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Ammonia volatilization during drought in perennial C₄ grasses of tallgrass prairie

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Abstract We measured foliar NH₃ volatilization as part of our study of the decrease (up to 40%) in shoot N concentration during drought in three perennial C₄ grasses of tallgrass prairie. Volatilization of recently expanded leaves was quantified using cuvettes and acid traps for *Spartina pectinata*, *Andropogon gerardii*, and *Schizachyrium scoparium*, a mesic, intermediate, and xeric species, respectively. In general, volatilization decreased during drought, approaching zero as stomates closed, and increased with plant N status and drought tolerance. Prior to drought, NH₃ volatilization was greater in xeric than mesic species (179 and 131 vs. 115 ng m⁻² s⁻¹ for individual leaves of *S. scoparium* and *A. gerardii* vs. *Sp. pectinata*). During a 2–3 week drought, whole-shoot volatile N losses can exceed 5% of total plant N in these species, accounting for 2–10% of the decrease in shoot percent N (again, xeric > mesic). Drought-induced N retranslocation of shoot N to roots and rhizomes is responsible for c. 63% of the decrease in percent N in *Sp. pectinata*, 28% in *A. gerardii*, and 8% in *S. scoparium*. The remainder of the decrease in percent N is attributable to growth dilution of existing shoot N, accounting for 34, 65, and 87% of the decrease in shoot percent N during drought in *Sp. pectinata*, *A. gerardii*, and *S. scoparium*, respectively. Thus, the relative importance of volatilization, retranslocation, and dilution in decreasing foliar percent N during drought in prairie grasses is species dependent and related to drought tolerance.

Key words Ammonia volatilization · Drought · Nitrogen
Prairie grasses · Retranslocation

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Introduction

Volatile or gaseous loss of nitrogen from plant foliage can be substantial (Wetselaar and Farquhar 1980; Schjøerring 1991), in some cases exceeding 10% of total plant N over a 3–6 week period (Schimel et al. 1986; San Jose et al. 1991; Weiland and Ta 1992). This lost N, volatilized primarily in reduced form as ammonia (and perhaps other amines; Weiland and Stutte 1979, 1980, 1985; Wetselaar and Farquhar 1980), may decrease photosynthesis (Heckathorn 1994). However, it may also prevent accumulation of toxic levels of NH₃ in leaf tissues (Rabe 1990; Schjøerring et al. 1993b), as volatilization occurs when intercellular concentration exceeds ambient (Farquhar et al. 1980). When the reverse is true, NH₃ is absorbed by leaves; thus, plants may serve as sources or sinks for atmospheric NH₃.

Volatilization of NH₃ results when NH₄⁺-generating processes (e.g., protein degradation) exceed assimilation reactions, primarily those catalyzed by glutamate synthase (GOGAT) and glutamine synthetase (GS) (Schjøerring 1991). Therefore, evolution of NH₃ is often greatest when N remobilization rates are high, such as during reproduction and senescence, or when N availability is high (Rabe 1990; Schjøerring 1991 and references therein). Only 10–30% of volatilized N appears to be associated with photorespiration (Weiland and Stutte 1985; Morgan and Parton 1989), so rates of volatilization are similar among C₃ and C₄ species (Schjøerring 1991).

Measurements of volatilization from foliage of individual species have been limited almost exclusively to agronomic plants (Schjøerring 1991; but see Stutte and Weiland 1978; Weiland and Stutte 1979 for data from four weed species), even though NH₃ exchange has been studied in a number of ecosystems (Langford et al. 1992; Schlesinger and Hartley 1992). Ecosystem-level measurements by Langford et al. (1992) at the Konza Prairie Research Natural Area in Kansas suggest that prairie canopies may take up ambient NH₃ at certain times during the growing season. However, this study also demonstrates that NH₃ volatilization from canopies of tallgrass

prairie may be substantial at other times, such as early in the growing season when soil N uptake and plant growth is rapid, and hints that volatilization may increase during drier periods of the summer. An increase in NH_3 loss during drought is consistent with the observation by Weiland and Stutte (1979) of an increase in volatilization in one of two cultivars of unirrigated soybeans, but contrary to the results of Parton et al. (1988) in which volatilization decreased in mildly water-stressed wheat.

We measured NH_3 volatilization during drought in three dominant grasses representing a range of drought tolerance to identify possible interspecific differences in the response of volatilization to water stress. In a previous study (Heckathorn and DeLucia 1994), we documented drought-induced N retranslocation from shoots to root and rhizomes in these same species. In general, we observed greater N remobilization in mesic than xeric species. This suggests that volatile N losses during drought may be greater in mesic species.

Nitrogen availability may also influence N remobilization (Hayes 1986), and thus volatilization, in prairie grasses. Further, N availability, which can vary substantially in tallgrass prairie with precipitation, grazing, fire, and topography (Hobbs et al. 1991; Seastedt et al. 1991; Schimel et al. 1991), can itself affect rates of N volatilization. However, the effect of N availability on volatilization is not well understood and can vary with species and phenology (Schjøerring 1991). To determine the influence of N availability on volatilization in prairie grasses, we measured NH_3 loss from plants grown at two N fertilization levels.

Materials and methods

We examined the influence of drought and leaf N status on foliar NH_3 volatilization in three rhizomatous perennial C_4 grasses native to tallgrass prairie. These species encompass a range of drought tolerance from mesic to xeric in the following order: *Spartina pectinata* Link (prairie cordgrass), *Andropogon gerardii* Vitman (big bluestem), and *Schizachyrium scoparium* (Michx.) Nash (little bluestem) (Weaver and Fitzpatrick 1932; Heckathorn 1994).

Plants were grown in a greenhouse at the University of Illinois 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, v:v) under 15-h, 28°C days and 20°C nights. Minimum irradiance (natural plus supplemental) at pot height was $700 \mu\text{mol}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD). Half the plants of each species were fertilized (N:P:K) 4 and 6 weeks prior to imposition of drought, while the remaining plants received no fertilizer; all plants were watered daily at the soil surface. A 21-day controlled drought, similar in severity and duration to what plants might experience in the field (Heckathorn 1994), was imposed after 8 weeks of growth, as described in Heckathorn and DeLucia (1994).

Ammonia volatilization from recently expanded leaves of high and low N plants was measured prior to drought (pre-drought), at leaf water potentials at which leaf rolling began (mid-drought), and at water potentials at which stomatal closure was approximately complete (late drought) ($n=4-6$ previously unmeasured plants per species \times N status (2) \times H_2O status (3) = 24-36). Midday water potentials where leaf rolling occurred and stomates closed varied among species (see Results). Ammonia (and amine) volatil-

ization from four to ten leaf blades of a plant (i.e., parent plus tillers within a pot) was measured using 3-l teflon-coated fan-stirred plexiglass cuvettes and acid traps containing w/0.9 M H_2SO_4 and glass beads (2 mm diameter). Ambient air was pulled through cuvettes, because of persistent small cuvette leaks, and then pushed through acid traps at 2 l min^{-1} . Leaves were enclosed for 4-6 h between 10 and 4 p.m.; rolled water-stressed leaves were left rolled during measurements. A control cuvette without foliage was used to trap ambient NH_3 during this time, which was subtracted from foliage-containing cuvettes when calculating volatilization rates of leaves.

Because NH_3 is known to adsorb to teflon (Langford et al. 1992), cuvettes were immediately resealed after removing foliage and flushed for 1-2 h to collect any NH_3 adhering to cuvette walls. All cuvettes were then wiped with moistened paper towlettes. The towlettes were digested in acid and analyzed for N content. No additional N was recovered from the towlettes, indicating that flushing the cuvettes was sufficient to remove any adsorbed NH_3 . Ammonia (and amine) content of acid traps and total organic (Kjeldahl) N content of towlettes and acid-digested leaf tissue was determined colorimetrically (nitroferrocyanide reaction, Traacs 800, Bran-Luebbe, Buffalo Grove, Ill., USA).

Volatilization measurements were made in growth chambers, to minimize environmental variability, after allowing plants 24 h to acclimate to chamber conditions (equivalent to greenhouse conditions except for daytime air temperature). Air temperature within the cuvettes was maintained at 28-32°C by keeping growth chamber air temperature at 24°C and placing IR filters between the cuvettes and the light source. Cuvette leaf temperatures were monitored with fine-wire thermocouples and were within 3°C of

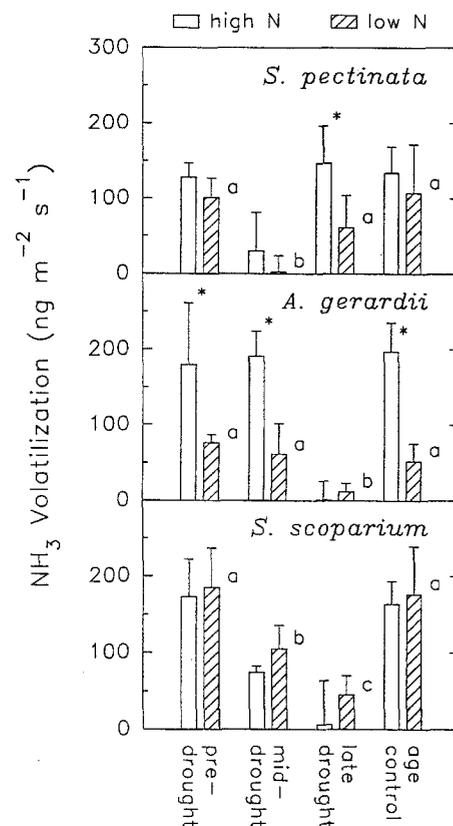


Fig. 1 Ammonia volatilization during drought from recently expanded leaves of *Spartina pectinata*, *Andropogon gerardii*, and *Schizachyrium scoparium* grown at two fertilization levels. Significant differences ($P < 0.05$) among drought stages (across N levels) are indicated by different superscripts and between N levels (within a drought stage) by an asterisk. Error bars = 1 SD (open columns high N, shaded columns low N)

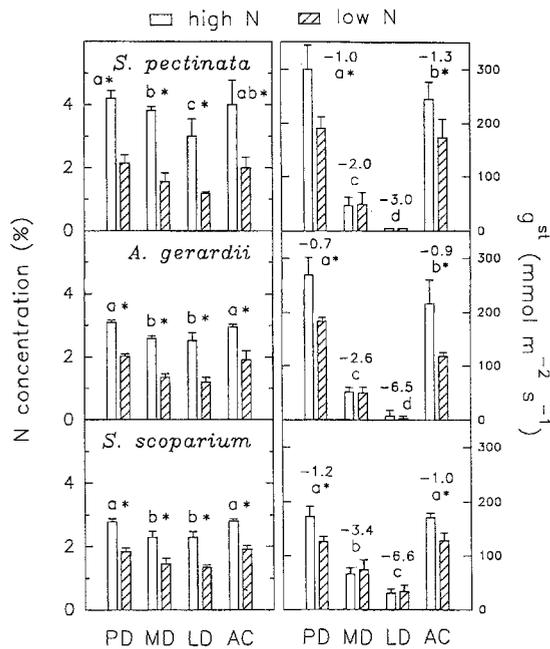


Fig. 2 Nitrogen concentration and stomatal conductance (g^{st}) during drought of recently expanded leaves of *Spartina pectinata*, *Andropogon gerardii*, and *Schizachyrium scoparium* grown at two fertilization levels (PD pre-drought, MD mid-drought, LD late drought, AC age control). Numbers inside right-hand panels are mean midday leaf water potentials (MPa) for high- and low-N plants combined. Significant differences ($P < 0.05$) among drought stages (across N levels) are indicated by different superscripts and between N levels (within a drought stage) by an asterisk. Error bars = 1 SD (open columns high N, shaded columns low N)

air temperature. Irradiance in the cuvettes was $1100 \pm 100 \mu mol\ m^{-2}\ s^{-1}$ PPFD.

Stomatal conductance and water potential were monitored on leaves both inside and outside the cuvettes using a null-balance porometer (LI-1600, LI-COR, Lincoln, Neb., USA) and pressure chamber (PMS Instrument Co., Corvallis, Ore., USA). Neither conductance or water potential changed significantly over the 4–6 h measurement period, nor differed appreciably between leaves in and out of the cuvettes. Therefore, we report only cuvette end-of-measurement period conductances and water potentials.

Results were analyzed statistically using three-way (species \times N status \times H₂O status) analysis of variance (ANOVA). Tukey's multiple-comparison test and Student's *t*-test were then used to identify significant differences among treatments and species. Variances were tested for homogeneity using Bartlett's test. Percentage data

were arcsine transformed prior to analysis; however, means and error bars in figures are untransformed values.

Results

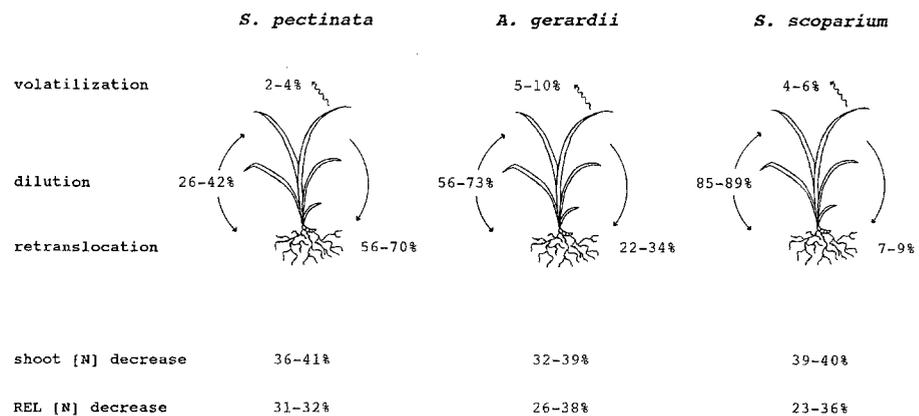
Ammonia volatilization varied among species and was influenced by water and N status (ANOVA, $P < 0.02$, 0.0001, and 0.0001, respectively). Volatilization in *Sp. pectinata* decreased through mid-drought, then increased dramatically late in the drought, at which time high N plants exhibited greater volatile N loss than low N plants (Fig. 1). Foliar volatilization remained high through mid-drought in *A. gerardii* before decreasing. Volatilization rates were greater in high-N plants of this species prior to late drought. Ammonia loss decreased through mid- and late drought in *S. scoparium*, and was not significantly affected by N status. Prior to drought, volatilization rates (across N levels) were significantly greater in *S. scoparium* than in *Sp. pectinata*; volatilization was intermediate in *A. gerardii*, but did not differ from the other species (one-way ANOVA and Tukey's, $P < 0.05$).

Leaf N concentration (%N, dry mass basis) was greater in high-fertilizer plants and decreased with drought in all species (Fig. 2). Foliar percent N decreased throughout the drought in *Sp. pectinata*, but did so through mid-drought only in the two more xeric species. Stomatal conductance (g^{st}) decreased throughout the drought in all species and was greater in high-N plants only at high water potentials (Fig. 2). Stomates were completely closed in the two more-mesic species during late-drought measurements (here g^{st} = cuticular conductance), but remained slightly open in *S. scoparium*. Leaf water potentials at the time g^{st} measurements were made (Fig. 2) differed between high- and low-N plants only in *S. scoparium* – mean water potentials were always higher (0.11–0.40 MPa higher depending on drought stage) in low-N plants (two-way ANOVA, $P < 0.01$).

Discussion

In general, but with notable exceptions, foliar NH₃ volatilization decreased during drought, approaching zero as

Fig. 3 Relative decrease in nitrogen concentration [N] of shoots and recently expanded leaves (REL) during a 2–3 week drought in *Sp. pectinata*, *A. gerardii*, and *S. scoparium*, and the proportion of that decrease attributable to foliar ammonia volatilization, shoot N retranslocation, and growth dilution during drought. Nitrogen concentration data and estimates of shoot N retranslocation are from two droughts, one of 2 weeks and the other of 3 weeks duration, described in Heckathorn and DeLucia (1994)



stomates closed, and increased with plant N status and drought tolerance (Fig. 1). Volatile N losses initially decreased during drought in the most mesic species, *Sp. pectinata*, then increased to pre-drought levels late in the drydown, despite complete stomatal closure and leaf rolling (Heckathorn and DeLucia 1991). In *A. gerardii*, a species of intermediate drought tolerance, volatilization remained high through mid-drought before declining, again despite decreasing stomatal conductance. For volatilization to increase, or even remain unchanged, as g^{st} decreases requires an increase in the NH_3 concentration gradient between leaf and atmosphere (Farquhar et al. 1980), indicating increased intercellular NH_3 levels during drought in *Sp. pectinata* and *A. gerardii*. There was no suggestion of such an increase in the most xeric grass, *S. scoparium*, as volatilization decreased throughout the drydown in this species.

High volatile-N losses in *Sp. pectinata* late in the drought, when growth is inhibited, appear to coincide with retranslocation of shoot N to roots and rhizomes in this species. In *A. gerardii*, continued high volatilization rates during mid-drought, when volatilization has decreased in the other two species, may also be related to shoot N retranslocation. *Sp. pectinata* retranslocates as much as 30% of shoot N to belowground tissues during drought while *A. gerardii* remobilizes up to 12% of shoot N; N retranslocation during drought is negligible in *S. scoparium* (Heckathorn 1994; Heckathorn and DeLucia 1994). Changes in N concentration of recently expanded leaves in this study suggest that shoot N is retranslocated late in the drought in *Sp. pectinata*, but early in the drought in *A. gerardii*.

In *Sp. pectinata*, 66 and 38% of the decrease in shoot N concentration occurred in the latter half of the drought in high- and low-N plants, respectively (Fig. 2), at a time when little photosynthesis (Heckathorn 1994; Heckathorn and DeLucia 1991), and hence growth, is occurring. Thus, growth dilution of existing foliar N cannot account for the decrease in leaf N concentration late in the drought. As discussed later, little of the decrease in foliar N concentration is attributable to volatilization in *Sp. pectinata*, indicating that drought-induced N retranslocation of shoot N is largely responsible for decreases in leaf N concentration in this species during late drought.

Leaf N concentration did not change significantly (3 and 10% for high- and low-N plants, respectively) over the second half of the drought in *A. gerardii* (Fig. 2); therefore, retranslocation of shoot N must have occurred prior to late drought in this species. As with *Sp. pectinata*, however, volatile N losses during drought in *A. gerardii* were high (in comparison to mid-drought plants of the other two species) when remobilization of shoot N was occurring and stomates were closing. This is consistent with increased volatilization in several agronomic species during flowering and fruit development, when extensive remobilization of plant N to seeds is occurring (Hooker et al. 1980; Schjörriering 1991, 1993a, b), and agrees with Stutte and Weiland (1978) and Weiland and

Stutte (1985) who also observed an uncoupling of volatilization and transpiration.

Volatilization rates were also influenced by plant N status and species in this study (Fig. 1). Nitrogen losses increased with N status in *Sp. pectinata* and *A. gerardii*, more so in the latter species, but were not significantly affected in *S. scoparium*. A trend towards greater volatilization in low-N plants of *S. scoparium* may perhaps be related to slightly higher water potentials. Differences among species were evident both in well-watered plants, where volatilization increased from mesic to xeric species, and in the pattern of volatilization throughout drought.

Maximum rates of volatilization observed in this study are within the range reported for agronomic species (Schjörriering 1991) and savannah, shortgrass, and tallgrass prairie communities (San Jose et al. 1991; Langford et al. 1992; using leaf area indices of 6, 2, and 4, respectively, to convert canopy-based rates to leaf-level fluxes). They are comparable to our own preliminary field measurements of the same species at Konza prairie (unpublished results). As mentioned earlier, Langford et al. (1992) observed increased NH_3 losses from prairie canopies during late summer. Although these authors did not provide data on plant water relations, nor indicate that these measurements were made on water-stressed plants, our data indicate that these late-season losses are not the result of drought. It is likely, then, that increased late-summer volatilization is associated with flowering and senescence of the dominant C_4 grasses, which occurs at this time of the growing season (Weaver and Fitzpatrick 1932).

Although the instantaneous rates of N loss in this study are small ($<200 \text{ ng m}^{-2} \text{ s}^{-1}$), we estimate that during a 2–3 week drought *Sp. pectinata* volatilizes 0.7–2.5% of total plant N, depending on plant N status. *A. gerardii* and *S. scoparium* lose 1.2–3.9% and 2.2–5.5% of total plant N, respectively. These estimates are based on a 14-h day during which the rate of volatilization is assumed to be constant (as in Schjörriering 1991), a 10-h night during which no N loss occurs, as is commonly used or conservative (Schjörriering 1991, 1993), and our own measurements of specific leaf mass and foliage mass throughout a drought. Our estimates of N loss may be somewhat conservative since they are based on volatilization rates of recently expanded leaves, which typically exhibit lower N loss rates than older foliage (Weiland and Stutte 1979; Schjörriering et al. 1993) and possibly younger foliage as well (Weiland and Stutte 1979).

Using our estimates of total volatilized N from this study and measurements of shoot N retranslocation and tissue N concentration from previous experiments conducted under comparable growth conditions and plant age (Heckathorn 1994, Heckathorn and DeLucia 1994), we can partition decreases in shoot N concentration during drought in these species among three processes – volatilization, retranslocation, and drought-related growth dilution. All other possible avenues for N loss (Wetselaar and Farquhar 1980) are accounted for or are

not pertinent to potted greenhouse plants experiencing drought (Heckathorn and DeLucia 1994).

As a result of volatilization, retranslocation, and dilution, shoot N concentration decreased 32–41% during drought, while N concentration of recently expanded leaves decreased 23–38% [Fig. 3; %N data and estimates of retranslocation are from Heckathorn and DeLucia (1994) from droughts of either 2-week or 3-week duration, hence the use of ranges to express changes indicated this figure]. Volatilization accounted for 2–10% of these decreases, depending on species. Retranslocation decreased shoot N concentration c. 63% in *Sp. pectinata*, 28% in *A. gerardii*, and 8% in *S. scoparium*. The remainder of the decrease in N concentration was attributable to drought-related growth dilution of existing shoot N, as growth was affected to a lesser extent than uptake of soil N during drought (Heckathorn and DeLucia 1994). Growth dilution of N during drought accounted for 34, 65, and 87% of the decrease in shoot N concentration in *Sp. pectinata*, *A. gerardii*, and *S. scoparium*, respectively.

Volatilization, retranslocation, and dilution all contribute to decreased shoot N concentration during drought, although the relative importance of each is species-dependent. In each species in this study, decreases in foliar N concentration during drought persist for more than a week following resumption of daily watering, resulting in decreased photosynthesis (Heckathorn 1994; Heckathorn and DeLucia 1994). During a single drought episode, volatilization plays the smallest role in decreases in shoot N concentration and post-drought photosynthesis in these species, but may have a large cumulative effect over the growing season because of recurrent drought typical of temperate grasslands (Borchert 1950; McNaughton et al. 1982).

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