Low-temperature Nitrogen Uptake and Use of Three Cool-season Turfgrasses under Controlled Environments

Daniel T. Lloyd
Division of Plant Sciences, Turfgrass Research Center, University of Missouri, 3600 East New Haven Road, Building 50, Columbia, MO 65201

Douglas J. Soldat†
Department of Soil Science, University of Wisconsin–Madison, 245 King Hall, Madison, WI 53706

John C. Stier
Department of Horticulture, University of Wisconsin–Madison, 381 Horticulture Building, Madison, WI 53706

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Abstract. Fall fertilization of turfgrass in northern climates is often considered to be agronomically beneficial, although research on nitrogen (N) uptake during cold temperatures is sparse and environmental concerns exist regarding nitrate leaching. Therefore, the objective of this study was to evaluate N uptake by creeping bentgrass (Agrostis stolonifera L.), kentucky bluegrass (Poa pratensis L.), and annual bluegrass (Poa annua var. repans L.) seeded and grown for 3 months and then acclimated in a growth chamber to one of three climate regimens corresponding to 15 Sept., 15 Oct., and 15 Nov. in Madison, WI. Grasses were fertilized at 0, 25, 49, or 98 kg ha⁻¹ N with ¹⁵N-labeled ammonium sulfate (10 atom %¹⁵N) by applying a liquid solution of 75 mL per pot (1 cm of solution in depth). Data collected included verdure biomass, root mass, and expectations (Liu et al., 2008). Throughout the growing season canopy photosynthesis were greatest in the November treatments, although these responses compared with 57% and 38% in October and November, respectively. Root mass and net growth increased in response to N application in the September regimen, but not in October or November regimens. N uptake was significantly lower in the November regimen compared with September with an average of 73% of fertilizer recovery in September compared with 57% and 38% in October and November, respectively. Root mass and net canopy photosynthesis were greatest in the November treatments, although these responses were generally unaffected by N application rate. The results of this study indicate that N uptake capacity is greatly reduced as average daily temperatures approach 0 °C. Nitrogen application rates should be adjusted downward to maximize uptake efficiency in cold temperatures.

Nitrogen is the mineral nutrient required in the greatest amount for cool-season turfgrass and is often applied as fertilizer to supplement the temporarily inconsistent plant-available N in the soil. Fertilizer N is applied to turfgrass at various times throughout the growing season generally totaling between 80 kg ha⁻¹ and 200 kg ha⁻¹ depending on management practices and expectations (Liu et al., 2008). Throughout temperate climates, fall is widely considered the most important time for N fertilization, often accounting for up to half of annual N applied (Bauer et al., 2012).

Many practitioners and researchers consider the ideal N application timing to be shortly after shoot growth ceases, a timing referred to as late-fall N fertilization (Baird, 2007; Danneberger, 2006; Koski, 1988; Kussow, 1988; Reicher, 2005; Rieke 1997, 1998; Snow, 1982). The conventional wisdom backing this recommendation is that the cooler air temperatures in fall allow a greater portion of assimilated N to be used for carbohydrate accumulation and root and rhizome development instead of being partitioned into shoot growth, as has been shown to occur when temperatures are optimal for shoot growth (Bowman, 2003). Previous research evaluating the benefits of late-fall N fertilization has yielded mixed results, likely as a result of regional, temporal, and climatic variability (Bauer et al., 2012). Improved color responses in the fall, winter, or spring have been observed consistently in the mid-Atlantic region (Powell et al., 1967), New England (Ledebor and Skogley, 1973; Mangiafico and Guillard, 2006; Wilkinson and Duff, 1972), the Midwest (Miltner et al., 1996; Walker et al., 2007; Wehner et al., 1988), and in the Pacific Northwest (Miltner et al., 2004). Root growth response to late-fall N fertilization has been less consistent with some researchers finding greater root mass increase in late fall or spring (Hamon and Juska, 1961; Moore et al., 1996), whereas others have found negative or insignificant root responses to fall-applied N (Mangiafico and Guillard, 2006; Powell et al., 1967).

The concept that turfgrass preferentially uses N for root and rhizome development in cool temperatures assumes sustained photosynthesis and N uptake and metabolism. Net photosynthesis by cool-season grasses has been shown to be higher in cooler temperatures because of diminished respiration (Powell et al., 1967), although generally photosynthesis of C₃ turfgrasses follows a quadratic response with optimal photosynthesis ≈20 °C. In perennial ryegrass (Lolium perenne L.), a species that has relatively less cold tolerance than Agrostis spp. or kentucky bluegrass, photosynthetic rates are sensitive to chilling temperatures and can be diminished for several days after a hard chill (Moore et al., 1990). Research directly measuring turfgrass N uptake in cool temperatures is limited to two studies in Michigan (Frank et al., 2006; Miltner et al., 1996). Miltner et al. (1996) reported that Kentucky bluegrass (Poa pratensis L.) had a 35% N uptake efficiency when 39 kg ha⁻¹ N as urea was applied on 23 Nov. after shoot growth ceased for the year. At the same location, Frank et al. (2006) determined only 18% of 25 kg ha⁻¹ N applied as urea was taken up by kentucky bluegrass when applied on 17 Oct. The differences between the two studies at the same location with the same grass highlight the large variability that can be observed in field research as a result of weather and edaphic factors. Uncertainty remains regarding capacity for turfgrass to assimilate N in the late fall, although for many other plants, researchers have shown that N uptake is greatly inhibited in temperatures below those of optimal growth resulting from limited xylem flow and down-regulated transporters responding to decreased plant demand (Dubey and Parnick, 2002).

The extent to which N uptake by turfgrass is inhibited by low temperature likely depends on environmental factors and turfgrass species. High rates of N fertilization during a time when turfgrass uptake and N immobilization decline increases the likelihood of fertilizer loss through denitrification and leaching, especially considering the high precipitation and low evapotranspiration (ET) rates characteristic of late fall in many parts of the temperate United States. Excess N fertilization at this time is a potential economic and environmental burden.

Additional research evaluating fall-applied N uptake and use by cool-season turfgrass is warranted because of a potential disconnect between environmental interests and perceived agronomic benefits through the often emphasized practice of late-fall N fertilization. Much of the research performed on late-fall N fertilization was performed in field settings, which may limit the transferability of the results resulting from regional, climatic, and site-specific conditions.
variables. In fact, no controlled environment research could be found evaluating low-temperature N uptake, metabolism, and use of turfgrass or the response differences among N rate, application timing, and turfgrass species in cool temperatures. As a result of the perceived importance of fall fertilization, the agronomic significance should be evaluated through controlled environment research accounting for climatic and spatial variables such as temperature, photoperiod, N rate, and turfgrass species composition. Therefore, the objective of this study was to evaluate N uptake potential, use, and plant metabolic response in a climate-controlled environment evaluating the responses of various cool-season turfgrass species to variable N rates and temperature regimens.

**Materials and Methods**

‘Midnight’ kentucky bluegrass, ‘Penncross’ creeping bentgrass (*Agrostis stolonifera* L.), and ‘True Putt’ annual bluegrass (*Poa annua* var. *reptans* L.) were established from seed at the rate of three pure live seeds/cm² in a greenhouse set to 24/18 °C day/night temperatures with a photoperiod of 14 h. Plants were grown in 10-cm-diameter polyvinyl chloride pipe cut to 30 cm depth, outfitted with a drain cap base, then filled with 85:15 (v/v) sand to peat root zone mix conforming to USGA specifications (Green Section Staff, 2004) and packed incrementally to a bulk density of 1.4 g cm⁻³. Plants were fertilized using a granular 14N:12.3P:10K product, which included urea, monoammonium phosphate, and methylene urea as N sources at the rate of 49 kg N ha⁻¹ N during seeding. Additional nutrients were supplied at 4 and 8 weeks after seeding using a mix of ammonium sulfate and potassium phosphate at 4 and 8 weeks after seeding using a mix of N sources at the rate of 49 kg N ha⁻¹ N during seeding. Additional nutrients were supplied at 4 and 8 weeks after seeding using a mix of ammonium sulfate and potassium phosphate at the rate of 25 kg ha⁻¹ N, 25 kg ha⁻¹ potassium, and 20 kg ha⁻¹ phosphorus. Irrigation was applied daily in a mist house for 14 d after seeding and three times weekly thereafter at 35 mm/week. Plants were clipped using hand shears three times weekly to the height of 13 mm until N treatments were applied. Fourteen weeks after seeding, the plants were transferred from the greenhouse into a growth chamber for cool temperature acclimation stage. Temperature regimens and photoperiod are outlined in Table 1. After the acclimation period, plants were fertilized with one of the four N rates using a liquid solution of ¹⁵N-labeled ammonium sulfate (10 atom % ¹⁵N). After labeled N was applied, plants were irrigated to 80% of soil moisture capacity based on weight to eliminate the potential for leaching losses.

Seven d after N treatment, net ecosystem CO₂ exchange (NEE) was determined by calculating the difference of CO₂ fixation from the turf canopy and respiration from the turf + soil ecosystem. Photosynthesis can be approximated from NEE values, but NEE more accurately provides a measure of plant and microbial metabolic response to N fertilization and temperature. An infrared gas analyzer with a modified canopy chamber provided with 500 μmol m⁻² s⁻¹ CO₂ was used to determine CO₂ exchange rates (LI-COR 6400; Li-COR, Inc., Lincoln, NE). The I-L custom canopy chamber (10 cm height, 10 cm diameter) consisted of a clear acrylic cylinder to allow light transmission with a ring around the base to form a seal on top of polyvinyl chloride columns. The mixing fan installed in the infrared gas analyzer was sufficient for mixing the chamber volume on factory settings. The chamber was allowed to equilibrate for exactly 5 min before photosynthesis measurements were recorded. Gas exchange measurements were recorded between 1100 and 1400 hr; canopy temperature and photosynthetically active radiation (PAR) were also recorded.

Before N applications, all plants were cut to 13 mm and allowed to grow unclipped until harvest. Plants were watered three times weekly to 80% of pot water-holding capacity to prevent moisture stress. Plants were destructively harvested 10 d after N applications. On harvest, soil columns were split lengthwise using a custom-designed stainless steel blade and intact halves were removed from the polyvinyl chloride pipe. One half was used for soil analysis, whereas the other half was used to quantify root biomass. Verdure from each column was removed at the soil surface using a razor blade and then dried at 60 °C for 24 h. Dried samples were cleaned of sand and debris using the vibrating pan method (Kreuser et al., 2011). Cleaned samples were then weighed to determine dry mass.

After verdure was removed, the soil column was dried at 60 °C for 48 h. After drying, the roots were separated from the root zone mix using a dry sieving technique. Peat was removed from the root samples using forceps and fine roots shed during this process were collected on an aluminum baking pan and added into the mass. Debris was discarded and clean root samples were weighed.

Dried and cleaned verdure and root samples were ground using a Wiley mill (Thomas

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### Table 1. Growth chamber conditions recorded for second run of cool-season grass response to September, October, and November temperature regimens.a

| Temp. regimen | Mean daily Minimum Maximum | PAR (μmol m⁻² s⁻¹) | CO₂ (μL L⁻¹) | Photoperiod (h d⁻¹) |
|--------------|---------------------------|-------------------|--------------|-------------------|
| September 16·1 | 10·9 (11) 22·7 (19) | 431 | 409 | 12·5 (12·3) |
| October 11·3 | 6·9 (6) 15·1 (14) | 466 | 380 | 11·0 (11·0) |
| November 1·8 | –2·7 (–3) 4·6 (5) | 405 | 397 | 9·6 (9·6) |

aChamber set points are presented in parentheses. PAR and CO₂ values reported are means of each regimen. Diurnal temperature set points did not deviate by more than 2 °C in 3-h intervals.

bTemperature regimens are presented to correspond to 40-year means of 15 Sept., 15 Oct., and 15 Nov. for Madison, WI.

PAR = photosynthetically active radiation.

### Table 2. P-values from analysis of variance for treatment effects on plant and soil response parameters.a

| Source of variation | df | Verdure biomass | Root mass | df | Total ¹⁵N uptake |
|---------------------|----|----------------|----------|----|----------------|
| Run 1 | | | | | |
| Temp. (T) | 2 | 0·014* | <0·001*** | 2 | 0·001*** |
| N rate (N) | 3 | 0·004*** | 0·007** | 2 | 0·001*** |
| Species (S) | 6 | <0·001*** | 0·011** | 4 | 0·028* |
| Run 2 | | | | | |
| Temp. (T) | 2 | <0·001*** | 0·040* | 2 | 0·001*** |
| N Rate (N) | 3 | 0·004*** | 0·940 | 2 | 0·002** |
| Species (S) | 6 | <0·001*** | 0·263 | 4 | 0·024* |

Three temperature regimens (T) correspond to 15 Sept., 15 Oct., and 15 Nov. in Madison, WI, and were each replicated in a separate run. Four nitrogen rates (N) were applied (0, 25, 49, and 98 kg ha⁻¹) to three turfgrass species (S) (creeping bentgrass, kentucky bluegrass, annual bluegrass).

* ** ***Significant at the 0·05, 0·01, and 0·001 P level, respectively.
Scientific, Swedesboro, NJ) to pass through a 0.25-mm sieve and packaged in tin capsules to contain 100 to 200 μg N for isotope ¹⁵N analysis using an automated carbon–nitrogen analyzer (PDZ- Europa, Crewe, U.K.).

The experiment was a completely randomized design of a four (N) × three (temperature) × three (species) factorial with three replications. The factorial experiment was conducted twice, in separate “runs,” which were treated similarly to a year or location effect in the statistical model. Because the “run” was a statistically significant main effect for all responses except net ecosystem exchange rate, we analyzed and presented the data separately for each run. Runs were combined for net ecosystem exchange. The statistical software JMP (Version 8; SAS Institute, Cary, NC) was used for analysis of variance. When appropriate, treatment means were separated by Tukey’s honestly significant difference test at the 0.05 level. Data were log (base 10) transformed whenever a result of N application from 0 to 96 kg ha⁻¹ was only observed for the September timing combination of N and species. No differences were observed in ¹⁵N uptake. In Run 1, ¹⁵N uptake in the September regimen was greater than the November regimen only at the 98 kg ha⁻¹ rate, whereas in Run 2, ¹⁵N uptake during the September regimen was greater than the November regimen regardless of N rate. The October regimen had intermediate ¹⁵N uptake, often statistically similar to both the September and November regimens (Fig. 1).

Root accumulation of ¹⁵N was markedly different between runs. In the first run, we observed significantly greater recovery of ¹⁵N in the November regimen compared with the September and October regimens (Fig. 1A). However, the opposite occurred in Run 2 (Fig. 1B). Root fertilizer N concentrations accounted for an average of 17% of total N taken up averaging 5.2 kg N ha⁻¹ (data not shown).

Shoot: root fertilizer N partitioning was significantly different between runs. In Run 1, temperature regimen significantly affected shoot: root N partitioning (P < 0.001) and 40% of ¹⁵N was partitioned to the roots in November compared with 13% and 12% in October and September, respectively. In Run 2, temperature regimen did not significantly affect shoot:root N partitioning (P = 0.14) with all temperature regimens accumulating between 14% and 17% of fertilizer N in the roots.

Net ecosystem CO₂ exchange was only affected by temperature regimen and species with no effect of N rate or any interactions (Table 7). NEE increased as temperature regimen decreased (Table 8). Statistically, creeping bentgrass had greater NEE during each temperature regimen compared with Kentucky bluegrass, although the difference was less than 2%.

### Results

Growth chamber conditions, including temperature, light intensity, CO₂ concentrations, and humidity, were continually monitored through computerized sensors and did not deviate substantially from the set points within runs indicate statistical significance at the 0.05 level according to Tukey’s honestly significant difference test at the 0.05 level. Data were log (base 10) transformed whenever residuals were not normally distributed.

### Table 4. Verdure biomass as affected by temperature regimen and nitrogen application rate.

| Nitrogen application rate | Timing | Verdure biomass (g m⁻²) |
|---------------------------|--------|------------------------|
| 0                         | 24.5   |
| 24.5                      | 48.9   |
| 96                        |        |
| **Timing**                |        |
| Run 1                     |        |
| Sept.                     | 178 C  |
| 240 B                     | 254 AB |
| 306 A                     |        |
| Oct.                      | 225 BC |
| 217 BC                    | 225 BC |
| 217 BC                    |        |
| Nov.                      | 217 BC |
| 220 BC                    | 227 BC |
| 240 BC                    |        |
| Run 2                     |        |
| Sept.                     | 249 CD |
| 277 BC                    | 321 AB |
| 348 A                     |        |
| Oct.                      | 215 DE |
| 220 DE                    | 232 CDE|
| 235 CDE                   |        |
| Nov.                      | 183 EF |
| 188 EF                    | 185 EF |
| 158 F                     |        |
| **Timing**                |        |
| Run 1                     |        |
| Sept.                     | 284 A  |
| 193 CD                    | 257 AB |
| Oct.                      | 245 AB |
| 188 CD                    | 235 ABC|
| Nov.                      | 227 BCD|
| 180 D                     | 254 AB |
| Run 2                     |        |
| Sept.                     | 299 AB |
| 269 BC                    | 329 A  |
| Oct.                      | 245 C  |
| 188 D                     | 245 C  |
| Nov.                      | 161 D  |
| 183 D                     | 188 D  |

### Discussion

The lack of growth response of the cool-season grasses in October and November temperature regimens is consistent with previous research suggesting a minimal shoot growth response to N in temperatures below
10 °C (Powell et al., 1967; Wilkinson and Duff, 1972). As noted in the introduction, the convention for the past several decades has been to recommend N application in the fall. Our results indicate that actively growing turfgrasses absorb applied N very efficiently (65% to 83%) regardless of N rate (Fig. 1). Fertilizing when shoot growth becomes unresponsive to N application still was relatively efficient (46% to 72%), especially at the lowest application rate. However, fertilizing when air temperatures approach 0 °C resulted in low and variable uptake of applied N (15% to 60%). These results build on the work of Bowman et al. (1989), who quantified the uptake potential of cool-season grasses by monitoring the rapid depletion in the soil of applied fertilizer. That study demonstrated the N uptake potential under ideal growing conditions in the field, whereas our study demonstrated the extent of N uptake under cool temperatures.

Root growth and NEE were the only measured parameters for which N rate was not a consistently significant main effect (Tables 2 and 7). These results suggest that although root growth may increase in response to cooler soil temperatures (Tables 5 and 6), this trend is not stimulated further through N fertilization. Our finding is consistent with previous research (Mangiafico and Guilard, 2006; Powell et al., 1967). It may not be surprising that we found few differences in root growth among the treatments because only 10 d passed between application and harvest. Although additional longer-term or field research would be desirable to test the hypothesis that fall N does not affect root growth, our data preliminarily indicate that N applied at these rates in these temperature regimens has little effect on short-term root growth.

The absence of an N effect on NEE further supports the hypothesis that N does not stimulate root growth when shoots are inhibited by cool temperatures. NEE was found to increase as temperature decreased, which matched the trend of increased root growth in cold temperatures in Run 1. Photosynthesis rates of cool-season turfgrasses at low temperatures are not well publicized. Our NEE rates were ≈75% lower than those published for creeping bentgrass growing in sand at optimal shoot growth temperatures (Pote et al., 2006). The daily PAR supplied in our controlled environments was midway between what our region experiences in September and October (Stier and Gardner, 2008), which generally seems to be sufficient to maintain high-quality turf. The relatively cool temperatures in our study may have limited regeneration of Ribulose-1, 5-bisphosphate (RuBP), whereas the slight increase observed between September and November conditions could have been the result of enhanced RuBisCO selectivity for CO2 (Sage and Kubien, 2007). Additional information on the interaction of photosynthetic rates, carbohydrate, and N uptake and metabolism of cool-season turfgrasses could help explain winter survival and regrowth in spring.

We were unable to conclusively document the effect of N partitioning between shoots and roots for N applications in cold temperatures. It appears that shoot:root partitioning was not significantly different between the September and October regimens, but in Run 1, strong partitioning of N to roots was observed, whereas in Run 2, this did not occur.

Table 6. Root biomass as affected by temperature regimen and turfgrass species.

| Timing | Creeping bentgrass | Kentucky bluegrass | Annual bluegrass |
|--------|-------------------|--------------------|-----------------|
| Run 1  |                   |                    |                 |
| Sept.  | 297 A             | 118 D              | 179 BC          |
| Oct.   | 290 A             | 145 CD             | 149 CD          |
| Nov.   | 341 A             | 210 B              | 284 A           |
| Run 2  |                   |                    |                 |
| Sept.  | 297 AB            | 192 D              | 205 D           |
| Oct.   | 311 AB            | 220 CD             | 253 BCD         |
| Nov.   | 365 A             | 133 E              | 277 ABC         |

*Temperature regimens correspond to 15 Sept., 15 Oct., and 15 Nov. in Madison, WI. Roots were harvested 10 d after nitrogen application. Different letters within runs indicate statistical significance of log transformed values at the 0.05 level according to Tukey’s honestly significant difference.

Fig. 1. Effect of temperature regimen and nitrogen application rate on 15N fertilizer recovery in roots and roots + verdure (total) for (A) Run 1 and (B) Run 2. Roots and verdure were harvested 10 d after nitrogen application. Temperature regimens correspond to 15 Sept., 15 Oct., and 15 Nov. in Madison, WI.
Table 7. Effect of temperature regimen and species on net ecosystem exchange rate.1

| Source of variation | Net ecosystem exchange (μmol m⁻² sec⁻¹) |
|---------------------|----------------------------------------|
| Temperature (T)     | <0.001***                              |
| N Rate (N)          | 0.168                                  |
| Species (S)         | <0.001***                              |
| T × S               | 0.468                                  |
| N × S               | 0.522                                  |
| T × N × S           | 0.526                                  |

*Three temperature regimens correspond to 15 Sept., 15 Oct., and 15 Nov. in Madison, WI. Different letters within main effects indicate statistical significance at the 0.05 level according to Tukey’s honestly significant difference.

Table 8. Effect of temperature regimen and species on net ecosystem exchange rate.2

| Log of net ecosystem exchange (μmol m⁻² sec⁻¹) | Main Effect Level |
|---------------------------------------------|-------------------|
| 2.01 C                                      | 15 Sept.          |
| 2.07 B                                      | 15 Oct.           |
| 2.21 A                                      | 15 Nov.           |
| 2.12 A                                      | Creeping bentgrass |
| 2.14 B                                      | Kentucky bluegrass |
| 2.09 B                                      | Annual bluegrass  |

*Three temperature regimens correspond to 15 Sept., 15 Oct., and 15 Nov. in Madison, WI. Different letters within main effects indicate statistical significance at the 0.05 level according to Tukey’s honestly significant difference.

Our results suggest that some of the widely held views on the importance of fall fertilization may not be as well understood as thought. The N uptake capacity of creeping bentgrass, annual bluegrass, and kentucky bluegrass declines substantially as temperatures decrease, although N uptake potential appears to be relatively high near the time after shoot growth stops. Waiting after this period greatly reduces N uptake potential. Because of the increased risk of N loss during the fall in humid, temperate regions resulting from seasonally high rates of precipitation and low rates of ET, agronomic recommendations for late-fall fertilization need to be re-evaluated. Additional field research is required to confirm the results of this controlled environment evaluation.

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