Altitudinal gradients of natural abundance of stable isotopes of nitrogen and carbon in the needles and soil of a pine forest in Nepal

S. P. Sah, R. Brumme

Institute of Soil Science and Forest Nutrition, University of Göttingen, Göttingen, Germany

ABSTRACT: This paper deals with natural abundance of ^{15}N and ^{13}C in the soil and needles of the pine forest (*Pinus roxburghii*, Sargent) along an altitudinal gradient. The study area lies in the elevation range of 1,200 m to 2,200 m in Kathmandu valley of Nepal. The higher altitude soil was found to be much more depleted of ^{13}C than the lower altitude soil. The decreasing trend of C-isotope (as well as the trend of N-isotope) might be attributed to the lower mineralisation rate and net nitrification rate at the higher altitude. The observed differences in isotopic N- and C-contents of needles and soils across altitudinal gradients in this study are a result of the combination of environmentally induced variations in physiological and morphological differences. For example, altitudinal variation in needle $\delta^{15}N$ and $\delta^{13}C$ at the research site indicates that the needle isotopic composition is related to nitrogen availability at a site.

Keywords: pine forest; Nepal; stable isotopes; carbon; nitrogen; soil; needles; altitudinal gradients

Natural abundance of isotopes offers a promising tool for the exploration of nutrient dynamics in forest ecosystems (NADELHOFFER, FRY 1994). A better understanding of N-dynamics is needed because of the intimate connection between the cycling of nitrogen and carbon in the biosphere (ÅGREN, BOSATTA 1996).

Since it has become known that plant tissues contain less $\delta^{13}C$ than the ambient air, studies of ^{13}C discrimination by plants have become a potential tool in global C-cycling studies. The relation between the stable isotope ratio and photosynthetic water-use efficiency has led to a wide-spread use of isotopic analyses in plant physiological ecology. The significance of isotopic variation lies in its broad correlation with photosynthetic water-use efficiency (FARQUHAR, SHARKEY 1982). Considerable effort has gone into the description of sources of variation in $\delta^{13}C$ and $\delta^{15}N$ which vary among species (DELUCIA et al. 1988; GOWER, RICHARDS 1990; MARSHALL, ZHANG 1994) and along an environmental gradient (DELUCIA, SCHLESINGER 1991; LAJTHA, GETZ 1993; PANEK, WARING 1995). Leaf carbon isotope discrimination reflects the rates of internal to external CO_2 concentrations and is an integrated, long-term measure of the effects of factors affecting inward CO_2 diffusion (leaf conductance) and CO_2 consumption (photosynthetic rate) (EHLERINGER et al. 1993).

Shifts in $\delta^{13}C$ and $\delta^{15}N$ at the intraspecific level are consistently observed over altitudinal gradients (KÖRNER et al. 1988; VITOUSEK et al. 1990; MARSHALL, ZHANG 1993; SPARKS, EHLERINGER 1997); however, the mechanisms underlying this trend are unknown. Ecologists have reported correlations of stable isotopes of N and C with the various abiotic factors over altitudinal gradients. These factors include soil moisture (BEERLING et al. 1996), air temperature (PANEK, WARING 1995), atmospheric CO_2 concentrations (EHLERINGER, CERLING 1995), and leaf morphological and physiological traits that vary with altitude. Levels of N in plant are positively correlated with altitude (KÖRNER 1989; SPARKS, EHLERINGER 1997). Likewise leaf mass per unit area increases with altitude (WOODWARD 1986; WILLIAMS et al. 1995) and is often correlated with $\delta^{13}C$ (VITOUSEK et al. 1990; KÖRNER et al. 1991).

In this study, we report trends in leaf and soil $\delta^{13}C$ and $\delta^{15}N$ of pine forests that occur across a broad altitudinal range. The objectives of this study were to examine the responses of single species that exhibit a continuous distribution over a broad elevational gradient. We anticipated that nutrient accumulation would be most rapid at low elevation (POST et al. 1985). We also expected that foliar nutrient concentrations would decline with increasing elevation (GRUBB 1977; TANNER 1985), reflecting slower nutrient cycling. Finally we anticipated that foliar $\delta^{13}C$ would be less negative (^{13}C enrichment) and foliar $\delta^{15}N$ less positive (^{15}N depletion) at high altitudes. We tested the following hypotheses: 1. carbon and nitrogen isotopes in the needles of the tree species shift consistently over altitudinal gradients and 2. shifts in isotope ratios are related with leaf and soil nutrient content.

METHODOLOGY

Site selection and their description

The present study deals with the Nagarjun hills of Kathmandu, Valley, Nepal. They are situated north of Kath-
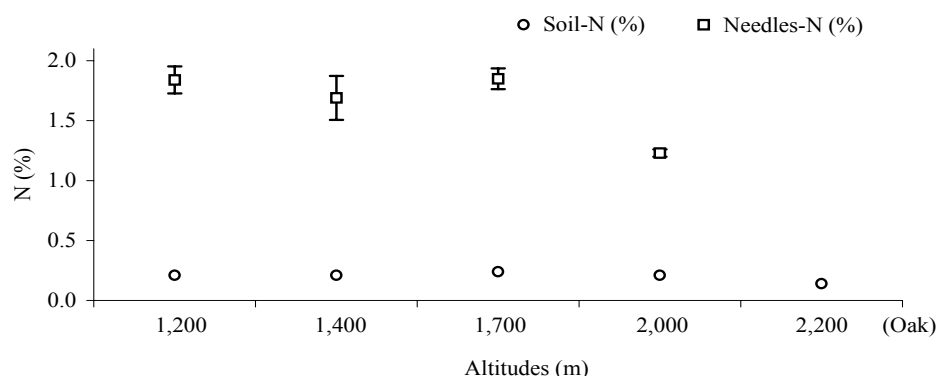
Fig. 1. N% soil and needles

mandu City and their total area is 15 km^2. The main range of the hills runs in east west direction with its highest point of 2,200 m which rises abruptly from the floor of Kathmandu valley of 1,200 m. The climate is typical monsoon; hot summer and cool winter. The maximum temperature goes up to 30°C in summer and minimum temperature in winter falls below the freezing point (–3°C). The annual rainfall is about 1,400 mm, mostly distributed only in the months of July and August and other months are almost dry. The site is mainly composed of *Schima* forest, mixed broad-leaved forest, pine forest and oak forest. This study was limited only to the south facing slope of the hill from 1,200 m to 2,200 m. This slope is mainly composed of pine forest (*Pinus roxburghii*, Sargent) up to an altitude of 2,000 m. Above this altitude, the hill consists of only deciduous oak forest (*Quercus lanuginosa* D.).

Five stands were selected from the bottom to the top of hills at the interval from 200 to 300 m altitude. A quadrate of 20 × 20 m was set up at each stand. From each quadrate, only *Pinus* sp. was selected for the sampling. Five trees were sampled at random from each quadrate. Following samplings were carried out in each quadrate:

Sampling

Samples of needles were collected from the selected sites in February (in dormant seasons). The needles sampled were quickly rinsed with de-ionised water to remove dust particles. All needle samples were dried at 60–80°C and milled using planetary mills.

Soil samples were collected randomly according to a sample grid system. The soil was sampled in 5 × 5m grid system according to diagnostic horizons. The stand consisted of no significant humus layer. Therefore, only the mineral soil layer at the depth of 20 cm was sampled. The collected soil samples were sieved through 2mm sieve prior to drying and grinding.

Analytical methods

All the plant and soil samples were dried at 70°C and samples were ground into a fine powder in a planetary mill. The elemental composition of plant and soil samples was analysed by the standard methods. The isotopes of C and N were measured on a Finnigan MAT Delta plus stable isotopic ratio mass spectrometer (IRMS) equipped with an elemental analyser for conversion of N into N_2, C into CO_2. The results of IRMS measurements were given in δ notation. The δ values of isotopes (N and C) are expressed as parts per 1,000 differences from standard atmospheric isotopes (SHEARER, KOHL 1993).

$$\delta X = (R_{sample}/R_{atmos} - 1) \cdot 1,000 \text{ (‰)}$$

where: X — ^{15}N and ^{13}C,
R_{sample} — X present in samples,
R_{atmos} — X present in atmosphere as standard.

The isotopic composition of soil nitrogen may vary from one site to another. Therefore, the relationship for the nitrogen isotope composition of plants and soil is also presented in terms of "enrichment factor" (MARIOTTI et al. 1981). If the substrate is a large reservoir with respect to the product, then the enrichment factor can be approximated as the difference between ^{15}N abundance in the sub-
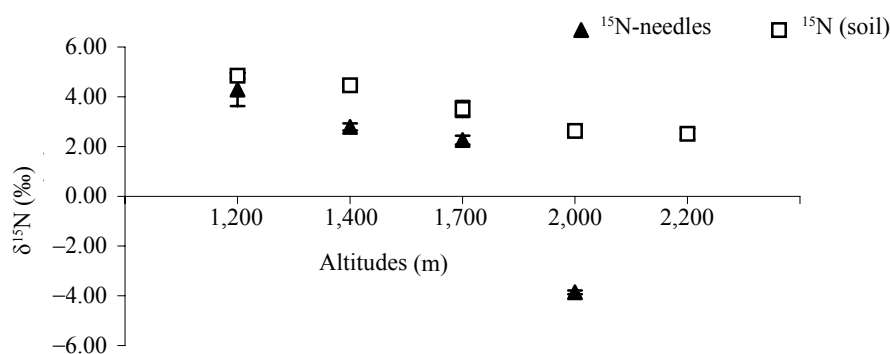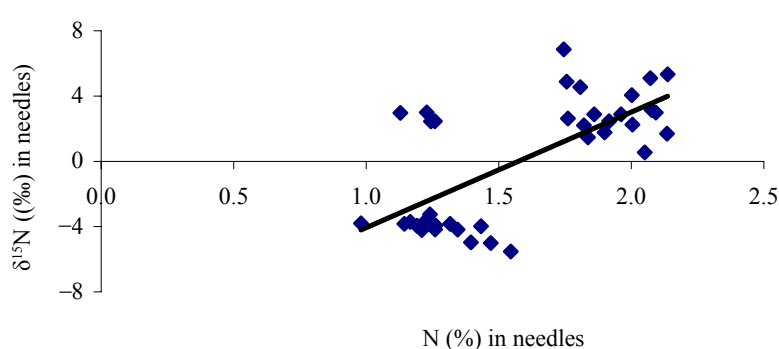

Fig. 2. ^{15}N soil and needles

$R^2 = 0.4678 \ (r = 0.68)$

Fig. 3. N% and ^{15}N relationships in needles/foliage

(Figure axes: y-axis $\delta^{15}N$ (‰) in needles, ranging −8 to 8; x-axis N (%) in needles, ranging 0 to 2.5)

strate (total soil nitrogen) and the product (foliar nitrogen), i.e. enrichment factor = $[\delta^{15}N_{\text{(needles)}} - \delta^{15}N_{\text{(soil)}}]$.

RESULTS

Altitudinal gradients of natural abundance of ^{15}N in plants and soil

N content of soil, in general, slightly decreased with the increasing altitudes (Fig. 1). Soil nitrogen content decreased ($r^2 = 0.36$) about 0.07% over an altitude of 1,000 m from 0.21% at 1,200 m to 0.14% at 2,200 m. However, the trend of heavier stable isotopes of N in soil along the above mentioned altitudinal gradients was opposite to the trends in their lighter elemental forms. $\delta^{15}N$ values in soil were higher at lower altitude (+ 4.85‰) than those found at the higher altitude (+ 2.51‰), i.e. the difference was about + 2.34‰ (Fig. 2). The decreasing trend of soil $\delta^{15}N$ ($r^2 = 0.97$) was significant with the increasing altitude. The %N and ^{15}N relationship indicated a slight positive correlation both in soil ($r^2 = 0.71$) as well as in needles ($r^2 = 0.47$) (Fig. 3).

Similar to soil, green needle nutrients slightly declined ($r^2 = 0.55$) with increasing altitude (Fig. 1). Needle nitrogen content decreased about 0.57% over 800 m, from 1.67 N% at 1,200 m to 1.23 N% at 2,000 m and this negative correlation trend, however, was not found significant ($r^2 = 0.55$). In the needles, $\delta^{15}N$ values, similar to %N, were lower at higher altitudes than at the lower altitudes, i.e. at the higher altitudes pine sp. was more depleted of $\delta^{15}N$ (−3.86‰) than at the lower altitude (+ 4.29‰), showing a large difference ($r^2 = 0.81$) of 8.15‰ over an altitude difference of 800 m (Fig. 2). When compared across all altitudes, the %N and $\delta^{15}N$ of foliage (Fig. 3) were positively correlated ($r^2 = 0.46$).

Altitudinal gradients of natural abundance of ^{13}C in needles and soils

The C content (Fig. 5) of soil ranged from 1.87% (higher altitude) to 2.91% (lower altitude), but this decreasing trend was not significant ($r^2 = 0.35$). The C/N ratio in soil increases slightly with altitude from 13.6 at the 1,200 m altitude to 14.1 at the 2,200 m altitude. It shows an slow increase of decomposition rate at the higher altitude. However, a distinct trend of their heavier stable isotopes of C in soil, similar to N-isotopes, was observed along the above mentioned altitudinal gradients. Soil $\delta^{13}C$ values were greater (i.e. ^{13}C enrichment) at lower altitudes (−16.26‰) than those found at higher altitudes (−23.57‰), i.e. ^{13}C-depletion in soil was stronger at higher altitudes than at lower altitudes (Fig. 6). The difference between lower altitudes and higher altitudes in soil $\delta^{13}C$ values was about −7‰. The decreasing trend of soil $\delta^{13}C$ ($r^2 = 0.82$) was weaker than that of soil $\delta^{15}N$ ($r^2 = 0.97$) with the increasing altitude (Figs. 2 and 6).

$R^2 = 0.7138 \ (r = 0.84)$
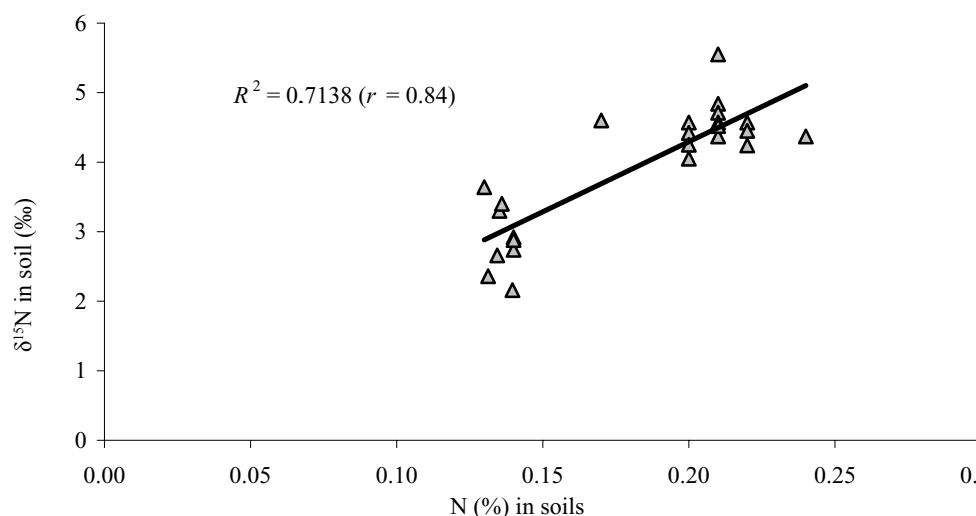
Fig. 4. N% and ^{15}N relationship in soils

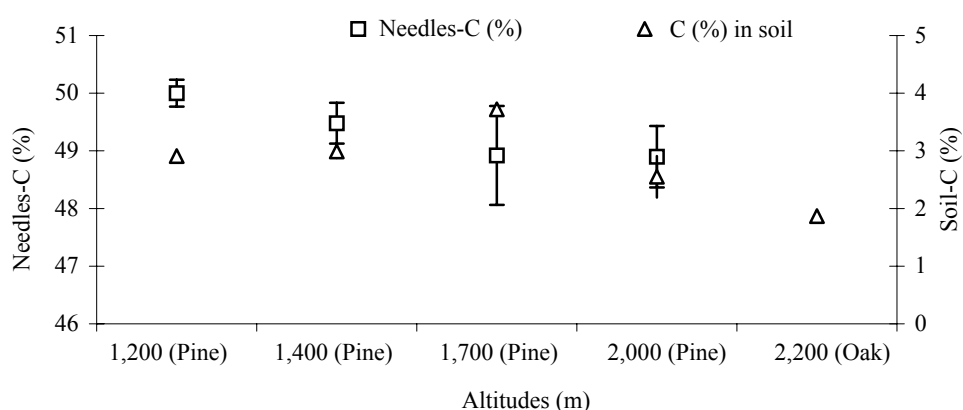(Figure axes: y-axis $\delta^{15}N$ in soil (‰), ranging 0 to 6; x-axis N (%) in soils, ranging 0.00 to 0.30)

Fig. 5. C% in needles and soil

As expected, C content of the needles was similar at all altitudes (Fig. 5). However, opposite to ^{15}N, carbon isotope ratios (δ^{13}C) increased slightly with altitudes in the needles of the trees, i.e. the trees growing at higher altitudes discriminated less against [13]C (increase in δ^{13}C) compared with trees at lower altitudes (Fig. 6). δ^{13}C in the needles at the different altitudes ranged from –27.86 to –26.87‰ along the altitudinal range of 800 m. A significant negative correlation ($r^2 = 0.87$) was obtained between δ^{13}C abundance and altitude (Fig. 6).

Trends of enrichment factors indicated more positive values of δ^{15}N at lower (0.56 ‰) altitudes than at higher altitudes (–8.55‰), i.e. larger (i.e. more positive or less negative) enrichment factors indicate smaller differences between the isotopic composition of soil N and foliar N (Fig. 7).

DISCUSSION

Altitudinal gradients of natural abundance of ^{15}N in needles and soil

The decreasing trends of N contents of soil with altitudes in our studies, in general, correspond to other studies (ZEWDU, HÖGBERG 2000; JHA et al. 1986). This trend is attributed to the soil erosion effect on the high steep slopes of the site. The steep slopes at higher altitudes cause

the nutrients leaching downwards, resulting in their accumulation at lower altitudes and it is reflected by the presence of higher soil nutrients at the lower altitudes in our study (see below). However, the trend of heavier stable isotopes N in soil along the above mentioned altitudinal gradients was opposite to their trends of lighter elemental forms. Opposite to elemental N, there was a significant decreasing trend of soil δ^{15}N ($r^2 = 0.97$) with the increasing altitude. Furthermore, a positive (but insignificant) correlation between %N and δ^{15}N was observed in soil across the altitudes ($r^2 = 0.71$) and the decreasing trend of N-isotopes might be attributed to the lower rates of both mineralisation and net nitrification at the higher altitude. Strong nitrification that occurs at N-rich sites produces ^{15}N depleted NO_3. If this NO_3 pool is selectively lost through leaching or denitrification, the residual inorganic pool will be dominated by isotopically heavier NO_3 and NH_4. This process explains why N-poor sites (high altitudes) are associated with more negative soil and foliar δ^{15}N. MA-RIOTTI et al. (1980) found similar results. They showed a decrease in δ^{15}N values of surface mineral soil from + 3.1‰ to + 0.31‰ along the 1,100–1,800 m altitudinal gradient and it was linked to the isotopic composition of undecomposed surface fresh plant material on surface soil and to differences in biodegradation and humification of organic matter. They showed much more positive δ^{15}N in Mull-humus than in Mor-humus. GARTEN and MIGROET
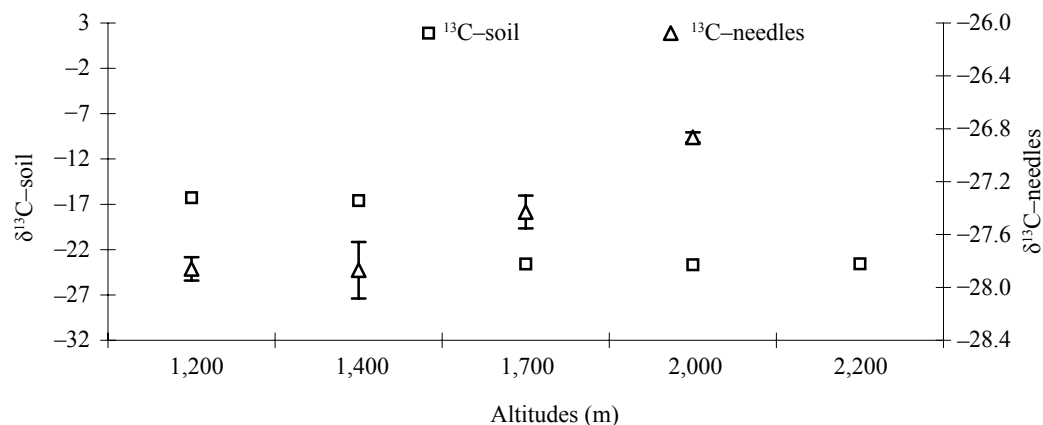

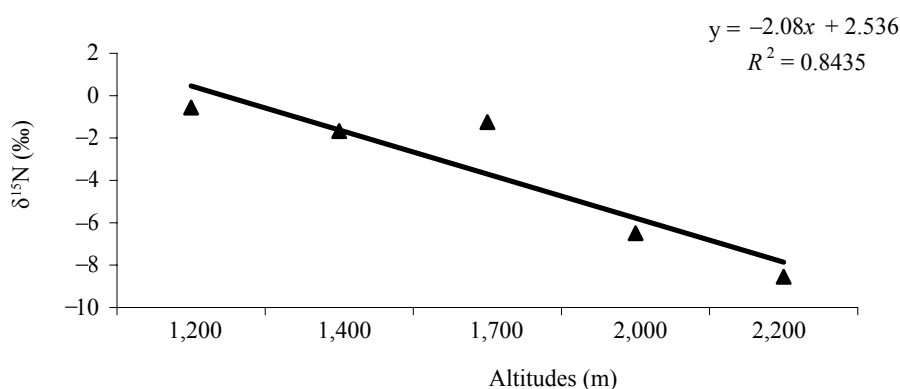Fig. 6. [13]C in soil and needles

$$y = -2.08x + 2.536$$
$$R^2 = 0.8435$$

Fig. 7. Enrichment factor of soil

(1994) did not find any consistent pattern of soil natural ^{15}N abundance along the altitudinal gradient of forest in the USA. They found δ^{15}N in the range of +3.6 to +5.4‰ from 8 sites in 8 different tree species.

Similar to soil, green needle nutrients also declined significantly ($r^2 = 0.55$) with increasing altitude (Fig. 1). A similar trend of foliar nutrient concentrations was reported from several studies (VITOUSEK et al. 1988; TANNER 1985). LEIGH (1975) attributed it to decreased nutrient uptake caused by low rates of transpiration at the higher altitude. But more recently leaf morphology and decreased nutrient availability caused by low rates of decomposition were considered more likely (GRUBB 1977; TANNER 1985). Other studies also reported the increase of %N in foliage with altitudes. Various explanations for such altitudinal trends in plant N have been suggested. Low temperature and short growing season at higher altitude reduce growth and might consequently have a concentrating effect on leaf N contents (KÖRNER 1989; FRIEND, WODWARD 1990). Another cause might also be the high N supply (BADDELEY et al. 1994; PITCAIRN et al. 1995) from atmospheric N deposition, as altitudinal increases in N deposition in some industrial regions were reported (FOWLER et al. 1988). In the needles, δ^{15}N values, similar to %N, were lower at higher altitudes than at lower altitudes, i.e. at higher altitudes pine sp. was more depleted of δ^{15}N (–3.86‰) than at lower altitudes (+ 4.29‰). When compared across all altitudes, %N and δ^{15}N of foliage were positively correlated ($r^2 = 0.46$). Similar results were obtained by other researchers (HOBBIE et al. 2000; GARTEN 1993).

Foliar δ^{15}N should reflect the δ^{15}N of soil N sources when N is limiting (HÖGBERG 1997; HÖGBERG et al. 1999). The decreasing foliage ^{15}N with altitude might be attributed to the net nitrification potential in soil, i.e. net nitrification potential of high altitude soil is less than at the lower altitude (GARTEN 1993) and this, in turn, causes lower availability of inorganic N in soil. As mentioned above, strong nitrification that occurs at N rich sites produces ^{15}N depleted NO_3. If this NO_3 pool is selectively lost through leaching or denitrification, the residual inorganic pool will be dominated by isotopically heavier NO_3 and NH_4. This process explains why net N poor sites (high altitudes) are associated with more negative soil and foliar δ^{15}N. The trend of enrichment factors supports our hypothesis too. Trends of enrichment factors indicated more positive values of δ^{15}N values at the lower (–0.56‰) altitudes than at the higher altitudes (–8.55‰), i.e. higher (i.e. more positive or less negative) enrichment factors indicate smaller differences between the isotopic composition of soil N and foliar N (Fig. 7). Similar results were obtained by GARTEN and MIGROET (1994). Enrichment factors were found to be correlated with net nitrification potential in soil (GARTEN, MIGROET 1994; GARTEN 1993). Foliar δ^{15}N values were found to be positively correlated with net nitrification potential in surface soil (GARTEN 1993). It shows a higher potential net N-mineralisation of soil at lower altitudes compared with higher altitudes and it is supported by the presence of higher nutrients at lower altitudes in our study. Similar conclusions were made by MILLER and BOWMAN (2002) from the study of alpine-tundra plants in the USA. GARTEN and MIEGROET (1994) did not find any consistent pattern of ^{15}N abundance in soil with elevations.

Altitudinal gradients of natural abundance of ^{13}C in needles and soils

The lighter C content of soil did not differ a lot with altitude. As expected, the ^{13}C-depletion was stronger at the higher altitude soil than at the lower altitude soil. This decreasing trend of soil δ^{13}C at the higher altitude was weaker ($r^2 = 0.76$) than that of soil δ^{15}N ($r^2 = 0.97$) with the increasing altitude. The decreasing trend of C-isotope might be attributed to the lower rate of mineralisation and net nitrification rate at the higher altitude. As expected, C content of the needles was similar at all altitudes. However, opposite to ^{15}N, carbon isotope ratios (δ^{13}C) in needles increased slightly with altitudes, i.e. the trees growing at higher altitudes discriminated less against [13]C (increase in δ^{13}C) compared with trees at lower altitudes (Fig. 6). This might be due to increases in the diffusional pathway length for CO_2 from atmosphere to the site of carboxylation and potentially decrease discrimination at the higher altitude (VITOUSEK et al. 1990). Several other studies reported a similar increase in δ^{13}C of needles/foliage along altitudinal gradients (KÖRNER et al. 1988, 1991; VITOUSEK et al. 1990; MARSHALL, ZHANG 1993). The δ^{13}C trend was correlated with leaf morphological and physiological traits that vary with altitudes. Correlated

leaf traits include leaf thickness (VITOUSEK et al. 1990; CORDELL et al. 1998), stomatal conductance (MEINZER et al. 1992), stomatal density, i.e. number of pores per leaf surface area (KÖRNER et al. 1989; WOODWARD, BAZZAZ 1988), leaf nitrogen content (SPARKS, EHLERINGER 1997; MORECROFT, WOODWARD 1996), and leaf mass per area (VITOUSEK et al. 1990). CORDELL et al. (1998) reported foliar $\delta^{13}C$ values increasing substantially from –29.5‰ at low elevation to –24.8‰ at high elevation. They attributed this significant increase in leaf mass per unit area as a function of elevation. MEINZER et al. (1992) speculated that $\delta^{13}C$ increases with altitude were due to decreases in maximum stomatal conductance, presumably decreases with stomatal density (WOODWARD, BAZZAZ 1988), which would lead to isotopic enrichment. HULTINE and MARSHALL (2000) recently concluded from their study of 4 coniferous tree species that the relationships between the above mentioned physiological traits over altitudinal gradients were mostly species-specific and only the relationship between leaf mass area (LMA) and $\delta^{13}C$ was observed in general, suggesting that internal resistance can limit CO_2 diffusion to sites of carboxylation to some extent in conifers. LMA increased with altitudes and was coupled with $\delta^{13}C$. This assumption was also supported by the results of VITOUSEK et al. (1990) from the Hawaiian tree species *Metrosideros polymorpha*. KÖRNER and DIMER (1987) suggested a potential cause for the foliar $\delta^{13}C$ enrichment at higher altitude due to higher photosynthetic capacities of trees at this altitude. KÖRNER et al. (1988) attributed such a trend associated with the presence of lower ratio of Pi/Pa of CO_2 in leaves of high altitude plants than in leaves of low altitude, and it is also supported by many studies (KÖRNER, DIEMER 1987; MORECROFT, WOOSWARD 1990, 1996). KÖRNER et al. (1991) suggested that both temperature and atmospheric pressure are responsible for the altitudinal trends in ^{13}C discrimination. They provided evidence that C-isotope discrimination during photosynthesis of C3-plants decreases with altitude and it was found to be associated with greater carboxylation efficiency at the higher altitude. Changing partial pressure of CO_2 and O_2 and changing temperature are possible explanations of this observation. The higher values of $\delta^{13}C$ at the higher altitude indicate a lower ratio of CO_2 partial pressure inside the leaf to that in the atmosphere (Pi/Pa) (MORECROFT, WOODWARD 1990), and a higher ratio of carboxylation efficiency to stomata conductance (FARQUHAR 1982). SPARKS and EHLERINGER (1997) found also the increase in $\delta^{13}C$ with increase in altitude in 3 different *Populus* sp. in the USA and they attributed it to the presence of the higher internal leaf CO_2 concentrations at low elevation. KÖRNER and DIMER (1987) and FRIEND et al. (1989) suggested that at the higher elevations plants exhibit unusually high carboxylation capacities in relation to their stomatal conductance and this would lead to a decrease in ^{13}C discrimination over elevation.

CONCLUSIONS

Overall, the results of the present study supported our hypothesis that the altitudinal differences would lead to

changes in isotopic N- and C-composition within a plant species. The observed differences in isotopic N and C contents of needles and soils across altitudinal gradients in our study are a result of the combination of environmentally induced variations in physiological and morphological differences. For example, altitudinal variation in needle $\delta^{15}N$ and $\delta^{13}C$ at the research site indicates that needle isotopic composition is related to nitrogen availability at a site.

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Výškové gradienty přirozeného zastoupení stabilních izotopů dusíku a uhlíku v jehličí a půdě v borových porostech Nepálu

S. P. Sah, R. Brumme

Ústav půdoznalectví a výživy lesa, Univerzita v Göttingenu, Německo

ABSTRAKT: Příspěvek se zabývá zastoupením izotopů [15]N a [13]C v půdách a jehličí borových porostů (*Pinus roxburghii*, Sargent) v kontextu výškového gradientu. Oblast výzkumu leží v nadmořské výšce 1 200 až 2 200 m n. m. v údolí Kathmandu v Nepálu. Bylo zjištěno, že půdy ve vyšších nadmořských výškách jsou více ochuzeny o obsah ^{13}C než půdy ve výškách nižších. Klesající trend C-izotopu lze podobně jako u N-izotopu přičíst nižší rychlosti procesů mineralizace a čisté nitrifikace ve vyšších výškách. Zjištěné rozdíly v obsahu izotopů N a C v jehličí a půdách v kontextu výškových gradientů vyplývají z kombinace změn podmínek indukovaných vnějším prostředím (fyziologické a morfologické rozdíly). Například uváděné změny $\delta^{15}N$ a ^{13}C podle nadmořské výšky oblasti výzkumu indikují skutečnost, že skladba izotopů v jehličí je ovlivněna dostupností dusíku na stanovišti.

Klíčová slova: porosty borovice; Nepál; stabilní izotopy; uhlík; dusík; půda; jehličí; výškové gradienty

Příspěvek se zabývá přirozeným zastoupením izotopů [15]N a [13]C v půdách a jehličí borových porostů (*Pinus roxburgii*, Sargent) v kontextu výškového gradientu v Nepálu. Oblast výzkumu leží v nadmořské výšce 1 200 až 2 200 m n. m. v údolí Kathmandu v Nepálu. Od té doby, kdy bylo zjištěno, že rostlinná pletiva obsahují méně $\delta^{13}C$ než okolní vzduch, staly se výzkumy založené na rozlišování izotopu [13]C v rostlinách potenciálním nástrojem v globálních studiích koloběhu uhlíku. V práci je stanovováno přirozené zastoupení izotopů [15]N a ^{13}C jak v půdách, tak v rostlinách v kontextu výškového gradientu. Trend většího stabilního izotopu N v půdách podle výškového gradientu byl opačný než trend lehčích elementárních forem. Byl zjištěn signifikantní trend poklesu půdního $\delta^{15}N$ ($r^2 = 0,97$) spolu se zvyšováním nadmořské výšky, a to může být způsobeno nižší rychlostí procesů mineralizace a čisté nitrifikace ve vyšších výškách. V jehličí byly hodnoty $\delta^{15}N$ stejně jako % N nižší ve vyšších výškách než na lokalitách nižších, tj. ve vyšších nadmořských výškách byla borovice (*Pinus roxburghii*, Sargent) více ochuzena o $\delta^{15}N$ (−3,86 ‰) než ve výškách nižších (+ 4,29 ‰). Snižování obsahu [15]N v jehličí spolu s nadmořskou výškou může být způsobeno potenciálem čisté nitrifikace v půdě. Půdy ve vyšších nadmořských výškách jsou více ochuzeny o obsah ^{13}C než půdy ve výškách nižších. Klesající trend C-izotopu lze podobně jako u N-izotopu přičíst nižší rychlosti procesů mineralizace a čisté nitrifikace ve vyšších výškách. Nicméně na rozdíl od izotopu ^{15}N se poměr izotopu uhlíku ($\delta^{13}C$) v jehličí mírně zvyšoval spolu s výškou, tj. stromy rostoucí ve vyšších nadmořských výškách diskriminují méně izotop [13]C (zvýšení $\delta^{13}C$) ve srovnání se stromy rostoucími níže. Může to být způsobeno zvyšováním délky difuzní cesty CO_2 z atmosféry na místo karboxylace a potenciálním snížením diskriminace ve vyšších výškách. Trendy ve faktorech obohacení indikují více pozitivní hodnoty $\delta^{15}N$ v nižších výškách (−0,56 ‰) než ve výškách vyšších (−8,55 ‰), tj. hodnotově vyšší (více pozitivní nebo méně negativní) faktory obohacení indikují menší rozdíly mezi skladbou izotopů v půdním N a v listovém N.

Corresponding author:

Ph.D. Shambu Prasad Sah, Department of Forest Ecology, University of Helsinki, PL BOX 27, Latokartanonkaari 7, FIN-00014 Helsingin Yliopisto, Helsinki, Finland
tel.: + 358 9 191 581 26, fax: + 358 9 191 581 00, e-mail: sambhu.sah@helsinki.fi