbon acquisition and N conservation. We postulate that the same trade-off between carbon and nitrogen may exist for drought-induced N retranslocation. Availability of inorganic N is very low throughout the growing season in tallgrass prairie soils (Knapp and Seastedt 1986, Seastedt and Hayes 1988; and C. W. Rice, *personal communication*), and N is the primary nutritional limitation to productivity in this ecosystem (Risser and Parton 1982, Hayes 1986). Furthermore, soil N availability decreas-

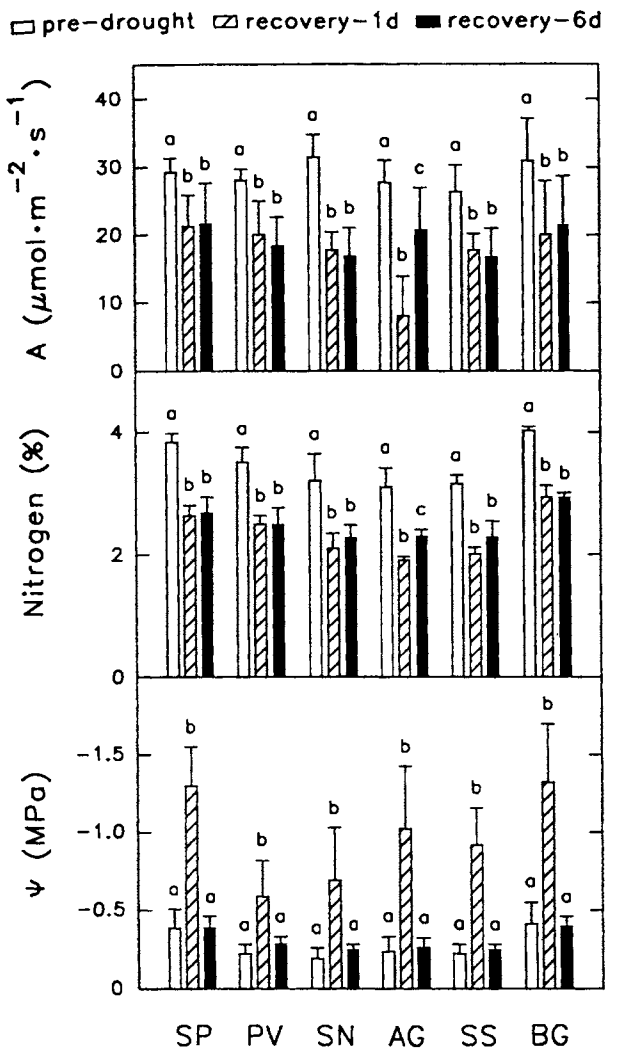

FIG. 7. Net CO_2 assimilation (A), nitrogen concentration, and midday water potential (Ψ) of recently expanded leaves of *Spartina pectinata* (SP), *Panicum virgatum* (PV), *Sorghastrum nutans* (SN), *Andropogon gerardii* (AG), *Schizachyrium scoparium* (SS), and *Bouteloua gracilis* (BG). Open bars are pre-drought plants, shaded bars are post-drought plants 1 d following resumption of daily watering, and solid bars are plants 6 d after watering. Significant differences ($P < 0.05$) among treatments are indicated by different superscripts. Error bars = 1 SD.

es with decreasing soil moisture (Stanford and Epstein 1974).

A large part of the growing season in tallgrass prairie is characterized by extended periods of limited water availability (Brown and Bark 1971, Knapp 1984), and thus extremely low available soil nitrogen. Consequently, perennial grasses accumulate most (e.g., >85%; McKendrick et al. 1975) of their annual N prior to onset of the summer drought, ≈30–40% of which can come from recycling plant N from the previous year (Clark 1977, Adams and Wallace 1985). Thus, by retranslocating 25% of shoot N to rhizomes or roots, prairie grasses could protect nearly 20% of total plant N from loss to herbivory, fire, or volatilization, which represents ≈30% of N acquired annually from the soil.

Evolution of prairie species is heavily influenced by combined selective pressures of fire, grazing, seasonal drought, and low available soil N (McNaughton et al. 1982). Fire is thought to have occurred every 1–4 yr over much of the prairie (Bragg and Hulbert 1976, Reichman 1987), and the potential for loss of foliar N via fire increases during summer droughts. The potential for loss to herbivory (e.g., cattle and bison grazing) is everpresent. Because of low soil N, plants may be forced to replace lost foliage N with that stored in the rhizome during summer months, possibly decreasing survival and future growth (Vinton and Hartnett 1992).

Plants at Konza prairie experience 5–6 periods of 7 d or more without rain during an average growing season (S. A. Heckathorn and E. H. DeLucia, *unpublished data*). We hypothesize that drought-induced retranslocation of shoot N to roots or rhizomes in prairie grasses limits potential loss of N to herbivory, fire, and volatilization during periods when drought curtails uptake of soil N and efficient photosynthetic utilization of leaf N. A cost associated with this strategy may be decreased carbon assimilation following precipitation. Because prairie grasses generally experience multiple droughts during the growing season, the carbon cost of retranslocating shoot N may increase with the magnitude of retranslocation, setting limits on the amount of N remobilized and on the benefits of retranslocation.

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