Nitrate and Ammonium Uptake by Nitrogen-deficient Perennial Ryegrass and Kentucky Bluegrass Turf

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Abstract. Nitrogen uptake by two N-deficient turfgrass species was characterized by measuring N depletion from a complete nutrient solution. The uptake rate of both NO$_3^-$ and NH$_4^+$ was enhanced up to 6-fold in N-deficient perennial ryegrass (Lolium perenne L.) compared to N-sufficient controls, reaching a maximum of about 0.3 and 0.4 g N/m$^2$ per hr for NO$_3^-$ and NH$_4^+$, respectively. Deficiency-enhanced uptake exceeded uptake by controls for about 42 hr following resupply of N. Nitrogen uptake was enhanced to a similar degree by N deprivation in Kentucky bluegrass (Poa pratensis L.). Mowing had no effect on NO$_3^-$ uptake by N-deficient perennial ryegrass turf, whereas mowing inhibited uptake by N-sufficient turf by $\approx 60\%$. Deficiency-enhanced uptake was found to be the result of an increased capacity for N absorption ($I_{max}$) rather than an increased affinity for N ($K_m$). $I_{max}$ values increased from 0.24 and 0.73 mg N/g dry weight per hr for N-sufficient ryegrass turf for NO$_3^-$ and NH$_4^+$, respectively, to 1.44 and 2.68 mg N/g dry weight per hr for N-deficient turf. $K_m$ values increased slightly, from 14 $\mu$M for both N forms for N-sufficient turf to 24 and 39 $\mu$M for NO$_3^-$ and NH$_4^+$, respectively, for N-deficient turf.

Turfgrass management is fundamentally different from that of agricultural crops because the primary goal is to maintain appearance and vigor rather than high yields. This goal may be achieved, at least in part, through the judicious use of N fertilizers. Nitrogen is applied to turf every 1 to 4 months in amounts ranging from 25 to 50 kg N/ha. However, unlike the situation with most agronomic crops, there is very little published information on the uptake and metabolism of N applied to turf. In a field study, Kentucky bluegrass turf absorbed N very rapidly. A typical application of 50 kg N/ha, supplied either as NO$_3^-$ or NH$_4^+$, was removed from the soil in 2 days with depletion rates during the first 24 hr as high as 40 kg N/ha. It was proposed that the rapid depletion was the result of the high root length density of the turf and an enhanced capacity for N absorption due to N deficiency (2).

A nutrient deficiency in a plant is often associated with enhanced root absorption of the deficient nutrient (23, 24) as compared with unstressed controls. Such a response has been reported for K$^+$ (13), PO$_4^{3-}$ (8, 12, 22), and SO$_4^{2-}$ (9, 23). Similarly, NO$_3^-$ uptake is increased by N deprivation in various species. For example, Champigny et al. reported a 3-fold increase in uptake by wheat seedlings following 7 days of N deprivation (5). Nitrate and NH$_4^+$ absorption by barley roots was stimulated up to 2.5-fold and 3.6-fold, respectively, following 4 days of N stress (25). Comparable increases have been reported for barley (11) and corn (14) using split-root techniques in which only part of the root system is deprived of N. This literature suggests that enhanced N uptake in response to N deficiency may be fairly common. However, most published studies of deficiency-enhanced uptake have used seedlings to examine the response, have investigated only NO$_3^-$ as the N source, and have limited the nutrient stress period to 7 days or less. Data are lacking on the comparative uptake of NO$_3^-$ and NH$_4^+$ uptake by mature plants, and also on the effects of longer-term N deprivation, such as might typically occur in the field. Turfgrasses often withstand periods of weeks to months between N applications and, as a result, experience cycles of moderate to severe N deficiency. Mowed turfgrass may thus represent a system in which deficiency-enhanced N uptake is important in N acquisition under field conditions. However, we did not find data in the literature reporting the effects of N deprivation on N uptake by mowed turfgrasses. This paper characterizes NO$_3^-$ and NH$_4^+$ absorption by turfgrass using a nutrient solution culture system. The effects of plant N status and mowing on N uptake by both N-deficient and N-replete turf are presented.

Materials and Methods

Plant culture. Nutrient solution culture was used to measure N uptake by turf grown in a controlled environment. The culture unit consisted of a rigid plastic container having a surface area of 167 cm$^2$ and holding 2.3 liters of nutrient solution. For each container, seeds of 'Manhattan II' perennial ryegrass were sown at a rate of 400 kg/ha$^{-1}$ on a sheet of glass wool supported by a rigid plastic mesh. The container was filled with tap water (moistening the glass wool and seeds by capillarity), covered with a plastic cap, and shaded with four layers of cheesecloth. Germination and subsequent establishment took place in a greenhouse operated at 23C day and 15C night under natural light. Seeds germinated in 7 days, after which the seedlings were uncovered and grown for an additional 7 days on tap water. Subsequently, the turf was established on a 0.25-strength Hoagland's solution (19), referred to as $+NS$, with the following composition: 3.75 mM NO$_3^-$, 1.5 mM K$^+$, 1 mM Ca$^{2+}$, 0.5 mM Mg$^{2+}$, 0.25 mM H$_2$PO$_4^-$, 0.5 mM SO$_4^{2-}$, 46 $\mu$M B, 9 $\mu$M Mn, 0.8 $\mu$M Zn, 0.3 $\mu$M Cu, 0.1 $\mu$M Mo, and 1 mg Fe/liter as Fe-EDDHA. A solution in which the NO$_3^-$ salts were replaced by SO$_4^{2-}$ salts (referred to as $-NS$) was substituted to produce N-deficient turf. The initial pH of both solutions was 6.0. Supplemental Fe as FeSO$_4$·7H$_2$O was periodically added at a rate of 0.4 mg Fe/liter to prevent incipient chlorosis. Solutions were aerated and were changed with each mowing (every 4 to 7 days, depending on growth rate). The turf cultures were mowed regularly to a height of 4 cm starting 3 weeks after seeding and continuing during the preculture period. Nine to 12 weeks after seeding, the turf was dense, with four to five tillers per plant, and had developed a healthy root system. Cultures were then used for uptake experiments.
'Columbia' Kentucky bluegrass was included for comparison in the first experiment. Culture was similar to that described above, except that the container used had a volume of 1.8 liters and a surface area of 145 cm². Further, the growing period was extended to 9 months before measuring N uptake to produce a relatively mature turf, as evidenced by rhizome development.

A controlled environment growth chamber operated at 24°C during the 16-hr light period and at 18°C during the 8-hr dark period was used in Expt. 3. Relative humidity was ~80% and PPFD at plant height was 400 μmol·s⁻¹·m⁻², supplied by incandescent and cool-white fluorescent lamps. Turf cultures were acclimated to the growth chambers for 1 week before treatment.

The effect of N deficiency of N uptake (Expt. 1). This experiment, conducted in the greenhouse in Apr. and May 1986, was designed to examine the uptake of NO₃-N and NH₄-N by turfgrass varying in degree of N deficiency. Four levels of N deficiency were imposed by transferring cultures of both species to −NS at 28, 14, and 7 days before N application and measurement of N uptake. Controls were grown on +NS through the 4-week pretreatment period during the 28-day pretreatment period and 30.4 mol·day⁻¹·m⁻² during the 4-day uptake period. All cultures were mowed 24 hr before N application. A 4 × 2 (deficiency level × N form) factorial arrangement of treatments in a completely randomized design was used, with four replicates per treatment.

Turf cultures were removed from the −NS pretreatment solution at 0900 hr on day 1 of the experiment and the roots were rinsed with −NS and allowed to drain. Each culture was then transferred to 2.3 liters of −NS, to which either KN0₃ or (NH₄)₂S0₄ was added to a final concentration of 1.5 mM N. A 3-ml sample from each container was taken 10 min later to establish the initial N concentration following equilibration with the root-free space. Samples were then taken at 1- to 4-hr intervals during the first 24-hr period, at 1- to 8-hr intervals during day 2, and then at 4- to 12-hr intervals during days 3 and 4 to determine the time course of N uptake. Net uptake was determined by measuring the depletion of N from solution corrected for loss of solution due to evapotranspiration and sampling. Because uptake rapidly depleted both the NO₃-N and NH₄-N, especially during the first 24 hr, KNO₃ or (NH₄)₂S0₄ was added to the uptake solutions as required to maintain the concentration above 1 mM N. The pH was adjusted frequently with KOH or H₂S0₄ to maintain it at 6.0 ± 0.5. Solutions were replaced at 24 hr and thereafter brought to volume daily with −NS. Cumulative uptake data were fit to a series of cubic equations from which a cubic spline curve was drawn. Uptake rates were estimated from the first derivative of the curve evaluated at the sampling time points and are presented as mg N absorbed/culture per hr.

The effect of mowing (Expt. 2). Since defoliation may reduce N stress in grass swards (17, 18), the response of NO₃ uptake to mowing was investigated in the greenhouse. Perennial ryegrass was grown for 14 days in −NS solution (N-deficient turf) or in a complete +NS solution (plus-N controls). Groups of four cultures from each N treatment were mowed either 4, 2, 1, or 0 days before N was added to initiate uptake (the 0-day mowing took place 30 min before N addition). Nitrate uptake was determined over 48 hr as described above, with the exception that 4 mM Mes [2-(2N-morpholino)ethanesulfonic acid] was included in the uptake solution for pH control. The four treatments were arranged in a completely randomized design with four replicates of each.

Iₘₐₓ and Kₘ (Expt. 3). By analogy to the Michaelis–Menten constants, Iₘₐₓ (maximum net uptake rate) and Kₘ (concentration at which net uptake rate was half the maximum value) were estimated on perennial ryegrass cultures deprived of N for 7 days compared to +N controls using the method of Claassen and Barber (6). The experiment was performed in the growth chamber using cultures mowed 24 hr before the experiment. Uptake was measured in a flow-through chamber holding 1.5 liters of aerated nutrient solution, recirculated at two exchanges/min to minimize diffusion limitation. To overcome the initial lag period of low NO₃ uptake by N-deficient cultures, NO₃ uptake was induced starting 6 hr before the experiment with additions of 1 mg NO₃-N per culture every 2 hr. Plus-N controls were acclimated to a low-N solution containing 0.18 mM NO₃-N for 2 hr before initiating the experiment.

Roots were rinsed and allowed to drain. The cultures were then transferred to the flow-through chambers containing −NS and the roots equilibrated for 15 min. Uptake was initiated by the addition of either KNO₃ or (NH₄)₂S0₄ to a final concentration between 0.143 and 0.286 mM N, depending on expected uptake rates. Depletion data were fit to a series of cubic equations as above and uptake rates were calculated as the negative of the first derivative of the curve. Uptake rates could thus be associated with actual measured N concentrations; Iₘₐₓ and Kₘ were estimated from a Lineweaver–Burk plot of these data (29).

N analyses. Nitrate and ammonium concentrations in the solution samples, tissue extracts, and digests were measured directly by the method of Carlson (3, 4). Nitrate in the tissue was determined using a water extract of the dried tissue. Total N in the tissue was measured by Kjeldahl digestion. Results are reported on a dry-weight basis as the means of four samples ± SD.

Results

Growth and N content of the tissue. The turf cultures responded rapidly to the −N treatment. Yield and reduced N in the tissue decreased dramatically, whereas root dry weight increased after 7 days of N deprivation (Table 1). Clipping yield and Kjeldahl-N decreased to a comparable degree by N deprivation in both species.

<table>
<thead>
<tr>
<th>Species and pretreatment</th>
<th>Clipping yield (g·day⁻¹·m⁻²)</th>
<th>Root dry wt (g)</th>
<th>Kjeldahl-N (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perennial ryegrass</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>+ N (control)</td>
<td>20.7 ± 2.1</td>
<td>2.95</td>
<td>5.8 ± 0.06</td>
</tr>
<tr>
<td>− N 1 week</td>
<td>11.5 ± 1.4</td>
<td>4.67</td>
<td>4.3 ± 0.08</td>
</tr>
<tr>
<td>− N 2 weeks</td>
<td>5.9 ± 0.7</td>
<td>5.02</td>
<td>3.7 ± 0.07</td>
</tr>
<tr>
<td>− N 4 weeks</td>
<td>3.4</td>
<td>5.74</td>
<td>2.3 ± 0.3</td>
</tr>
<tr>
<td>Kentucky bluegrass</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>+ N (control)</td>
<td>13.4 ± 1.0</td>
<td>3.75</td>
<td>4.9 ± 0.1</td>
</tr>
<tr>
<td>− N 1 week</td>
<td>9.7 ± 0.8</td>
<td>4.64</td>
<td>4.3 ± 0.1</td>
</tr>
<tr>
<td>− N 2 weeks</td>
<td>6.8 ± 0.9</td>
<td>4.65</td>
<td>3.5 ± 0.1</td>
</tr>
<tr>
<td>− N 4 weeks</td>
<td>2.4</td>
<td>4.93</td>
<td>2.6 ± 0.3</td>
</tr>
</tbody>
</table>

*Values are means of four samples ± SD, except root dry weight and percentage of root N are based on one sample.

+Clippings were bulked from all eight cultures due to very low yield in the 4-week −N treatment.

Nitrate and ammonium uptake by perennial ryegrass. Nitrate absorption was initially slightly greater in the controls than in the other three treatments (Fig. 1 A and B). However, uptake by the N-deficient turf increased rapidly during the first 8 to 10 hr, reaching a maximum rate of about 5 mg N/culture per hr, or 4- to 6-fold that of the +N controls. Uptake by +N controls was relatively constant at 0.7–1.0 mg N/culture per hr. The peak rate by N-deficient cultures decreased during the next 10 to 14 hr, coincident with the dark period. A similar pattern of uptake was observed throughout the remaining 3 days. Four weeks of N stress resulted in a lower maximum uptake rate than either 1 or 2 weeks; by 24 hr the 4-week cultures had absorbed 53 mg NO$_3^-$-N vs 69 mg N by both the 1- and 2-week cultures (Fig. 1A). During the 2nd day, however, uptake by the 4-week treatment exceeded both the 1- and 2-week -N treatment, resulting in essentially identical total uptake (103–106 mg N) by 50 hr. For comparison, this is equivalent to 63 kg N/ha. Nitrogen-deficient perennial ryegrass turf is thus capable of absorbing a quantity of NO$_3^-$-N approximating that of a normal application in <2 days. This agrees with the field observation that N-deficient turf absorbed ≈30 kg N/ha during the first day following fertilization with either NO$_3^-$-N or NH$_4^+$-N (2).

The effect of N deficiency on NH$_4^+$-N uptake was generally similar to that on NO$_3^-$-N (Fig. 2), with the exception that there was no apparent lag period. The initial maximum uptake rate of 5- to 6-fold the control value quickly declined (Fig 2B) to values 2 to 3 times the controls. Uptake rate was essentially identical between stress treatments for the first 10 hr, after which the 4-week -N treatment maintained higher uptake rates through 62 hr. By 80 hr, NH$_4^+$ uptake by the N-deficient treatments had reached control levels.

Minus-N cultures absorbed NH$_4^+$ equivalent to a typical 50 kg N/ha application by 38 hr. By 96 hr, uptake totalled nearly 200 mg N/culture, (Fig. 2A) or 128 kg N/ha. Nitrate uptake over this same period averaged 150 mg N/culture, or 90 kg/ha. Nitrate and ammonium absorption by Kentucky bluegrass. The results using Kentucky bluegrass (Figs. 3 and 4) are qualitatively very similar to perennial ryegrass, with N-deficiency again increasing uptake of both NO$_3^-$ and NH$_4^+$ by 2- to 5-fold. Induction of NO$_3^-$ uptake required about 4 to 6 hr for full expression, while no induction of NH$_4^+$ uptake was observed. Cumulative uptake increased with longer periods of N deprivation, unlike perennial ryegrass. The two species also differed in the total amount of N absorbed in 4 days, expressed on an area basis. N-deficient Kentucky bluegrass absorbed an average of 50 and 77 kg N/ha, while perennial ryegrass absorbed 86 and 114 kg N/ha as NO$_3^-$ and NH$_4^+$, respectively.

The effect of mowing on nitrate uptake by perennial ryegrass. Mean clipping yield of N-deficient and N-replete controls at
Fig. 4. Cumulative uptake (A) and uptake rate (B) of NH$_4^+$ by Kentucky bluegrass as a function of four levels of N stress (0, 1, 2, and 4 weeks). Values are means of four samples ± SE.

Fig. 5. Effect of mowing on cumulative uptake (A) and uptake rate (B) of NO$_3^-$ by perennial ryegrass deprived of N for 14 days. Turf was mowed 4, 2, 1, or 0 days before measuring uptake. Values are means of four samples ± SE.

The time of this experiment were 7.3 ± 0.4 and 25.1 ± 1.2 g dry weight/day per m$^2$, respectively. Mowing had little effect on NO$_3^-$ uptake by cultures deprived of N for 14 days (Fig. 5), whereas it had a marked effect on uptake by +N controls (Fig. 6). The pattern and magnitude of uptake by N-stressed plants was similar to that described above, with a maximum uptake rate of 6 to 7 mg N/culture per hr occurring at 6 hr.

Cumulative uptake by +N control cultures increased with time after mowing (Fig. 6). There was a 3-fold difference in uptake rate between cultures mowed 4 days before the experiment and those mowed 30 min before measuring uptake. Cultures mowed the day of the experiment had the greatest initial uptake rate, which then quickly declined to very low values. Regression of cumulative uptake over consecutive 24-hr periods for all four mowing treatments indicates a linear correlation between uptake rate by +N controls and days after mowing, with a slope of 0.24 mg N/culture per hr per day and an $R^2$ value of 0.94.

Table 2. $I_{\text{max}}$ and $K_m$ values for perennial ryegrass 'Manhattan II' in response to N deficiency. N-stressed (-N) cultures were deprived of N for 7 days. A second set of measurements were made 2 days later in the case of +N cultures.*

<table>
<thead>
<tr>
<th>Type of culture</th>
<th>$I_{\text{max}}$ (mg N/g dry wt per hr)</th>
<th>$K_m$ (µM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>+N NO$_3^-$N</td>
<td>Day 0 0.24 ± 0.01</td>
<td>14 ± 1</td>
</tr>
<tr>
<td></td>
<td>Day 2 0.85 ± 0.08</td>
<td>19 ± 1</td>
</tr>
<tr>
<td>NH$_4^-$N</td>
<td>Day 0 0.73 ± 0.11</td>
<td>14 ± 6</td>
</tr>
<tr>
<td></td>
<td>Day 2 1.09 ± 0.14</td>
<td>8 ± 1</td>
</tr>
<tr>
<td>-N NO$_3^-$N</td>
<td>1.44 ± 0.07</td>
<td>24 ± 5</td>
</tr>
<tr>
<td>NH$_4^-$N</td>
<td>2.68 ± 0.19</td>
<td>39 ± 2</td>
</tr>
</tbody>
</table>

*Values are the means of four replicates ± sd.

$I_{\text{max}}$ and $K_m$. Because of very low uptake rates by mowed, +N cultures, measurements were repeated on these cultures following an additional 2 days of growth. Within the low N concentrations used, both NO$_3^-$ and NH$_4^+$ uptake followed typical uptake kinetics, with saturation occurring at very low N concentrations. $I_{\text{max}}$ of N-deficient turf was ≈5-fold and 2- to 4-fold greater than that of +N turf for nitrate and ammonium, respectively (Table 2) and are similar to the maximum uptake rates reported above. $K_m$ values for NO$_3^-$ absorption were similar between +N and -N cultures, ranging from 14 to 24 µM. By contrast, the $K_m$ for NH$_4^+$ absorption by N-deficient cultures
increased to 39 μM from the 8- to 14-μM value measured with +N turf. $I_{\text{max}}$ had increased significantly in +N cultures following 2 days of additional growth, while the $K_m$ values were similar on both days.

Discussion

Nitrogen uptake rates by N-deficient Kentucky bluegrass grown in solution culture are very similar to those reported for a field-grown Kentucky bluegrass (2). Further, the N uptake rates by perennial ryegrass in this study are consistent with the N depletion rates reported for field-grown perennial ryegrass (2). Kjeldahl-N of bluegrass clippings in the present study (4.9%, 2.6%) was similar to unreported data from the field study (4.7%, 3.2%) for N-fed and N-starved turf, respectively. The turf cultures used in this study have the advantage over commonly used seedling systems in that the turf system consists of a large population of relatively mature turf plants, minimizing the effect of variability between individuals. Additionally, results may be expressed on a land-area basis, permitting comparison with field data.

Although the pattern of NO$_3^-$ and NH$_4^+$ uptake by N-deprived turf was quite different during the first 6 hr, with NO$_3^-$ uptake exhibiting the characteristic lag period, cumulative uptake of the two N forms over the first 12 hr was nearly identical. In the case of NO$_3^-$, this short-term rapid uptake may be associated with filling of the root vacuole, as proposed by Glass et al. (15). Following an initial rapid loading of the vacuole, a new, reduced uptake rate would be attained, regulated by assimilation and translocation. It is also possible that the decrease in uptake might be related to depletion of root carbohydrates (1, 20, 31). This would be the case particularly with NH$_4^+$ uptake, since the root is the primary site of NH$_4^+$ assimilation (26). Nitrogen absorption would thus be regulated by a number of factors, with the different patterns of uptake over the first 12 to 18 hr suggesting separate controls for NO$_3^-$ and NH$_4^+$.

Mowing had little effect on the rapid uptake by N-deficient turf, which indicates that new leaf tissue functioned neither as a critical source of assimilates nor as a necessary sink for absorbed N. Since carbohydrates accumulate in plants deprived of N (7, 8, 30, 31), uptake by N-deficient roots may be relatively independent of current photosynthates (1, 28). By comparison, +N cultures were very sensitive to mowing, with the lowest uptake rates occurring 1 day after removing new leaf blades. This situation is most easily explained as the result of diverting available carbohydrates to the rapidly expanding leaves (32).

Nitrogen uptake was enhanced after 7 days of starvation, consistent with observations that increased uptake capacity is established soon after imposition of nutrient stress (9, 10, 22). Shoot growth had declined and root growth had increased by 7 days (Table 1). Increased uptake was only partially due to the larger root system, since uptake per unit root dry weight also increased as much as 3- to 4-fold. This is very similar to the increases in NO$_3^-$-N uptake reported for barley (25) and for wheat (5, 30). Extending the period of N deprivation from 1 to 2 or 4 weeks had little additional effect on N uptake. The response in perennial ryegrass is thus relatively stable, with enhanced uptake remaining fully expressed over as long as 4 weeks of N deprivation. This contrasts with reports that, after reaching a maximum after 2 to 3 days of nutrient stress, deficiency-enhanced uptake capacity declines with longer periods of stress (5 to 10 days) to levels often below that of unstressed controls (8, 23, 25). This difference might be related to the ability of mature plants to remobilize N reserves and maintain uptake systems.

The $I_{\text{max}}$ of perennial ryegrass increased while the $K_m$ changed very little in response to N deprivation (Table 2). Lee and Drew (24) also reported large increases in $I_{\text{max}}$ but no change in $K_m$ for NO$_3^-$ uptake by barley. The $K_m$ values found in this study for NO$_3^-$ uptake (14 to 24 μM) are similar to the values of 14 to 17 μM reported for barley (24), 27 μM for wheat (16), and 33 μM for ryegrass (27). Goyal and Huffaker (16) and Lycklama (27) also report $K_m$ values for NH$_4^+$ uptake of 50 μM and 40 μM, respectively, similar to the 39 μM by N-deficient ryegrass in this study. The present results suggest that perennial ryegrass responds to N stress primarily by increasing the capacity ($I_{\text{max}}$) rather than the affinity ($K_m$) of the uptake mechanism. Increased capacity is considered to be due to either synthesis of new carriers (7, 21) or activation of existing carriers (21), and is thought to represent an adaptation to dwindling soil nutrient levels, thereby allowing the plant to maintain relatively constant tissue nutrient concentrations and growth (7, 13, 25). This interpretation has been criticized (11, 12), especially for ions of low mobility in the soil, such as PO$_4^-$ and NH$_4^+$, or those present at low concentrations (12).

The results of this investigation, in which N uptake by two turfgrass species is enhanced by N-deficiency, support the interpretation that the rapid disappearance of NO$_3^-$-N and NH$_4^+$-N fertilizers applied to turf in the field is due largely to plant absorption (2). Uptake of both NO$_3^-$ and NH$_4^+$ is enhanced by N deprivation to a similar degree. Mowing had little effect on enhanced uptake by N-deficient turf cultures, whereas uptake by +N cultures was reduced by mowing.

Literature Cited
