NOTES

Intraseasonal variation in the $\delta^{15}N$ signature of taiga trees and shrubs

Knut Kielland, Bruce Barnett, and Don Schell

Abstract: We examined the stable isotope ratios of nitrogen from six dominant taiga species over three distinct phenological periods during the growing season. Temporal changes in the isotopic signature varied among species, but were not consistent within a given growth form. Despite large variation between nitrogen concentrations in new, mature, and senescent foliage, the seasonal fluctuations in $\delta^{15}N$ were small with the exception of aspen, a tree species growing on the most fertile sites. In the absence of strong within-season variation in isotope signature, we conclude that this parameter reasonably well integrates the plant–nitrogen relations over the growing season for most species, with the caveat that this parameter may show significant temporal variation in species from high-nitrogen environments. We found a significant, positive relationship between nitrogen concentration and $\delta^{15}N$ values in mature and newly flushed foliage, suggesting that plant enrichment in $\delta^{15}N$ is associated with increased soil nitrogen turnover.

Résumé : Nous avons examiné les rapports des isotopes stables de l'azote de six espèces dominantes de la taïga sur trois périodes phénologiques distinctes durant la saison de croissance. Les changements temporels dans la signature isotopique ont varié selon les espèces, mais n'étaient pas consistants à l'intérieur d'une forme de croissance donnée. En dépit de la forte variation entre les concentrations azotées du feuillage nouveau, mature et sénescent, la fluctuation saisonnière de $\delta^{15}N$ était petite à l'exception du tremble, une espèce arborée croissant sur les sites les plus fertiles. En absence d'une forte variation intra saison dans la signature isotopique, nous concluons que ce paramètre peut être estimé avec un seul échantillonnage durant la saison de croissance pour la plupart des espèces, avec la mise en garde que les valeurs d'abondance naturelle en ^{15}N peuvent présenter des variations saisonnières significatives chez les espèces d'environnements riches en azote. Nous avons observé une relation significative et positive entre la concentration inter-spécifique en azote et les valeurs de $\delta^{15}N$ dans le feuillage mature ainsi que celui nouvellement formé; cela suggère que l'enrichissement en $\delta^{15}N$ de la plante est associé à l'accroissement du turnover de l'azote du sol.
[Traduit par la Rédaction]

Introduction

The analysis of natural ^{15}N abundance ($\delta^{15}N$) has recently been used in the context of the physiological ecology of arctic and subarctic plants (Schulze et al. 1994; Michelsen et al. 1996; Nadelhoffer et al. 1996; Kielland 1997). Whereas differences in plant $\delta^{15}N$ values are believed to reflect variation in both soil and plant processes over spatial and temporal scales, nitrogen isotope values of plant tissues have largely been considered to be time invariant in ecological studies. The premise of such constancy is paramount for adequate interpretation of this ecological variable. However, large fluctuations in rates of soil nitrogen transformations and the corresponding soil nitrogen pools during the growing season (Giblin et al. 1991; Sveinbjörnsson et al. 1995), coupled with temporal variation in plant nitrogen uptake (Chapin and Tryon 1982; Kielland and Chapin 1994), suggest not only that these factors influence interspecific variation in $\delta^{15}N$ signatures per se, but also that such signatures may change during the growing season. In particular, interspecific differences in the relative importance of storage versus current uptake to meet annual nitrogen requirements could affect the seasonal $\delta^{15}N$ signature, independent of other factors such as rooting depth or absorbed nitrogen form (Schulze et al. 1994; Nadelhoffer et al. 1996; Kielland 1997). Here we examine the $\delta^{15}N$ signature in the foliage of six dominant taiga species (four trees and two shrubs), at three distinct phenological periods during the growing season, to test the null hypothesis that nitrogen isotope values are independent of plant phenology within the growing season.

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Methods

The study was conducted near Fairbanks, Alaska (64°51′N, 147°43′W, elevation 305 m), in three different types of upland taiga forests: black spruce (SB), white spruce (SW), and birch aspen (BA). These forest types exhibit large differences in rates of organic matter turnover and nitrogen cycling (Fox and

Fig. 1. Foliar $\delta^{15}N$ (‰) of taiga trees and shrubs at different phenological stages. Species designations are PIMA, *Picea mariana*; PIGL, *Picea glauca*; VAVV, *Vaccinium vitis-idea*; POTR, *Populus tremuloides*; BEPA, *Betula papyrifera*; SAAL, *Salix alaxensis*. Different letters designate statistical difference at $P < 0.05$. Mean and SE are shown. $n = 8$.

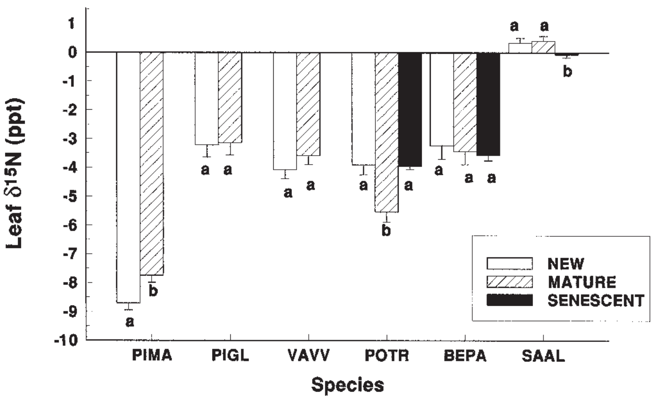
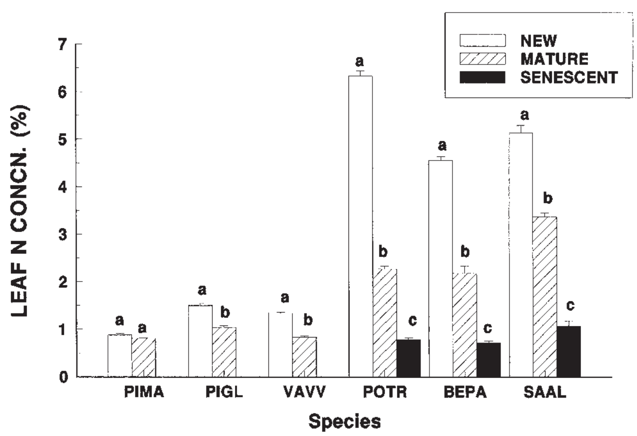


Fig. 2. Foliar nitrogen concentrations of taiga trees and shrubs at different phenological stages. Species designations and significance are as in Fig. 1.



Van Cleve 1983; Van Cleve et al. 1983). The soils are Histic Pergelic Cryaquepts (SB) and Alfic Cryochrepts (SW and BA), derived from a loess parent material (Viereck et al. 1983). The black spruce is underlain by permafrost. The pH ranges from 4 to 6 (Van Cleve et al. 1983).

The species sampled were *Picea mariana* (Mill.) BSP and *Vaccinium vitis-idea*, (SB); *Picea glauca* (Moench) Voss and *Salix alaxensis* (Anderss.) Cov. (SW); and *Betula papyrifera* Marsh. and *Populus tremuloides* Michx. (BA). For each species eight individuals were marked and repeatedly sampled over the growing season. The phenological stages sampled were spring leaf flush (last week in May for deciduous species and first week in June for evergreen species); mature, fully expanded foliage (20 July); and senescent leaves of deciduous species (mid-September).

We sampled foliage from 10 shoots of each species along a 120-m transect in each forest type at each sampling date. The samples were dried at 60°C, ground in a Wiley mill (40 mesh), and analyzed for total N and $\delta^{15}N$ on a Europa 20–20 mass spectrometer at the University of Alaska Fairbanks. Tissue $\delta^{15}N$ was calculated by conventional means (e.g., Michelsen et al. 1996; Kielland 1997) with nitrogen in air as the reference (Shearer and Kohl 1989). The data were analyzed by repeated-measures one-factor ANOVA using SAS (SAS Institute Inc. 1990).

Results

Despite large differences in soil nitrogen dynamics among these forest types (Flanagan and Van Cleve 1983), with one exception, we found only small changes in foliar $\delta^{15}N$ values over the season (Fig. 1). The mature evergreen needles tended to be enriched relative to newly flushed needles, whereas the opposite was generally true for the deciduous species. Aspen was the only species that showed substantial variation between newly flushed and mature leaves.

Foliar nitrogen concentrations varied seasonally over 8-fold within a deciduous species (aspen), and over 7-fold between deciduous and evergreen species (aspen – black spruce) at a given sampling date (Fig. 2). Among the deciduous species, aspen exhibited the greatest variation in seasonal nitrogen concentration (CV = 92%) and willow the least (CV = 64%).

We found a significant positive relationship between foliage nitrogen concentration and $\delta^{15}N$ signature in both mature (Fig. 3*a*) and newly flushed leaves (Fig. 3*b*) across species, although this relationship was stronger for mature foliage. No consistent trend was observed within a given species.

Discussion

The range of $\delta^{15}N$ values reported here overlap those reported elswhere for *Picea* in taiga forests (Schulze et al. 1994), but in the absence of similar data for the other species it is difficult to know how widely these results can be generalized.

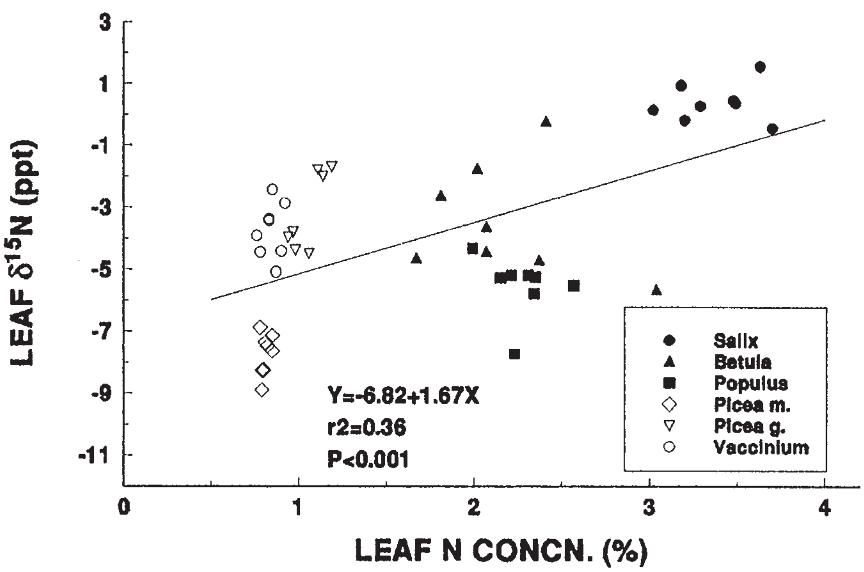
We suggest that the change in leaf $\delta^{15}N$ of aspen between early to midseason is in part explained by the seasonal changes in soil nitrogen acquisition. Aspen stands exhibit higher rates of nitrogen mineralization and nitrification than other upland forest types (Van Cleve et al. 1983; Paré and Van Cleve 1993). Moreover, aspen has a high capacity for nitrate absorption relative to other upland tree species (Chapin et al. 1986). Because nitrification tends to discriminate against ^{15}N (Feigin et al. 1974), species that assimilate nitrate from nitrifying soils should be isotopically lighter than species relying primarily on ammonium (Frank and Evans 1997). Thus, one possible explanation for the depleted $\delta^{15}N$ signature of aspen during midseason may be due to larger proportion of its annual nitrogen uptake in the form of nitrate, though we recognize that the complexity of soil nitrogen transformations could confound this interpretation (Garten and Van Miegroet 1994).

The positive relationship between the isotope signature and nitrogen dynamics across forest types (Van Cleve et al. 1983, 1993; Fig. 3) suggests that plant isotope enrichment is functionally related to increased soil nitrogen turnover (Garten and Van Miegroet 1994). Data on foliar $\delta^{15}N$ values across gradients of nitrogen mineralization in the Arctic (Giblin et al. 1991; Nadelhoffer et al. 1996) are consistent with this hypothesis.

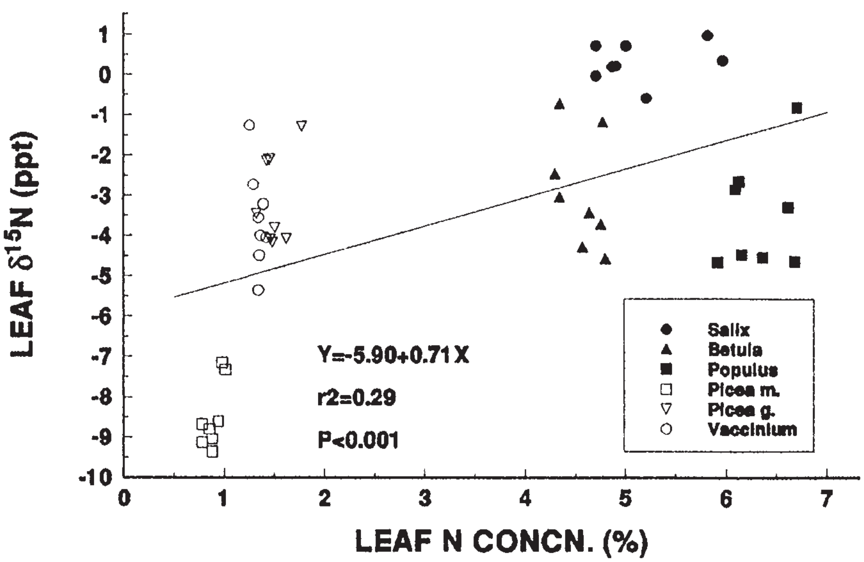
We have shown that interspecific variation in the $\delta^{15}N$ signature of taiga species can be large (–8.5‰ to +0.5‰). We conclude, however, that the absence of significant changes in foliar $\delta^{15}N$ during the growing season validates previous studies

Fig. 3. Relationship between nitrogen concentrations and $\delta^{15}N$ in (*a*) mature and (*b*) newly flushed foliage.

(a)



(b)



involving one-time sampling, with the caveat that $\delta^{15}N$ may show significant within-season variation in species from soil with high nitrogen turnover. The latter circumstance could lead to biased interpretations regarding soil nitrogen relations in these species.

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