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Stable Nitrogen Isotopes in a Forested Watershed in Taiwan

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Abstract

Differences in rates and patterns of nitrogen cycling have been correlated with nitrogen stable isotope measurements in forest ecosystems of tropical and temperate regions, but limited similar work has been conducted in sub-tropical forests. This study investigated patterns in stable N isotopic composition in a subtropical forest in Taiwan by sampling three soil profiles and overstory and understory foliage. Soil $\delta^{15}N$ in the forest floor ranged from -1.8 to 1.8%. Mineral soils had higher $\delta^{15}N$ (4.1 to 6.0%). Foliage $\delta^{15}N$ in overstory trees ranged from -6.6 to -2.0%, and understory foliage $\delta^{15}N$ ranged from -5.0 to -1.2%. There was a weak correlation between foliar % N and $\delta^{15}N$ (r²=0.214). Compared to results from similar surveys in tropical and temperate forests, foliar $\delta^{15}N$ values were generally lower. These results help highlight the need for improved knowledge regarding the relationships between patterns in N stable isotopes and processes affecting rates of N cycling, especially as related to wider scale patterns in forest ecosystems within the east-Asia region.

Key Words: foliar ¹⁵N, forest soils, nitrogen, stable isotopes, Taiwan

Introduction

Nitrogen is often a limiting nutrient in terrestrial ecosystems. In tropical forests, however, nitrogen is generally considered to be relatively more available then in temperate forests (Vitousek 1984; Vitousek and Sanford 1986). Interest in improving our understanding of the factors affecting rates of ecosystem N cycling among different ecosystem types has become intensified by the recognition of possible deleterious effects of elevated N inputs to many types of ecosystems, including forests. Much attention has been focused on the possibility of "nitrogen saturation" in forested ecosystems, especially in North America (Aber et al. 1989; Stoddard 1994) and Europe (Skeffington 1990; Gundersen et al. 1998). Some early studies indicated that

differences in hydrology and patterns in N cycling from those in watersheds in North America and Europe were responsible for the differences in temporal patterns in stream chemistry found in several watersheds in Japan (Mitchell et al. 1997). Much more information about rates of N cycling from regions other than North America and Europe is still needed to increase our understanding of the variation in forest ecosystem nitrogen cycling processes among different forest types and regions.

An approach increasingly being used to help interpret patterns of N cycling in forest ecosystems is stable isotope analysis. Investigating forest soil profiles (changes with soil depth) is a simple method that has been used to compare among forest types or environments to provide some fundamental insights into N cycling (Hogberg et al. 1996).

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Surveys of soil and plant tissue 15 N natural abundance can also be used to help understand nitrogen dynamics in forest ecosystems. Although some 15 N data from tropical and sub-tropical forests are available (Yoneyama et al. 1993; Piccolo et al. 1996; Kuang et al. 2010; Fang et al. 2011), most studies of this kind have been conducted in temperate regions. In this study I investigated patterns in δ^{15} N natural abundance in soils and vegetation in a forested watershed in northeastern Taiwan. The objective of this study was to conduct a survey of 15 N natural abundance of soils and vegetation collected along a hillslope in a forested watershed in Taiwan.

Leaf nitrogen concentrations may vary based on either changes in nitrogen availability or intrinsic differences among growth forms (e.g. evergreen versus deciduous; Aerts and Chapin 2000). Leaf nitrogen concentrations in turn are directly related to carbon assimilation rates (Evans 1989). As a result, leaf nitrogen concentration can indicate plant strategies for carbon acquisition and tissue turnover, with nitrogen concentration generally increasing in this order: evergreen species < forbs and graminoids < deciduous species (Aerts and Chapin 2000).

Foliar δ^{15} N values are known to be influenced by climate and moisture (Handley et al. 1999; Amundson et al. 2003). Stable isotopes are a useful tool for evaluating soil nitrogen dynamics because isotope ratios record the net effect of isotope fractionation processes on a particular ecosystem pool. Natural abundance nitrogen stable isotope measurements have been used to evaluate N cycling patterns (Nadelhoffer and Fry 1994; Emmett et al. 1998), to examine potential N sources to vegetation (Schmidt and Stewart 1997) and to determine types of plant and mycorrhizal associations (Michelsen et al. 1998). In a few studies, natural abundance of ¹⁵N of soil and foliage has been used to identify areas with higher rates of nitrification (Garten 1993; Garten and Van Miegroet 1994; Emmett et al. 1998). Several studies have suggested that among non-mycorrhizal plants, VA (vesicular-arbuscular) plants are generally higher than in ¹⁵N than ectomycorrhizal plants (Michelsen et al. 1996; 1998; Schimdt and Stewart 1997). Hobbie et al. (2000) reported that foliar N concentration and δ^{15} N were correlated at nitrogen limited sites, and attributed this pattern to differences in plant and mycorrhizal interactions. Using a modeling approach combined with a seedling experiment, Hobbie and Colpaert (2003) showed that and the varying fraction of N retention through mycorrhizal activity can explain patterns between N availability and foliar $\delta^{15}N$.

Studies of nitrogen transformations in tropical forest soils have indicated that, generally, rates of nitrification and nitrogen mineralization are higher in tropical soils compared to temperate soils (Matson et al. 1987; Neill et al. 1995). One early study of nitrogen cycling in a subtropical rainforest identified a pattern of more rapid rates of nitrification and nitrogen mineralization compared to temperate forests (Chandler and Goosem 1982). Later, Hiroto and Haibara (1994) used a laboratory incubation method to compare mineralization potentials at two slope positions in forest soils in Japan. They found that soil from lower elevation had higher mineralization rates and were positively correlated with total N concentration. Ohrui and Mitchell (1998) used a similar approach to compare amounts of inorganic N released from mineral soils in two Japanese forests. Their results indicated that higher nitrification rates occurred in near-stream areas compared to soils at a higher elevation.

Since there are fewer studies using stable isotopes in forests within the east-Asia region relative to the number of studies in tropical and temperate forests, I used data from tropical and temperate forests in other regions to compare with results from this study site. Overall, there is much evidence that there are differences in rates and patterns in N cycling between tropical and temperate forests. Because many N cycling processes result in isotopic fractionation, some predictable patterns in $\delta^{15}N$ among components of forest ecosystem occur (Nadelhoffer and Fry 1994). Martinelli et al. (1999) used this approach to test the hypothesis that tropical forests, in general, contain N that is more enriched in ¹⁵N. This should occur because tropical forests are often characterized by comparatively open N cycles (larger inputs and outputs relative to internal N cycling). The mechanisms for N losses in forests leave the N remaining in the forest (soil and vegetation N pools) enriched in ¹⁵N. This hypothesis was supported using a broad survey of δ^{15} N values for vegetation and soils collected from many parts of the world. The results from Martinelli et al. (1999) offer additional evidence regarding some fundamental differences between tropical and temperate forests. For this study, I was interested in whether a similar pattern could be found in a

subtropical forest in Taiwan. This survey is among the first surveys of $\delta^{15}N$ values for soil and vegetation for this subtropical forested watershed in northern Taiwan.

Materials and Methods

Study site

The Fushan Experimental Forest is located about 40 km southeast of Taipei, Taiwan (24°34'N 121°34'E; Fig. 1). Fushan is a moist, subtropical, evergreen forest with a rich flora of over 500 species (Mabry et al. 1998). Soil and vegetation samples for this study were collected from experimental watershed 1 (WS1; area 37 ha). The underlying geology in WS1 is metamorphosed sedimentary rocks such as argillite and slate (Tang and Yang 1976). WS1 has a SE facing aspect and elevation ranges from about 670 to 1,100 m. Dominant tree species in the study area include *Castanopsis carlesii* (Helmsl.) Hayata, *Litsea acuminata* (Blume) Kurata, and *Diospyros morrisiana* Hance. Common understory

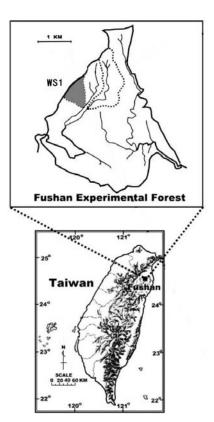


Fig. 1. Map showing the location of the Fushan Experimental Forest and the study watershed (WS1).

plants are *Lasianthus microstachys* Hayata, *Helicia formosana* Lour, *Alsophila podophylla* Hook, and *Blastus cochinchinensis* Lour. Mean annual precipitation is about 4,000 mm and mean annual temperature is 18.2°C (Hsia and Hwong 1999). Soil surveys have indicated that Ultisols and Inceptisols are the most common soil types within the watershed (Lin et al. 1996).

Sampling and analysis

Three hillslope locations were selected and soil pits were excavated by hand to a depth approaching 100 cm. Mineral horizons were sampled at 10 cm intervals, sieved (2 mm), and oven-dried (60°C) prior to analysis. Two rock specimens were also collected from the lower mineral soil, cleaned with deionized water, dried, and pulverized for isotope analysis. At each location, a 10x10 cm sample of the litter layer was also collected. Foliage samples were collected from the middle third of the tree canopy in dominant tree species in the immediate area adjacent to each soil pit. Leaves from two or three twigs containing green foliage without visible insect damage were combined for each sample. Understory foliage was sampled in a similar manner from two to four randomly clipped branches or bracts and composited. Foliage samples were oven-dried (60°C) and pulverized to a fine mesh with a dental amalgamator device prior to analysis.

Elemental and stable isotopic composition was determined using a Finnigan Delta-Plus isotope ratio mass spectrometer interfaced to an elemental analyzer. Typical precision for duplicate isotopic analyses was 0.2%. The isotopic composition of a sample is expressed using the standard notation as a difference from a standard: $\delta^{15}N$ (‰)=[R_{sample}/R_{standard}-1]x1,000. R refers to the ratio of the heavy to the light isotope. Linear regression and correlation were used to examine relationships between N concentration and stable isotope composition. All statistical analyses were conducted using SAS v9 (SAS Institute, Cary, NC, USA).

Results

Descriptive soil characteristics for WS1 are shown in Table 1. Some additional information on soils in WS1 is given in Lin et al. (1996) and Owen et al. (2003). Soil N

Table 1. Soil description in WS1 at the Fushan Experimental Forest

Depth (cm)	Description
0-4	Brownish black (10 yr 2/2, m) silt loam; fine granular; very friable; sticky and slightly sticky; very fine to coarse, abundant free growing roots; clear, smooth boundary.
4-14	Orange (7.5 yr $6/8$, m) silt loam; fine to medium subangular blocky; friable to firm; sticky and sticky; fine to coarse, abundant free growing roots; gradual, smooth boundary; $20\% \le 20$ cm diameter stones.
14-24	Yellow orange (7.5 yr 7/8) silt loam; fine to medium subangular blocky; friable to firm; sticky and sticky; fine to coarse, frequent free growing roots, gradual smooth boundary; $30\% \le 10$ cm diameter stones.
24-34	Orange (7.5 yr 6/8) silt loam; medium subangular blocky; friable to firm; sticky and sticky; fine to coarse, frequent distorted roots; diffuse, smooth boundary; 40% sharp angular stones.
34-54	Light brown (7.5 yr 5/8) silt loam; medium subangular blocky; firm; sticky and sticky; fine to coarse, frequent free growing roots, gradual, smooth boundary; 40%, 10 to 22 cm platy to blocky stones.
54-90+	Orange (7.5 yr 6/8) silt loam; medium subangular blocky to massive; firm to very firm; sticky and sticky; diffuse, smooth boundary; up to 70%, > 50 cm blocky angular stones.

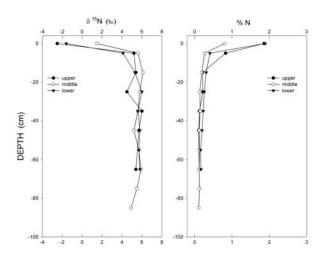


Fig. 2. Soil $\delta^{15}N$ and N concentration profiles at 3 sampling locations in Fushan Experimental Forest WS1.

concentration in the forest floor was lowest at the middle hillslope location and ranged from 0.80 to 1.86% N (Fig. 2). In mineral soil horizons, soil N concentrations did not change notably with depth or among the three soil profiles and ranged from 0.11 to 0.83% N. Soil δ^{15} N profiles showed a sharp increase below the litter horizon at each location (Fig. 2). δ^{15} N of the two rock samples were similar (2.5 and 2. 4‰). The range for δ^{15} N values in the litter horizon was from -1.8 to 1.8‰. For mineral soils, higher δ^{15} N values were found (4.2 to 6.0‰). Below the litter horizon, δ^{15} N values changed little with depth at all sampling locations.

There was a significant relationship between soil N con-

centration and soil $\delta^{15}N$ value at each of the hillslope locations. The best fit regression lines for the three soil profiles were $\delta^{15}N_{soil}{=}-4.275$ [% $N_{soil}]+6.668$ (r $^2{=}0.8592$, p ${<}0.001$); $\delta^{15}N_{soil}{=}-5.858$ [% $N_{soil}]+6.445$ (r $^2{=}0.8512$, p ${<}0.001$); and $\delta^{15}N_{soil}{=}-4.345$ [% $N_{soil}]+6.559$ (r $^2{=}0.9819$, p ${<}0.001$) for the upper, middle, and lower locations, respectively.

Overall, foliar % N and δ^{15} N were weakly correlated (r^2 =0.214, p=0.0347; Fig. 3). If non-mycorrhizal *H. formosana* was not considered, the correlation for all plants increased (r^2 =0.360, p=0.0052). For understory and subcanopy plants, the relationship was non-significant (r^2 =0.315, p=0.116; Fig. 3). Foliar N concentration in overstory plants varied from 1.3% to 1.7% N and foliar N concentrations in understory plants ranged from 1.7 to 3.4% N. However, the N concentration in one non-mycorrhizal understory plant (*H. formosana*) in the Proteaceae showed the lowest N concentration (1.3% N). Understory plants in the Urticaceae had foliar N concentrations over 3% N (Table 2).

Foliage $\delta^{15}N$ values for overstory trees ranged from -6.6 to -2.0‰, and understory foliage $\delta^{15}N$ values ranged from -5.0 to -1.9‰ (Table 2). Foliar $\delta^{15}N$ values of both groups were not significantly different at the three hillslope locations. Interestingly, understory plants near the lowest and highest foliar N concentrations all showed high $\delta^{15}N$ values, with plants in the Urticaceae having high N concentrations and the Proteaceae specimen having low foliar N concentration.

Discussion

Forest soil profiles often show a general trend of increasing $\delta^{15}N$ with depth; this trend has been observed in many forest soils throughout the world (Hogberg et al. 1996). This pattern results from several processes involving iso-

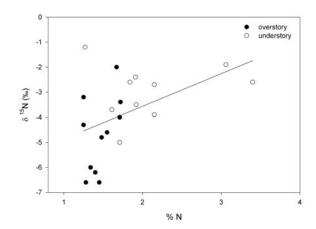


Fig. 3. Relationship between foliar $\delta^{15}N$ and N concentration in Fushan Experimental Forest WS1. The equation for the best-fit line is $\delta^{15}N$ = 1.3025 (%N)- 6.169 (r^2 =0.214, n=20).

topic fractionation during nitrogen cycling, leading to plant uptake of N that is depleted in ¹⁵N, and because of internal N cycling through mycorrhizal fungi that also results in the transfer of N that is depleted in ¹⁵N to host plants (Hobbie et al. 2000; Hobbie and Ouimette 2009). Both of these mechanisms results in the transfer of N which is depleted in ¹⁵N to the soil surface via litterfall. Thus, for nitrogen, plants are nearly always isotopically lighter than the soil supporting their growth (Nadelhoffer and Fry 1994). Isotopic fractionation during decomposition, soil food web processing, and denitrification also contribute to this pattern (Hobbie and Ouimette 2009).

The results for WS1 showed that N concentration in one non-mycorrhizal understory plant (H. formosana) in the Proteaceae had the lowest N concentration (1.3% N). Understory plants (Urticaceae) had foliar N concentrations over 3% N (Table 2). Members of the Proteaceae are generally non-mycorrhizal and adapted to nutrient poor habitats (Diaz 1996). For example, Schimdt and Stewart (1997) reported that non-mycorrhizal Proteaceae had higher δ^{15} N values than mycorrhizal species in Australian heathlands.

Table 2. Plant δ^{15} N, %N and mycorrhizal type by hillslope location in WS1

Location	Strata	Species	Family	Type	$\delta^{15}N_{plant}$	%N
Lower	Understory	Pellionia radicans	Urticaceae	VA/Non	-2.6	3.40
	Understory	Pellionia radicans	Urticaceae	VA/Non	-1.9	3.06
	Overstory	Meliosma squamulata	Sabiaceae	VA	-4.3	1.25
	Overstory	Tutcheria shinkoensis	Theasceae	Ecto/VA	-4.8	1.48
	Overstory	Cyclobalanopsis glauca	Fagaceae	Ecto	-3.4	1.72
	Overstory	Tutcheria shinkoensis	Theasceae	Ecto/VA	-4.6	1.55
	Overstory	Engelhardtia roxburghiana	Juglandaceae	VA	-2.0	1.67
Middle	Understory	Lasianthus microstachys	Rubiaceae	VA	-2.4	1.91
	Subcanopy	Helicia formosana	Proteaceae	Non	-1.2	1.27
	Subcanopy	Blastus cochinchinensis	Melastomataceae	VA	-3.5	1.92
	Subcanopy	Stauntonia hexaphylla	Lardizabalaceae	VA	-5.0	1.71
	Overstory	Tutcheria shinkoensis	Theasceae	Ecto/VA	-3.2	1.25
	Overstory	Listea acuminata	Lauraceae	VA	-6.0	1.34
Upper	Understory	Lasianthus microstachys	Rubiaceae	VA	-3.9	2.15
	Understory	Astronia ferruginea	Melastomataceae	Ecto/VA	-3.7	1.61
	Understory	Lasianthus japonicus	Rubiaceae	VA	-2.7	2.15
	Subcanopy	Blastus cochinchinensis	Melastomataceae	Ecto/VA	-2.6	1.84
	Overstory	Listea acuminata	Lauraceae	VA	-6.6	1.28
	Overstory	Listea acuminata	Lauraceae	VA	-6.2	1.40
	Overstory	Litsea acuminata	Lauraceae	VA	-6.6	1.45
	Overstory	Cryptocarya chinenisis	Lauraceae	VA	-4.0	1.71

Table 3. Enrichment Factors (EF= $\delta^{13}N_{plant}$ - $\delta^{13}N_{soil}$) reported from selected studies on ^{13}N natural abundance in vegetation and	soils in
North America and Europe	

Site	Description	EF min	EF max	Reference
GSMNP	Mixed	-7.9	-5.8	Garten, 1993
Sweden	Conifer	-3.6	0.0	Näsholm et al. 1997
NITREX sites	Mixed	-8.0	-1.2	Emmett et al. 1998
Fu-shan WS1	Upper	-11.9	-9.3	This study
Fu-shan WS1	Middle	-11.9	-9.1	This study
Fu-shan WS1	Lower	-9.5	-6.7	This study

Several earlier studies of soil and vegetation natural abundance ¹⁵N in forests used "enrichment factors" (EF= $\delta^{15}N_{plant}$ - $\delta^{15}N_{soil}$) to help reduce the uncertainty resulting from spatial variability observed for soil and tissue $\delta^{15}N$ values (Marrioti et al. 1981; Garten and Van Miegroet 1994; Näsholm et al. 1997). Enrichment factors have been shown to be positively correlated with rates of net N mineralization and nitrification (Garten and Van Miegroet 1994) and can be useful indicators of N supply (Näsholm et al. 1997). Enrichment factors in WS1 were generally more negative than those reported for temperate forested sites (Table 3). This finding indicates that there is a larger difference between $\delta^{15}N_{plant}$ and $\delta^{15}N_{soil}$ in WS1 compared to results from studies in several temperate forests (Garten 1993; Näsholm et al. 1997; Emmett et al. 1998). Though additional research will be needed to identify the N cycling mechanisms that result in the larger difference between plant and soil N stable isotope composition, this difference might be related to processes leading to N losses, such as gaseous losses through denitrification or export of dissolved inorganic and organic nitrogen via groundwater and surface waters (Houlton et al. 2006). In some watersheds, especially where N-rich sedimentary bedrock occurs, rockderived N is an important component of N cycling (Holloway and Dahlgren 1999). Some areas of Taiwan contain sedimentary bedrock and ascertaining the role of underlying geology in watershed N cycling should be a focus of future work. The results included here for rock $\delta^{15}N$ in WS1 are some of the first available for rock δ^{15} N in northern Taiwan (Yui et al. 2009). Though the number of samples was limited, rock δ^{15} N in WS1 (2.5%) was higher than mineral soil δ^{15} N (4.2 to 6.0%), suggesting the possibility than loss of N during rock weathering occurs with a systematic trend in N isotopic composition.

Some earlier studies showed that rates of microbial N transformations may be related to stable N isotope composition of soils (Garten 1993; Hogberg et al. 1996). Topographic position may affect the rates of many microbial processes in soils and thereby affect soil and foliar δ^{15} N values. For example, nitrification rates in soils are influenced by temperature, moisture, and nitrate concentration (Binkley and Hart 1989). During nitrification, the remaining ammonium should become enriched in ¹⁵N and the nitrate produced depleted in ¹⁵N (Hogberg et al. 1996). Relative to ammonium, nitrate is more easily leached from soils, though NH₄ concentrations in soil solution in WS1 are often undetectable (Owen, unpublished data). Average soil solution NO₃ concentrations at 15 cm depth were 11 μmol N/L and about 25 μmol N/L at 50 cm depth, ranging from 2 to 49 µmol N/L (Owen, unpublished data).

Since the earlier studies mentioned above, more recent approaches to understanding large-scale patterns in plant and soil $\delta^{15}N$ and modeling the distribution of N stable isotopes have utilized a steady state approach (Handley et al. 1999; Amundson et al. 2003). This approach relies on the concept that the soil total N pool is at a steady-state; the isotopic composition of the inputs and outputs determines the isotopic composition of the soil N pool. In steeply sloping and highly dissected terrain, which is a common landscape feature in Taiwan (Meybeck et al. 2001), further research should be directed towards a better understanding of patterns in soil and plant N stable isotope composition to test whether the steady state model applies to steeply sloped watersheds subject to disturbance such as landslides, typhoons and earthquakes.

Where studies have shown net rates of N mineralization and nitrification to vary among hillslope positions in forest soils, higher rates occurred at footslope locations (Hiroto and Haibara 1994; Koba et al. 1998). In WS1, there is little evidence to suggest that net nitrification rates are different at the higher and lower elevation sites (Owen et al. 2010). Thus differences in net nitrification and mineralization rates seem unlikely to be related to patterns in foliar $\delta^{15}N$ in WS1.

More information about stable isotopic composition of specific forms of N would be useful to better understand patterns in N cycling in forests in east-Asia (Hobbie and Colpaert 2003). The limited data available (Koba et al. 1998; 2010) suggest that measurements of the isotopic composition in both soil extractable pools and soil solution NO₃ and NH₄ could contribute to understanding regional differences in rates and patterns in N cycling. Currently there are no measurements of the N stable isotope composition of atmospheric inputs, soil solution or denitrification products available for forests in Taiwan. Work by Houlton et al. (2006) used stable N isotope measurements to highlight the magnitude of denitrification losses in affecting the distribution of δ^{15} N in tropical forests. In WS1, the influence of N losses via denitrification is not yet known, but the similarity in foliar and soil $\delta^{15} N$ values among the three hillslope locations is consistent with other studies in WS1 indicating that rates of soil microbial processes such as N mineralization and nitrification did not vary greatly between upper and lower locations in the watershed (Owen et al. 2010).

Conclusion

In summary, these results for soil and vegetation stable N isotopic composition from this subtropical forest in Taiwan are consistent with data from other forest ecosystems. Isotopic patterns in this subtropical forest seem to conform more closely to patterns in temperate forest than to patterns in tropical systems. The results of this study show that $\delta^{15}N$ of total soil N in the three hillslope locations did not vary greatly among the profiles. Understory and overstory foliage $\delta^{15}N$ showed generally few differences between the lower and upper hillslope location. Additional research on the relationships between inorganic and organic N availability, mycorrhizal-plant N cycling, and N stable isotope composition will be necessary to increase our understanding of patterns in N cycling in this watershed in addi-

tion to expand our range of regional patterns in east-Asia. Processes that deserve intensive study for understanding N cycling in subtropical forests in Taiwan and the east-Asia region include the influence of disturbances such as landslides, typhoons, and earthquakes, rates of N-fixation, N export to surface and groundwater, and N losses via denitrification.

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