Defoliation tolerance and ammonium uptake rate in perenni-
al tussock grasses

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Abstract

Siphe clarezi, Ball, has been shown to be more tolerant to defo-
iliation and a superior competitor to S. tenues Phillip and S.
ambigua Speg. 3 perennial grasses native to semiarid rangelands
in central Argentina. Mechanisms contributing to its great defoli-
ation tolerance and competitive ability, however, are largely
unexplored. We examined tolerance to defoliation and ammoni-
um uptake rates on defoliated and undefoliated plants of those
species at 10, 25, and 50 ppm NH4+ using NH4NO3 solutions
containing 60 atom % 15N excess. By mid-spring, greater
regrowth following defoliation in S. clarezi than in S. tenues or S.
ambigua indicated greater defoliation tolerance in the first than
in the other 2 species. Siphe clarezi had similar of higher ammo-
nium uptake rates than S. tenues and S. ambigua. Higher ammo-
nium uptake rates in S. clarezi thus appear to be one of the
mechanisms most likely contributing to its greater competitive
ability and defoliation tolerance when compared to the other 2
species. Defoliated plants of all 3 species had similar or greater
ammonium uptake rates than undefoliated plants. These results
suggest that photosynthetic canopy reestablishment may be
achieved without sacrificing root function in these perennial
grasses, at least as long as carbon reserves do not become a limit-
ning factor. Ammonium uptake rates increased when NH4+ con-
centrations increased in the labeled solutions in S. clarezi, S.
tenues and S. ambigua. This result demonstrates the capacity of
the root system for increasing nutrient acquisition during periods
of high resource availability.

Key Words: competitive ability, defoliation, 15N, perennial
grasses, uptake rate

Differences in resource acquisition and competitive ability
among species within the same plant community have been
linked to a variety of plant traits and mechanisms (Nye and
Tanner 1977, Caldwell 1994). Ammonium uptake rate and com-
petitive ability are positively related (Jackson and Caldwell
1990; Caldwell 1994) mainly in low-productivity environments
where belowground resource competition is intense (Cooper and
Jackson 1997). In addition, greater competitive ability has been reported

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as one of the major mechanisms contributing to greater defola-
tion tolerance in perennial grasses (Brice and Richards 1995).
Physiological plasticity of the root system in its nutrient uptake
capacity is also important in nutrient-poor environments
(Larigauderie and Richards 1994). This physiological root plas-
ticity allows for a disproportionate increase in ammonium uptake
rate (i.e., uptake kinetics) per unit root mass or length whenever
an N-rich patch is found (Caldwell 1994; Jackson et al. 1999).
This mechanism can be particularly important when soil resource
availability is temporally or spatially unpredictable, and when

Resumen

Se ha demostrado que Siphe clarezi tiene una mayor tolerancia a la defoliación y capacidad competitiva que S. tenues y S. ambigua, 3 especies de gramíneas perennes nativas en los pasti-
zales naturales semiáridos del centro de Argentina. Los mecani-
mismos que contribuyen a determinar su mayor tolerancia a la defo-
lación y capacidad competitiva, sin embargo, todavía no se han
investigado. Se examinaron la tolerancia a la defoliación y las tasas de absorción de amonio en plantas defoliadas y no defoli-
adas de estas especies a 10, 25, y 50 ppm NH4+ usando soluciones de NH4NO3 que contenían un enriquecimiento de 15N del 60%.
A mediados de primavera, una mayor producción de rebrote
luego de la defoliación en S. clarezi que en S. tenues y S. ambigua
indicó una mayor tolerancia a la defoliación en la primera que
en las otras dos especies. Siphe clarezi tuvo tasas de absorción de
amonio similares o superiores, pero no menores, que S. tenues y S.
ambigua. MAStas de absorción de amonio parecen ser uno de los mecanismos que contribuyen a determinar la mayor
capacidad competitiva y tolerancia a la defoliación en Siphe clarezi
que en las otras dos especies. Las plantas defoliadas de
tas especies tuvieron tasas de absorción de amonio similares
o mayores que las plantas no defoliadas. Estos resultados sug-
ieren que la restitución de la superficie fotosintética se puede
obtener sin sacrificar la función radial en estas especies, siem-
pre y cuando las reservas de carbono no sean un factor limitante.
Las tasas de absorción de amonio fueron mayores cuando se
incrementó la concentración de NH4+ en las soluciones marcadas
en Siphe clarezi, S. tenues y S. ambigua. Este resultado demues-
tra la capacidad, del sistema radial para incrementar la
adquisición de nutrimentos durante periodos de alta disponibilidad
de recursos.
duration and magnitude of nutrient pulses are insufficient to compensate for costs associated with root morphological plasticity (Grime 1994). Carbohydrate flow from stems to roots has a direct role in regulating plant nitrogen uptake (Ridoutt and Raper 1994). Mechanisms of soil resource acquisition can then be directly or indirectly affected after defoliation by either reducing plant photosynthetic capacity or preferentially allocating carbon to shoot growth (Briske and Richards 1995). In this manner, herbivory may modify competitive interactions among plant species in grazed communities (Briske 1991). Defoliation can reduce (Sanderson et al. 1997), have no effect or even increase (Wallace 1981, Pelley and Detling 1980) N uptake rates. An understanding of the ways plants respond to defoliation is useful in predicting competitive outcomes after grazing in natural systems (Wallace and Macko 1993).

_Spisum clavatum_ Ball (big needlegrass), _S. tenax_ P. Beal (thin needlegrass) and _S. ambiguus_ Sp. (viscacha hole straw), all perennial grass species, have shown different responses to continuous, long-term grazing in rangelands of the south of the Physiographical Provinces of the Monte and Espinal (Busso 1997). _Spisum clavatum_ is an example of a palatable (Cano 1988), dominant, highly competitive grass species in enclosures or lightly grazed areas (Busso 1997; Giorgetti et al. 1997, Saint Pierre et al. 2002). Mean values for neutral detergent fiber and crude protein in this species are 69% and 13.7%, respectively at the vegetative developmental stage (Menotre and Distel, 1997). Under moderate continuous grazing, _S. clavatum_ is replaced by other comparatively less palatable, perennial grasses like _S. tenax_ (Busso 1997). This species has mean values of 71.9% for neutral detergent fiber and 12.9% for crude protein at the vegetative stage of development (Torrea et al. 2000). Selective heavy grazing of these palatable perennial grasses, however, will eventually lead to their replacement by other unpalatable, early-successional, less competitive species (Briske 1991, Anderson and Briske 1999). Thus, _S. clavatum_ and _S. tenax_ have been replaced by the unpalatable _S. ambiguus_ under continuous, severe grazing conditions in semiarid rangelands of central Argentina (Torrea et al. 1997). Mean values in _S. ambiguus_ are 9.4% for lignin and 8.9% for crude protein early in the growing season (Giorgetti, Montenegro and Rodriguez, unpublished data).

Fig. 1. A) Daily rainfall (mm; vertical bars) and PAN evaporation (mm; solid line), and B) Absolute maximum and minimum, and mean monthly soil temperatures measured at 9900 hours at 0.05, 0.10, and 0.50 m soil depth during 1990 at a meteorological station located at the study site.
Parallel studies conducted at our study site have shown a greater competitive ability and tolerance of defoliation in S. clavata than in S. tenax and S. ambiguus (Saint Pierre 2002). For example, regrowth has been greater in S. clavata than in the other species after 2 successive defoliations (Saint Pierre et al. 2000a, 2000b). This has been associated with greater relative growth rates for green tiller length and height, and higher tiller production in S. clavata than in S. tenax and S. ambiguus (Saint Pierre et al. 2000a). Root proliferation towards root-free disturbed soil has also been greater on defoliated and undercut plants of S. clavata than on those of S. tenax and S. ambiguus (Saint Pierre et al. 2002). However, studies have not been conducted to determine if ammonium uptake rates could be another mechanism contributing to the greater defoliation tolerance and competitive ability in S. clavata than in the other 2 species.

We evaluated defoliation tolerance and competitive ability in defoliated and undercut plants of S. clavata, S. tenax and S. ambiguus. Competitive ability was determined by measuring ammonium uptake rates at different NH₄⁺ concentrations using (NH₄)₂SO₄ solutions containing 60 atom % ¹⁵N. We predicted that: (1) defoliation tolerance and ammonium uptake rates are greater in S. clavata than in S. tenax and S. ambiguus, and (2) ammonium uptake rate is reduced by defoliation in all 3 species.

Materials and Methods

Study area

Research was done from May to December 1998 at the field site of the Experimental Farm of Patagonas (40°59'S, 52°54'W, 40 m elevation), 22 km north of Carmen de Patagonas. It was conducted in a community that had been protected from domestic herbivores since 1996, because it contained abundant populations of late- and earlier-serial perennial grasses. The study site is within the Physiographical Province of the "Mountains" (Cabrera 1976). The community is characterized as an open alder-berry habitat with mostly perennial grasses (Pegguy et al. 1997). The soil was classified as a Typic Haploxeralf with a 20 cm thick A horizon with a loamy clay-sandy texture; 16.9 g kg⁻¹ organic carbon; 28.7 ppm available phosphorus and 1.23 g kg⁻¹ total nitrogen. A 6°C heat zon was found below 0.20 m soil depth followed by a BC horizon between 0.28 and 0.43 m depth. A C₃ horizon was below 0.43 m depth with very few roots. Long term (1901-1950) average annual climate values are: 331 mm precipitation, 14.6°C temperature, 60% relative humidity and 13 km/hour wind speed. More recent records for precipitation (1981-2000), however, raise the previous average annual value to 442.9 mm. Average minimum (August) and maximum (January) temperatures are 7.9°C and 43°C, respectively. Monthly precipitation and pan evaporation during the research period were recorded by a meteorological station at the study site. Thermal records are also provided for soil temperature since it has big effects on root respiration, and respiration affects ammonium uptake (Fig 1).

Treatments and measurements

Seventy two plants, 24 of each of the 3 species (S. clavata, S. tenax and S. ambiguus), were marked on 22 May. On each plant, shoot circumference was measured at the soil surface. The study area within the 2-year-exclusion cover had a good plant cover partly because it had been grazed appropriately in previous years. Most plots were done to one stand in this community. However, and similar to that reported by Bruvo et al. (2000a), we selected those without nearby neighbors within a radius of at least 0.30 m to decrease the probability of including roots from adjacent species. Half of the plants was defoliated to 5 cm stubble height on 17 September (apical meristems were not removed from the plants) and 12 October (apical meristems at the reproductive stage of development were removed), while the other half remained undercut (controls). No clipping was imposed on all studied tussocks during the previous growing season, so the current year aboveground growth could be evaluated in both defoliated and undercut plants. Thus, only dry weight production after defoliation (regrowth) was measured in this study on defoliated plants of all 3 species. Comparison of dry weight production on a per plant basis was prevented because of inherent plant basal area variation among species (mean values of 1 standard error (cm²) were: 53.2 ± 5.7 in S. clavata, 72.5 ± 6.3 in S. tenax and 111.2 ± 13.2 in S. ambiguus). Therefore, dry weight production data will be reported on a per basal area basis. All plant tissues obtained above elaging height were oven-dried at 60°C and then weighed.

Three destructive harvests were conducted during spring on the following dates: 6-10 days after the first defoliation (26 September), 6-10 days after the second defoliation (22 October), and at the end of the growing season (4 December). Entire plants including a block of soil approximately 25 (length) x 25 (wide) x 30 (depth) cm were excavated. Although these soil samples did not capture the entire root system, they did contain many fine lateral roots. Also, Becker et al. (1997) found that root weight density of field-grown S. tenax and Piptopteris repens were significantly higher than those in greenhouse grown. Treatment effects were significant in all measurements.

Footnotes for the N absorption experiment were manually washed from the soil, floated in water and retained if they were ≥1 mm in diameter and had a light color characteristic of young roots. By using excised roots, we removed them from their 'ecological reality.' The excised root assay was designed to provide relative comparisons of ammonium uptake, and there is evidence that the rate of uptake of ammonium in excised grass roots is representative of intact root uptake if measurements are completed within the first 2 hours after excision (Bloom and Caldwell 1988). Then, we took precautions to complete the N uptake experiments within 2-2.5 hours after soil sample collection in the field, precautions which have been followed extensively in this type of study (i.e., Jackson et al. 1990, Deemer and Bronke 1999, Busso et al. 2001). During separation, roots were maintained in aerated, 0.5 mM CaCl₂ solutions at 20°C. Roots from individual plants were separated into 3 subsamples of 0.5-1 g dry weight, wrapped in cheese cloth bags, and equilibrated for 1 hour in a 0.5 mM CaCl₂ solution at 20°C. Roots were immersed for 10 minutes in solutions of (NH₄)₂SO₄ (60 atom % ¹⁵N) which contained 10, 25 or 50 ppm NH₄⁺. Typical soil solutions ammonium concentrations at the site were 6.68-18.03 ppm (mean±SEM, n=9; range: 5.18-24.60 ppm) on soil samples taken up to 30 cm depth in mid winter (16 July 1998). This value is similar to that reported by Sánchez and Lazcano (1999) in another rangeland in central, semiarid Argentina. The highest concentration was selected to represent enriched soil patches where solution concentrations were approximately 2 times higher than typical values found in native soils. Differences in the spatial and temporal distribution of nutrient transformation and consumption
Table 1. Dry weight production (regrowth) per basal area basis on defoliated plants of S. clarizioi, S. sen&ium, and S. ambigius on early (26 September) and mid-spring (22 October) and at the end of the growing season (4 December). Each value is the mean ± 1 s.e.m. of n = 4. Means within rows followed by a different letter are statistically different (P < 0.05).

<table>
<thead>
<tr>
<th>Sampling Date</th>
<th>Regrowth production</th>
<th>S. clarizioi</th>
<th>S. sen&amp;ium</th>
<th>S. ambigius</th>
</tr>
</thead>
<tbody>
<tr>
<td>26 September</td>
<td>0.001 ± 0.0004a</td>
<td>0.001 ± 0.011a</td>
<td>0.003 ± 0.016b</td>
<td></td>
</tr>
<tr>
<td>22 October</td>
<td>0.009 ± 0.0036a</td>
<td>0.007 ± 0.007b</td>
<td>0.010 ± 0.006b</td>
<td></td>
</tr>
<tr>
<td>4 December</td>
<td>0.042 ± 0.013a</td>
<td>0.019 ± 0.009a</td>
<td>0.010 ± 0.003a</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Ammonium uptake rates (µg N g root dry weight−1 hour−1) of S. clarizioi, S. sen&ium, and S. ambigius after defoliation treatments (Table 1). All 3 sampling dates, ammonium uptake rates were similar at lower NH₄⁺ concentrations on defoliated and undefoliated plants of S. clarizioi, S. sen&ium, and S. ambigius showing greater (P < 0.05) ammonium uptake rates than defoliated and undefoliated plants of S. clarizioi after 25 ppm NH₄⁺ concentrations (Table 2). Rates of ammonium uptake were greater (P < 0.05) on defoliated than on undefoliated plants in S. ambigius. Ammonium uptake rates of S. clarizioi showed greater (P < 0.05) ammonium uptake rates than defoliated plants of S. sen&ium at the lowest NH₄⁺ concentration by the end of the growing season (Table 2). At this time, ammonium uptake rates were similar among species or defoliation treatments at 25 ppm NH₄⁺. At 50 ppm

<table>
<thead>
<tr>
<th>Sampling Date</th>
<th>Uptake Rates</th>
<th>S. clarizioi</th>
<th>S. sen&amp;ium</th>
<th>S. ambigius</th>
</tr>
</thead>
<tbody>
<tr>
<td>26 Sept.</td>
<td>57.8 ± 2.4a</td>
<td>59.9 ± 2.4a</td>
<td>54.6 ± 2.4a</td>
<td></td>
</tr>
<tr>
<td>10 ppm</td>
<td>45.7 ± 2.4a</td>
<td>47.7 ± 2.4a</td>
<td>52.7 ± 2.4a</td>
<td></td>
</tr>
<tr>
<td>22 Oct.</td>
<td>57.7 ± 2.4a</td>
<td>82.1 ± 2.4a</td>
<td>36.4 ± 2.4a</td>
<td></td>
</tr>
<tr>
<td>4 Dec.</td>
<td>50.0 ± 2.4a</td>
<td>85.8 ± 2.4a</td>
<td>53.6 ± 2.4a</td>
<td></td>
</tr>
<tr>
<td>25 ppm</td>
<td>44.2 ± 2.4a</td>
<td>90.9 ± 2.4a</td>
<td>45.3 ± 2.4a</td>
<td></td>
</tr>
</tbody>
</table>

Results

Dry weight production after defoliation (regrowth) was similar or greater (P < 0.05) in S. clarizioi than in S. sen&ium and S. ambigius (Table 1). In all 3 sampling dates, ammonium uptake rates were similar or greater (P < 0.05) at higher than lower NH₄⁺ concentrations on defoliated and undefoliated plants of S. clarizioi, S. sen&ium, and S. ambigius (Table 2).
Discussion

By mid-spring, Stipa clavata showed greater regrowth following defoliation than S. tenax and S. ambigua. This indicates greater defoliation tolerance in S. clavata than in S. tenax and S. ambigua. A rapid photosynthetic surface area restabilization is characteristic of perennial grasses tolerant to defoliation (Caldwell et al. 1991, Briese and Reichardt 1995, Briese and Hendrickson 1996). In addition, greater growth of any given species may have implications in the capacity for soil resource acquisition. For example, when 2 perennial grass species (Schenziachne scoparia and Poa pratensis) grew near each other, the species with greater growth was potentially released from nutrient limitation as a result of lower growth in the other species. Under this condition, the species with greater growth may have used the advantage of unused resources by P. pratensis which indicated a significant competitive intensity (Van Auken and Bush 1997).

Proportional increases in the magnitude of ammonium uptake rate over a relatively wide range of increasing NH₄⁺ solution concentrations indicates that an efficient uptake kinetics is an important component for ammonium acquisition in S. clavata, S. tenax, and S. ambigua. A similar conclusion was reached by Dermer and Briese (1995) on several C₃ and C₄ perennial grass species. Increases in nutrient uptake as a result of higher soil resource availability in low-nutrient adapted plants would demonstrate the capacity of the root system in these species to take advantage of greater soil resource levels when they are available (Crick and Grime 1987). Since presence of nearby plants can sub-stantially modify ammonium uptake rate of target individuals (e.g., Wallace and Macks 1993), targets whose soil was chosen such that they had no neighbors within a radius of at least 0.3 m. Similar distances among plants in low-nutrient availability studies demonstrated ammonium uptake rates in perennial grasses (Jackson and Caldwell 1991, Baso et al. 2003). Books of ammonium uptake were stalliar or greater, but not lower, in S. clavata than in S. tenax and S. ambigua at high concen- tration. This suggests a greater efficiency for ammonium uptake in S. clavata than in the other 2 species. On average for all the time steps, ammonium concentration and defoliation treatment, ammonium uptake rates were 15% greater in S. clavata (18.7 µg N g root dry weight h⁻¹) than in S. tenax (18.3 µg N g root dry weight h⁻¹) and S. ambigua (16.8 µg N g root dry hour⁻¹). Even though the number of replicate plants used in our investiga- tion is similar to that used in other studies of ammonium uptake (i.e., Dermer and Briese 1995, Baso et al. 2001), it may be that it was not high enough as to detect more significant differences among species. Our results are similar to those reported by Baso et al. (2001), who found that the late-serial (Petriciota sericea) (Texas grass) had significantly greater rates of N uptake than the late-serial (Bouteloua curtipendula) (sidewheat grass) in only 3 out of 21 comparisons.

The greater ammonium uptake rate in S. clavata than in the other 2 species, in agreement with the first hypothesis, con- firms the positive correlation between competitive ability and ammonium uptake rate which has been reported by several authors (Nye and Tinker 1977, Jackson and Caldwell 1991, Wallace and Macks 1993, Caldwell 1994). However, differences in competitive ability may also be the result of other characteristics such as physiological processes and carbon allocation patterns within any species (Di Tommaso and Larsson 1991). For example, a greater root proliferation capacity in S. clavata than in S. tenax and S. ambigua also appears to be important in determining its greater competitive ability in comparison to the other 2 species (Saint Pierre et al. 2002). Determination of the relative con- tribution of different mechanisms to plant competitive ability poses a new and interesting and difficult challenge for future research.

Greater rates of ammonium uptake on defoliated than on undefoliated plants of all 3 species leads to rejection of the second hypothesis. Defoliation of some grass species has resulted in decreased nutrient uptake rates on nutrit- ious soils as a result of increased carbon allocation for shoot regrowth (Davidson and Milthorpe 1966, Overy et al. 1989). Similar results were obtained in Agropyron desertorum (Fisch. ex Link) Stuntz., and Sporobolus pyramidal (Caldwell et al. 1987). Carbon can be the limiting factor when plants grow in nutrient-rich environments (Lambert et al. 1998). In nutrient-poor environments, however, high ammonium return to the soil can occupy- pions reserves more rapidly than those of carbohydrates (Chapin and Slack 1979). Because of this, plants could maintain or even increase nutrient uptake rates after defoliation as the expense of using fresh carbohydrates coming from aboveground, remnant tissues (Chapin and Slack 1979). For example, shoot biomass was stimulated after a moderate defoliation in the grasses Erigeron vaginatinum L. and Dactylis glomerata Leysselt: when these species grew in a nutrient-limited environ- ment (Chapin and Slack 1979). It is possi- ble that defoliation of a greater frequency and/ or intensity than those used in our study could lower ammonium uptake rates below values on undamaged controls in S. clavata, S. tenax, and S. ambigua. This would allow determination of the point where multiple defoliation levels decrease root reserve carbohydrates such that ammoni- um uptake can no longer be maintained at high rates (Chapin and Slack 1979).

Greater capacity to rapidly modify root growth (Crick and Grime 1987) and greater root invasion rates (Essienas and Caldwell 1989) have reported in grasses of relatively greater competitive ability. Plants with large root systems or their root proliferation capacity can cover greater soil volumes and thus gather a greater share of soil resources (Caldwell et al. 1989). We reported small root physiological and morphological plasticity as complementary rather than competitive traits (Caldwell et al. 1989). Root proliferation capacity at N micrograms taken-up per g root dry weight per hour, without counteracting total root system extension when raising comparisons on a per plant basis (Caldwell et al. 1989). We reported small root physiological and morphological plasticity as complementary rather than competitive traits (Caldwell et al. 1989).

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2002), with greater ammonium uptake rates most of the time, was also the most grazed tolerant (Saint Pierre 2002, Saint Pierre et al. 2000a, 2000b). Grazing reduces productivity and defoli- ation tolerance in the late-seral S. clareaei than in the earlier-seral S. tenella and S. ambigua where S. clareaei as a dom- inant species in well managed grasslands. Our results are consistent with the hypoth- esis that late-seral species have a greater competitive ability than earlier-seral species (Wilson and Keddy 1986, Hendon and Briske 2002). At the study site, per- centage contribution to total perennial grass biomass increased from 3.4 to 14.6% in S. clareaei and decreased from 27.5 to 13.1% in S. ambigua in areas which were excluded from domestic herbivory and had not been exposed to any disturbance dur- ing a 9-year period (Giorgetti et al. 1995). At the same time, frequency increased from 7.5 ± 0.5 to 15 ± 8.7% (mean ± 1 standard deviation) in S. clareaei and decreased from 65.1 ± 3.2 to 32.5 ± 11.1% in S. ambigua (Giorgetti et al. 2000). S. tenella and S. ambigua showed a similar regrowth production after defoli- ation. Except on 4 December at 50 ppm, where underfertilized S. tenella had sig- nificantly lower ammonium uptake rates than defoliated S. ambigua, or where defoliated S. tenella showed significantly greater ammonium uptake rates than undefoliated S. ambigua, the two species also had simi- lar (P > 0.05) rates of ammonium uptake during the study period. These results indi- cate that S. clareaei, and S. tenella most of the time, had a competitive ability that would be similar in S. clareaei and S. ambigua. Our data suggest a com- petitive hierarchy of the form S. clareaei > S. tenella > S. ambigua. A parallel study at the same research site confirmed this com- petitive hierarchy. When labelled (15)N-NH3 was introduced into the soil between any two species of defoliated and undefol- iated plants of the 3 species, mean total N acquisition per basal area basis was signific- antly greater in S. clareaei (0.0093 mg N atom excess cm
-2) than in S. tenella and S. ambigua (Saint Pierre 2002). At the same time, S. tenella and S. ambigua did not show significant differences in total N acquisition from the soil (mean = 0.011 mg N atom excess cm
-2 in S. tenella and 0.007 mg N atom excess cm