

Retranslocation of shoot nitrogen to rhizomes and roots in prairie grasses may limit loss of N to grazing and fire during drought

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Summary

1. It has previously been shown that perennial C₄ grasses of tallgrass prairie retranslocate up to 30% of shoot nitrogen (N) to rhizomes and roots in response to water stress and that retranslocation contributes to drought-related decreases in shoot N concentration and photosynthetic capacity, resulting in decreased post-drought carbon gain for 1–2 weeks.

2. In this paper the following hypothesis is tested: under N-limited conditions, the benefits of retranslocation may include limiting loss of shoot N to grazing (or fire) during drought, resulting in increased end-of-season whole-plant biomass, N content, and reproduction. All shoot tissue was removed from young N-limited plants either before or after drought, thereby preventing or allowing the opportunity for retranslocation, and the effects of each clipping treatment on biomass and N content after flowering and senescence were determined.

3. In *Spartina pectinata*, a mesic species that remobilizes 20–30% of shoot N during drought, plants clipped before drought (no retranslocation) had decreased biomass, N content, and tiller (but not seed) production relative to plants clipped after drought. In contrast, *Schizachyrium scoparium*, a xeric species that retranslocates little shoot N, exhibited decreased biomass, N content, and tiller and seed production in plants clipped after drought: the result of growth-related increases in total shoot N during drought, and thus greater N loss in plants clipped after drought. Time of clipping had no effect on *Andropogon gerardii*, a species of intermediate drought tolerance that retranslocates ca. 10% of shoot N during drought.

4. These results support the hypothesis that drought-induced shoot N retranslocation to below-ground tissues represents a trade-off between N protection and post-drought carbon assimilation in prairie grasses.

Key-words: Nutrients, remobilization, tallgrass prairie, water stress

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Introduction

Perennial C₄ grasses of tallgrass prairie retranslocate as much as 30% of shoot N to roots and rhizomes in response to drought, with mesic species appearing to retranslocate shoot N to a greater extent than xeric species (Heckathorn & DeLucia 1994). Retranslocation can account for up to 70% of the 30–40% decline in shoot N concentration during drought in these species (the remainder is due to growth dilution and volatilization) and by itself can account for 20% or more of the decrease in photosynthetic capacity

(Heckathorn 1995; Heckathorn & DeLucia 1995). Whole-plant recovery of foliar N concentration and maximum photosynthesis requires 1–2 weeks, resulting in a decrease in potential post-drought carbon gain (Heckathorn 1995; Heckathorn & DeLucia 1994).

Although water-stress-related movement of nutrients has now been observed in several species (see Heckathorn & DeLucia 1994 and references therein), the ecological and physiological significance of this retranslocation has not been studied. Drought-induced retranslocation of shoot N in prairie grasses may represent a compromise between carbon acquisition and N conservation (Heckathorn & DeLucia 1994). Del Arco, Escudero & Garrido (1991) presented a similar hypothesis to explain patterns of retranslocation of N

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from abscising leaves during seasonal drought in woody species of central Spain. They suggested that prolonged leaf retention and photosynthetic activity in xeric species during the dry season comes at the expense of inefficient resorption of foliar N prior to leaf abscission. We reasoned that for prairie grasses, retranslocation of shoot N may limit losses of foliar N to fire and herbivory at a time when uptake of soil N and efficient photosynthetic utilization of leaf N are limited by water availability and stomatal closure. A potentially negative consequence of N retranslocation is decreased post-drought carbon gain.

The adaptive significance of retranslocation in tallgrass prairie may be related to the extremely high levels of herbivory (McNaughton 1991), the high frequency of fire (Risser 1985; McNaughton, Coughenour & Wallace 1982) and the low availability of inorganic soil N in tallgrass prairie (Knapp & Seastedt 1986; Seastedt & Hayes 1988). Available soil N decreases further during drought (Stanford & Epstein 1974; McNaughton *et al.* 1982; Chapin 1991), which is common in tallgrass prairie (Brown & Bark 1971; Knapp 1984; Heckathorn 1995). Consequently, N is the most limiting mineral resource in tallgrass prairie (McNaughton *et al.* 1982; Risser & Parton 1982; Hayes 1986, and prairie species accumulate 80–90% of their annual N before the dry portion of the growing season (McKendrick, Owensby & Hyde 1975; Adams & Wallace 1985). Retranslocation may thus protect what is often irreplaceable shoot N from loss to herbivory and fire during summer drought.

For mesic species that experience drought infrequently, the seasonal photosynthetic costs of retranslocation may be small, but for xeric species that usually experience multiple droughts during the growing season, the carbon costs of N retranslocation (i.e. the integrated post-drought decrease in CO₂ assimilation) may be substantial. In this study, the following hypothesis was tested: under N-limited growth conditions, drought-induced retranslocation of shoot N to below-ground tissues can limit loss of N to herbivory (and fire) during drought, thereby increasing end-of-season whole-plant biomass, N status, and reproduction. To test this hypothesis, shoot tissue was removed from young N-limited plants either before or after drought. Plants clipped before drought had no opportunity to remobilize shoot N to root or rhizomes, whereas plants clipped after drought had the opportunity to remobilize shoot N. The effects of each clipping treatment on plant biomass and N content after end-of-season senescence were then measured. To the authors' knowledge, this study and related work examining the photosynthetic costs associated with drought-induced shoot N retranslocation (Heckathorn 1995; S. A. Heckathorn, unpublished results) are the first studies to extend beyond documenting such retranslocation and explore the ramifications of nutrient movement induced by water stress.

Materials and methods

The consequences of shoot tissue removal and drought were examined in three rhizomatous perennial C₄ grasses native to tallgrass prairie. *Spartina pectinata* Link (Prairie Cordgrass), *Andropogon gerardii* Vitman (Big Bluestem) and *Schizachyrium scoparium* (Michx.) Nash (Little Bluestem) encompass a range of drought tolerance from mesic to xeric (i.e. *Spartina pectinata* is the most mesic and *Schizachyrium scoparium* is the most xeric; Weaver & Fitzpatrick 1932; Heckathorn 1995). These species also represent a range of abilities to retranslocate shoot N during drought: *Spartina pectinata* and *Schizachyrium scoparium* are the extremes, retranslocating up to 30% and 5% of shoot N, respectively, during a 2–3 week drought (Heckathorn & DeLucia 1994).

Plants were grown in a greenhouse at the University of Illinois from mixed seed collected from many plants at the Konza Prairie Research Natural Area (Manhattan, KS). Individual plants (24 per species) were grown in 22-L pots containing loam, calcite clay, and sand (1 : 1 : 1, v : v : v) under 15 h, 30 °C days and 20 °C nights. Maximum daytime irradiance (natural plus supplemental) at pot height was 700–2000 µmol m⁻² s⁻¹ photosynthetic photon flux (PPF). Plants were watered daily at the soil surface, to prevent leaching of foliar N, and a commercial NPK fertilizer was applied weekly.

A 21-day controlled drought, similar in duration and severity to what might be experienced in the field, was imposed after 8 weeks of growth as in Heckathorn & DeLucia (1994). Briefly, the rate at which water stress was imposed was controlled by monitoring leaf water potential and by weighing plants (in their pots) daily and partly replenishing water lost over the previous 24 h, such that *ca.* 50% of the decrease in plant water status occurred over the first half of the 21-day drought. Both clipped and unclipped plants were drought stressed to the point of complete stomatal closure; i.e. to approximately -4 MPa midday leaf water potential for *Spartina pectinata*, -6 MPa for *A. gerardii* and -7 MPa for *Schizachyrium scoparium*. A subset of plants ($n = 8$ per species) was clipped to 3 cm above the soil surface at the start of the drought, thereby eliminating any opportunity for retranslocation of shoot N during drought (Fig. 1). A second subset of plants was clipped at the end of the drought, and thus had the opportunity to retranslocate shoot N. Because it was expected that any protective benefits of N retranslocation would be realized only under N-limited growing conditions, it was necessary to demonstrate that total seasonal available N was limiting for clipped plants. To demonstrate this, control plants remained unclipped and well watered throughout the drydown, so that it could be determined whether clipping and drought together decreased total plant N content.

Daily watering was resumed after the drought, but fertilization was not (neither drought-stressed nor control plants received fertilizer during the drought), thus establishing 'seasonal' limitations on available N for each plant. Plants were grown for an additional three months until flowering and senescence occurred, at which time all plants were harvested and separated into roots, rhizomes/crowns, shoots, and infructescences. Tissues were dried at 60 °C for 48 h and weighed. Plant material, including tissue removed by clipping, was then analysed colorimetrically for total organic nitrogen content following acid digest (nitroferrocyanide reaction, Traacs 800, Bran-Luebbe, Buffalo Grove, IL).

Results were analysed statistically with a two-way (species × clipping treatment) analysis of variance (ANOVA). Tukey's multiple-comparison test was used to identify significant differences among treatments and species. Variances were tested for homogeneity with Bartlett's test.

Results

Total end-of-season biomass and N content were greater in *Spartina pectinata* plants clipped after the drought than in plants clipped before, but there was no difference in biomass and N content between 'before' and 'after' plants of *A. gerardii* (Fig. 2). In *Schizachyrium scoparium*, plants clipped before the drought had greater biomass and N than plants clipped after, a reversal of the situation observed in *Spartina pectinata*. Biomass and N content of unclipped well-watered controls exceeded clipped plants in all species. The N content of tissue removed by clipping was greater for plants clipped before drought in *Spartina pectinata*, but greater for plants clipped after drought in *A. gerardii* and *Schizachyrium scoparium*. In contrast, more biomass was removed from plants clipped after drought than from plants clipped before drought in all species (data not shown)

The trends observed for above-ground tiller production were similar to those for total biomass and N

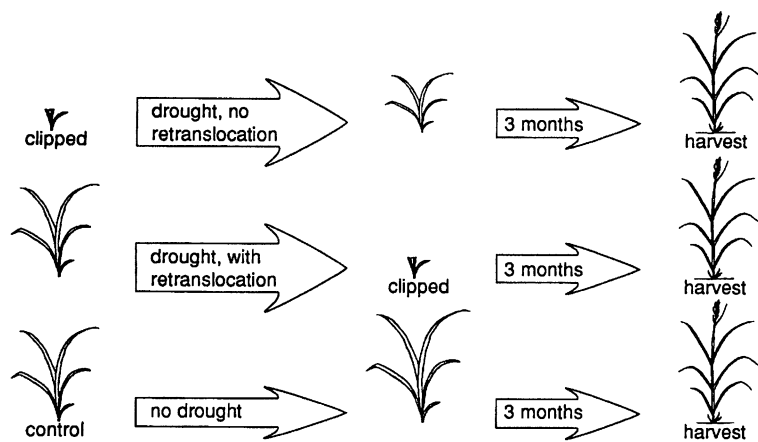


Fig. 1. Diagram of experimental design illustrating timing of clipping treatments and harvest.

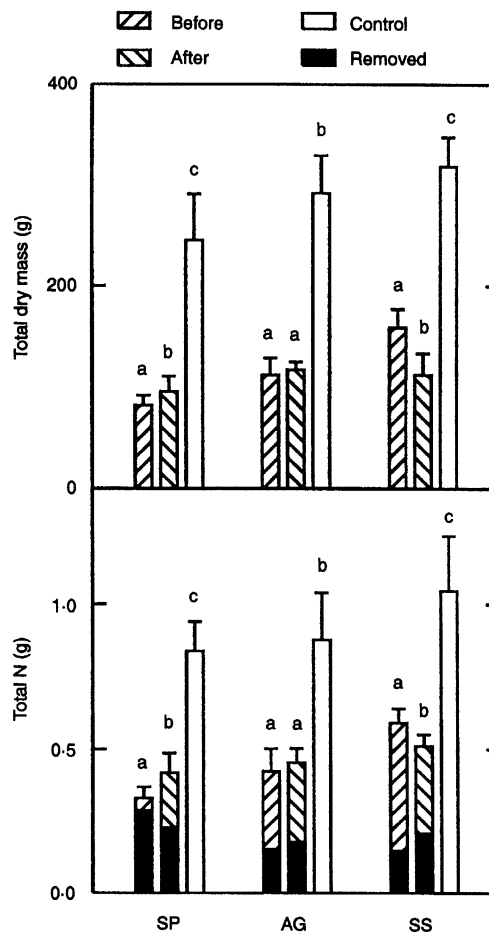


Fig. 2. Total end-of-season biomass and N content of *Spartina pectinata* (SP), *Andropogon gerardii* (AG) and *Schizachyrium scoparium* (SS) plants clipped before or after drought (hatched bars) or plants remaining unclipped and well watered (open bars). Also shown is the total N content of tissue removed by clipping (solid overlay). Significant differences ($P < 0.05$) among clipping treatments (excluding removed tissue) are indicated by different superscripts; no significant differences were observed when removed tissue was included in the analysis. Error bars = 1 SD.

(Fig. 3). Plants clipped after drought produced more tillers in *Spartina pectinata* than plants clipped before, whereas the reverse was true for *Schizachyrium scoparium*; tiller number was the same for plants clipped before and after drought in *A. gerardii*. Control plants produced more tillers than either set of clipped plants in *Spartina pectinata* and *Schizachyrium scoparium*, but not in *A. gerardii*, in which controls produced no more tillers than clipped plants.

As with measures of vegetative productivity, *S. scoparium* plants clipped after drought exhibited decreased infructescence mass and N content relative to plants clipped before, but no difference was observed between *A. gerardii* plants clipped before and after drought (Fig. 3). In contrast to vegetative growth, *Spartina pectinata* also exhibited no difference in infructescence mass and N in plants clipped before and after drought. Controls had greater infructescence mass and N than either group of clipped plants in all species.

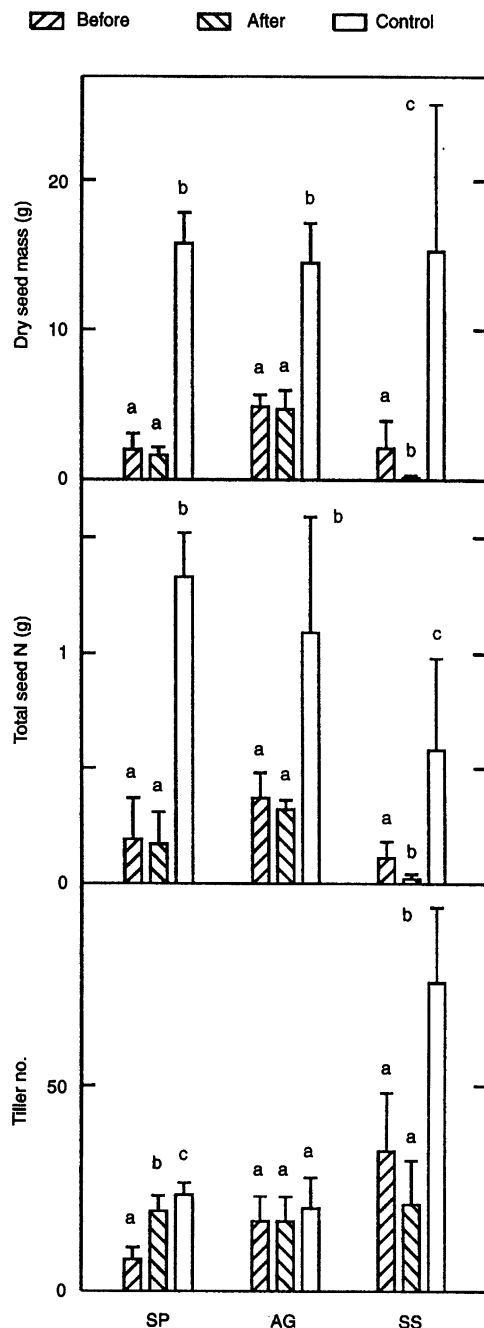


Fig. 3. Total end-of-season infructescence (seed) mass and N content and above-ground tiller number of *Spartina pectinata* (SP), *Andropogon gerardii* (AG) and *Schizachyrium scoparium* (SS) plants clipped before or after drought (hatched bars) or plants remaining unclipped and well watered (open bars). Significant differences ($P < 0.05$) among clipping treatments are indicated by different superscripts. Error bars = 1 SD.

Discussion

Under N-limited growth conditions, drought-induced retranslocation of shoot N to roots and rhizomes can limit loss of N to simulated herbivory (i.e. clipping) during drought, increasing end-of-season whole-plant biomass and N content. Eliminating the opportunity for retranslocation (clipping before drought) in *S. pectinata*, a mesic species that remobilizes 20–30% of

shoot N during drought, decreased total plant biomass, N content, and tiller production relative to plants that had the opportunity to retranslocate shoot N. Retranslocation did not increase infructescence biomass and N content, however. These results would presumably have been similar had shoot N been lost to fire rather than clipping.

In contrast to *S. pectinata*, *Schizachyrium scoparium*, a xeric species that retranslocates little shoot N during drought, exhibited decreased biomass, N content, and tiller and seed production in plants clipped after drought. No effect of timing of clipping was observed in *A. gerardii*, a species of intermediate drought tolerance that retranslocates ca. 10% of shoot N during drought. *S. scoparium* and *A. gerardii* are frequently subjected to drought (e.g. Weaver & Fitzpatrick 1932; Knapp 1984) and probably fix a significant fraction of their seasonal C during and after intermittent drought, so the C costs associated with retranslocation (i.e. decreased post-drought C gain) may be greater in these xeric grasses. In contrast, *Spartina pectinata* experiences prolonged drought infrequently and does not remain photosynthetically active during drought as do *Schizachyrium scoparium* and *A. gerardii* (Heckathorn & DeLucia 1995; Heckathorn 1995). The results of this study are thus consistent with the hypothesis that drought-induced shoot N retranslocation to below-ground tissues represents a trade-off between N protection and post-drought carbon assimilation in prairie grasses.

The potential protective benefits of shoot N retranslocation appear to be related to the magnitude of retranslocation relative to soil N uptake during drought. More N was removed from plants clipped before than plants clipped after drought in *Spartina pectinata*, presumably because net retranslocation of shoot N to roots and rhizomes occurred during drought. However, the reverse was true for the two more xeric species. In *A. gerardii*, and especially in *Schizachyrium scoparium*, more N was removed by clipping after drought than before because soil N uptake continued during drought to the extent that there was an increase in total shoot (and plant) N. No significant differences in total N existed between clipping treatments in any of the species when the N content of clipped tissue was added to end-of-season plant N values (the sum of hatched and solid bars in Fig. 2). Therefore, differential effects of clipping treatments on end-of-season biomass, N status, and tiller number were explained primarily by differences in the total N content of tissue removed by clipping.

The lack of difference between clipping treatments in the sum of removed N plus end-of-season N also indicates that patterns in final plant biomass and N content were not the result of the 21-day differential as to when plants were clipped; i.e. plants clipped both before and after drought had reached their full biomass and N potential by 'end-of-season' harvest in the greenhouse. These observations, and the fact that

biomass and N content of well-watered unclipped controls exceeded biomass and N content of both sets of clipped plants in all species, even if removed N was considered, together indicate that clipping and drought each imposed seasonal N limitations on clipped plants and that all clipped plants had reached this N limit by final harvest.

Under resource-limited conditions, shoot regrowth after grazing or fire is often at the expense of below-ground productivity, especially in taller grass species (Risser 1985; Georgiadis *et al.* 1989; McNaughton 1991). This can have detrimental effects on growth and survival the following year (Risser 1985; Vinton & Hartnett 1992). These past studies suggest that the protective benefits of drought-induced shoot N retranslocation in prairie grasses may extend beyond increasing end-of-season biomass, N content, and tiller number, as in this study, and affect overwinter survival or early-season growth the following spring. In addition, there are likely to be other ecological and physiological consequences associated with drought-related movement of nutrients that remain to be uncovered; the study described here represents only an initial foray into this previously unexplored subject.

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