Topographic Variations of Nutrient Cycling in a *Pinus Thunbergii* Parl. Plantation

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CONTENTS

Chapter 1

General Introduction

Nutrient cycling in a forest ecosystem

Ecosystem was defined by Tansley (1935) as *the whole system (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome - the habitat factors in the widest sense.* The ecosystem is considered to be a unit of biological organization made up of all of the organisms in a given area interacting with the physical environment. Through the interactions between organisms and the environment, energy and materials move among intra- and inter organisms. Therefore one of the best methods to evaluate an ecosystem is to analyze the energy flow and material circulation (Odum 1969).

Forest ecosystem has a huge structure built by the primary production of plants. The carbon compounds captured by plants were also used to maintain the physiological processes of themselves and support all organisms in the forest. In forest ecosystems, more than 90% of energy acquired by plants flow into the decomposition process (Wittaker 1970). Most of the materials and energy were accumulated in plants and soil. Consequently, the interactions between plants and the soil determine the structure and function of the forest ecosystem (Bormann & Likens 1979). To understand the structure and function of a forest ecosystem, it is important to study the resource foraging by plants in relation to the soil properties (Tilman 1988). In this dissertation, the author will examine the interactions between plants and the soil in a forest ecosystem, focusing on the accumulation and flow of materials.

Interaction between plant and soil

Plant response to soil

Natural environments show dramatic differences in nutrient availability. For example, the amount of nitrogen available to plants ranges 40-fold from a coniferous forest to a topical rain forest (Vitousek *et al.* 1982; Vitousek 1984). To compensate for the

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differences in nutrient availability, plants modify their nutrient foraging.

In response to low nutrient availability, plants maximize their nutrient uptake through a high root absorption capacity per unit root mass (Chapin 1980; Gray & Schlesinger 1983; Chapin *et al*. 1986) and a high root / shoot ratio (Chapin 1980; Keyes & Grier 1981; Cameau & Kimmins 1989). These effects of increased nutrient uptake, however, do not fully compensate for the reduced nutrient availability, so that nutrient concentration of plants and the total amount of absorbed nutrients generally decrease with decreasing nutrient availability.

Plants minimize their nutrient loss and reduce the nutrient demand at the lower level of nutrient availability. Leaf longevity increases with decreasing nutrient availability (Chabot & Hicks 1982; Reich *et al*. 1992). As nutrient availability decreases, nutrient resorption (translocation of nutrients from senescing leaves before abscision) increases (Small 1972; Flanagan & Van Cleve 1983; Chapin & Moilanen 1991; Pugnaire & Chapin 1993), and nutrient loss through leaching decreases (Tukey 1970). These factors contribute to the high nutrient-use efficiency of plants growing on infertile soils (Vitousek 1982, 1984).

Plants allocate a small part of dry matter and nutrients to leaves in response to the low nutrient availability. This small leaf allocation induces low productivity through low photosynthetic activity. Most plant characteristics of resource-poor environments have low potential growth rates and consequently reduced nutrient requirement (Grime 1977).

Effect of plant on soil

Plants exert a profound influence on soil properties (Jenny 1980). Plants can contribute to the development of soil by stabilizing the soil surface through the extension of root systems, and by serving organic matter and nutrients through litterfall (Charley & West 1975; Hirose & Tateno 1984).

Individual plant characteristics play an important role in determining soil fertility. In general, plant characteristics create positive feedbacks to patterns of nutrient cycling through nutrient uptake, use and loss (Melillo 1982; Pastor *et al*. 1984; Hobbie 1992; Vinton & Burke 1995). Plants that occur in low nutrient habitats grow slowly, use nutrients conservatively and produce poor quality litter that decomposes slowly. In contrast, plants in high nutrient habitats grow quickly, take up and lose nutrient rapidly, produce high quality litter that is readily decomposable.

Topographic variations of nutrient cycling in a forest ecosystem

On the global scale, soil properties differ along the climatic (temperature and precipitation) gradient or latitude. On a smaller scale, variations in soil properties can be seen along a topographic gradient even in a landscape (Robertson *et al*. 1988, 1993). Topography is known to play a critical role in modifying the soil properties (Shimel *et al*. 1985; Burke 1989; Zak *et al*. 1991; Brubaker 1993, 1994). In particular, the topographic effects on the movement of water and materials can determine or control the type and intensity of soil processes (Pennock *et al*. 1994). Topographic variations in nutrient cycling in forested ecosystems have been shown in the previous studies (Tsutsumi *et al*. 1984; Pastor *et al*. 1984; Garten *et al*. 1994).

Little is known, however, regarding the influence of topography on the spatial variations of soil properties and nutrient dynamics in a forest ecosystem. Soil properties and nutrient cycling determine the resource environment for plants. Topography produces spatial heterogeneity in resources (Robertson *et al*. 1988, 1993), and these spatial heterogeneity in resources enhanced species richness (Tilman 1982). For the management of forests containing many types of topographies, it is very important to elucidate the spatial variations in soil properties and resource utilization of plants along a topographic gradient .

Objectives of the study

The major aims of this research study are (1) to examine the patterns of stand structure and nutrient cycling in a forest ecosystem along a topographic gradient, and (2) to elucidate the variations of interactions between plants and the soil that induce the patterns of stand structure and nutrient cycling.

The interactions of plants with the soil are difficult to examine because the complex history of vegetation and soil development in the site inhibits an understanding of cause and effect relationship (Bazzaz 1983). The responses of a single plant species to the soil environment and their effects on soil properties need to be studied in order to elucidate plant-soil interactions. To examine the plant-soil interactions in isolation from other longer-term effects, a study plot was established in a 20-year-old *Pinus thunbergii* Parl. plantation in which natural vegetation was destroyed and surface soil was eroded

after repeated logging. In this paper, nitrogen and phosphorus are specifically determined because these nutrients are often limiting nutrients for plant growth in forest ecosystems (Binkley 1986).

The according chapters of this dissertation will provide a detailed explanation of the results of the various research studies conducted. Below is an overview of the content of each chapter:

- In Chapter 2, the topographic variations in soil properties and stand structure are examined. The morphological response of *P. thunbergii* and its effects on the forest structure are also investigated.
- In Chapter 3, physiological plasticity of *P. thunbergii* in nutrient uptake and nutrient use in response to nutrient availability are evaluated.
- In Chapter 4, the mechanisms which could account for the increase in nutrient-use efficiency of *P. thunbergii* in response to the lower nutrient availability are explored. Similarly the nutrient resorption efficiency and its relationship with factors that control nutrient resorption are examined.
- In Chapter 5, to evaluate the effects of nutrient use by plants on the environmental conditions, the decomposition processes of litter in relation to initial nitrogen concentration of litter and topographic positions are analyzed.
- In Chapter 6, general discussion of the topographic variations in the interactions between plants and soil, and their effects on the forest ecosystem are provided. Summary of the results of the preceding chapters are also contained in this chapters.

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Chapter 2

Topographic Variations of Soil Properties and Stand Structure
in a *Pinus thunbergii* Parl. Plantation

INTRODUCTION

Plant morphology changes in response to soil properties such as water and nutrient availability (Chapin 1980; Bloom *et al.* 1985). For example, the ratio of root to shoot biomass decreases with increasing soil fertility (Keyes & Grier 1981; Santantonio & Hermann 1985; Cameau & Kimmins 1989). Soil properties can vary greatly within a plant community and such phenomena result in spatial heterogeneity of the environment for plants (Robertson *et al.* 1988, 1993). The responses of plants to heterogeneous soil environments have important consequences for community structure (Tilman 1988). Grime (1994) reviewed recent experimental studies of plant responses to resource heterogeneity and re-examined the role of morphological plasticity of plants in exploiting environmental heterogeneity.

It is well known that soil properties vary widely along a topographic gradient from ridge top to valley floor (Brubaker *et al.* 1993, 1994; Garten *et al.* 1994). Changes in productivity and nutrient cycling along a slope have been studied in a deciduous broad-leaved forest (Katagiri 1988) and in a conifer plantation (Tsutsumi *et al.* 1983). Decomposition and accumulation of soil organic matter have been studied along a slope in an evergreen broad-leaved forest (Nakane 1975). In these studies, however, the long-term interaction between soils and plants included many species. The responses of a single plant species to a heterogeneous soil environment and their effects on soil properties need to be studied in order to elucidate soil-plant interactions.

The present study aims to investigate plant-soil interactions along a topographic gradient from ridge top to valley floor in a monospecific forest ecosystem. A study plot was established in a pine plantation in which natural vegetation was destroyed and surface soil was eroded after repeated logging. Therefore, the effects of accumulated soil organic matter before planting could be neglected.

To evaluate the heterogeneity of the soil environment and stand structure, the author measured the topographic variation in the following: 1) soil thickness and fine soil content; 2) soil moisture content; 3) accumulation of organic carbon in the forest floor and mineral soil; 4) aboveground forest structure; and 5) fine root biomass. The amount of soil overlying the bedrock and its texture play an important role in the soil's capacity to hold water and nutrients (Burke 1989). The accumulation pattern of organic carbon indicates the differences in decomposition rates and water and/or nutrient availability (Nakane 1975; Vogt *et al.* 1986; Katagiri 1988; Takeda & Kaneko 1988). Above- and belowground forest structure, such as tree density, stem diameter, height and volume, and fine root biomass were compared along a topographic gradient to evaluate the role of morphological plasticity of pine trees in response to heterogeneous environments. Soil-plant interactions in a forest ecosystem covering various topographies will be discussed by evaluating spatial heterogeneity of the accumulation pattern of organic matter in plants and the soil.

METHODS

Study site
The area of Mt. Tanakami, Shiga Prefecture, Japan had been deforested by repeated logging. Erosion of surface soil had prevented the restoration of a forest in this area (Tsutsumi 1963; Iwatsubo *et al.* 1982). In recent decades, an afforestation technique has been developed and implemented (Tsutsumi 1969; Iwatsubo & Tsutsumi 1982). After the construction of terraces along the contours of the hillside to prevent soil erosion, saplings of *Pinus thunbergii* Parl. were planted with *Alnus pendula* Matsum. and fertilizers were applied. A few years after planting, stems of *A. pendula* were cut down to prevent competition with *P. thunbergii*. *Pinus thunbergii* now dominates and covers a large area of Mt. Tanakami.

In this area, the forest canopy mostly consisted of *P. thunbergii*, while naturally regenerated *Pinus densiflora* Sieb. et Zucc. subdominated. Other naturally regenerated species such as *Clethra barbinervis* Sieb. et Zucc., *Quercus serrata* Thunb., *Ilex pedunculosa* Miq. and *Chamaecyparis obtusa* Endl. constituted a small part of the canopy. The subcanopy and shrub layer consisted of evergreen species such as *Eurya japonica* Thunb., *Ilex crenata* Thunb., *I. pedunculosa*, *Camellia japonica* L. and deciduous species such as *C. barbinervis*, *A. pendula*, *Q. serrata*, *Pourthiaea villosa* Decne., *Fraxinus sieboldiana* Blume and *Rhododendron reticulatum* D. Don.

The bedrock was granite which had been much weathered. The soil was sandy. The

mean annual temperature of the site was 12.4°C and annual precipitation was 1411 mm during the years between 1976 and1980 (Iwatsubo *et al.* 1982).

A study plot (34°55'N, 135°58'E, 420 m above sea level) of 40 m x 64 m (Fig. 2. 1) was set up in a *P. thunbergii* plantation which had been established in 1971. The direction of the plot was S55°E. The plot covered a steep ridge and an underground stream.

There were terraces for planting along the contours. Rocks appeared sparsely in the middle slope position. The amount of exposed rocks increased downslope. A riparian terrace exists between large wall-like rocks and the north side of the stream.
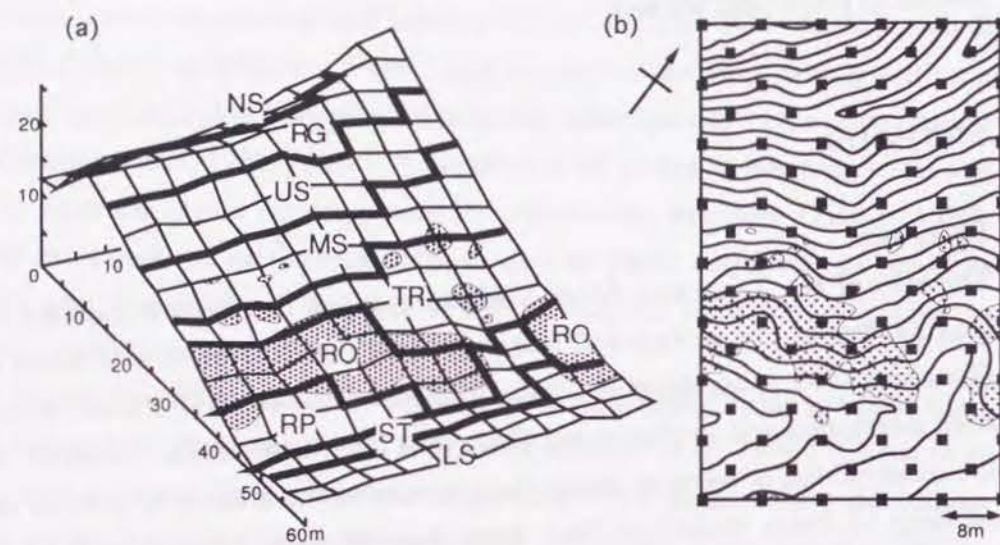

Fig. 2. 1. (a) Overview of the study plot. Shadowed areas indicate exposed rocks. The plot was divided into 4 X 4 m subplots and the 160 subplots were categorized into nine microsite types (see Table 2. 1). (b) Topographic map of the site and the locations of the 94 soil sampling points. Contour lines are drawn at intervals of 1 m. (see Table 2. 1 for abbreviations of microsite types for all figures.)

Topographic classification

The plot was divided into 160 subplots of 4 m x 4 m. To evaluate the smaller scale topographical variation, the elevation of every intersection of the 4 m x 4 m grids was measured. A map of exposed rocks in the plot was also made. On the basis of slope position (relative position from ridge top to valley floor along a slope), slope direction, and amount of exposed rocks, the 160 subplots were categorized into nine microsite types (Fig. 2. 1). The mean inclination and the number of subplots in each microsite

type are shown in Table 2. 1.

Table 2. 1 Number of subplots taken and mean inclination of the nine microsite types

Microsite type	Abbreviation	No. subplots	Mean inclination (°)
Lower slope	LS	23	13.3
Stream	ST	12	17.8
Riparian	RP	8	19.7
Rocky	RO	19	26.8
Transitional	TR	22	29.0
Middle slope	MS	20	29.7
Upper slope	US	20	29.7
Ridge	RG	21	32.2
North facing	NS	15	34.5
Whole		160	27.1

Tree census

Trees larger than 1 cm in DBH (stem diameter at breast height, 1.3 m above the ground) were identified in autumn, 1990. Tree height (H) and DBH were measured for the trees in the plot. Positions of the stem base were mapped.

Stem volume of a tree (V, dm^3) was estimated from H (m) and DBH (cm) by the following equations (Oohata 1991):

$$V = 0.0400 \, D_{0.1}^2 \, H,$$

$$D_{0.1} = 0.941 \, DBH + 0.734,$$

where $D_{0.1}$ is stem diameter at 10% of tree height.

To compare species diversity between microsite types, Shannon-Wiener's species diversity index (H', Pielou 1966) was calculated as follows:

$$H' = - \sum P_i \log_2 P_i$$

where P_i is the relative dominance in the number of stems of the *i*th species.

Soil sampling and analysis

The thickness of the soil overlying the bedrock was measured by a soil auger at 94 points (at every other intersection of the 4 m x 4 m grids, Fig. 2. 1). Soil samples were collected at the 94 points in July, 1991. Organic matter of the L-layer (fresh litter) and FH-layer (litter fragments and humus) were collected separately from a 20 cm x 20 cm quadrat. Samples of mineral soil were collected by removing a core (11.3 cm in diameter

and 5 cm deep). Soil samples were collected from two layers of mineral soil: 0-5 cm and 5-10 cm deep from the mineral soil surface. The soil samples were divided into litter, fine root (< 2 mm in diameter), coarse root (≥ 2 mm), fine soil (< 2 mm) and gravel (≥ 2 mm). The air-dried weight of each fraction was measured. Five grams of each fraction was oven-dried at 105℃ and weighed to obtain a dry weight ratio. The samples of L- and FH-layers were separately milled and carbon and nitrogen contents were determined using a CN-analyzer (Yanaco MT-600, Kyoto, Japan).

Statistical analysis

Analysis of variance (SYSTAT 1992) was used to determine differences between mean values of soil properties of the microsite types. The Tukey's HSD (Honestly significant difference) test was used for multiple comparisons. The mean values of soil properties in each microsite type were calculated by averaging the values from sampling points within each microsite type and on its borders.

RESULTS

Species composition

There were 2546 tree stems (DBH > 1 cm) in the plot including *P. thunbergii*, *A. pendula* and 37 other naturally regenerated tree species. Basal area of the plot was 25.2 m² ha⁻¹. *Pinus thunbergii* constituted 14.3% of the total number of stems and 67.2% of the total basal area. Naturally regenerated *P. densiflora* constituted 6.3% and 16.9%, respectively. The two *Pinus* species constituted composed 21% and 84%, respectively. Two deciduous species, *C. barbinervis* and *R. reticulatum* constituted 26.8% and 25.0% of the number of stems and 6.4% and 1.7% of the basal area. Sprouts of *A. pendula* constituted 11.9% of the number of stems and 2.9% of the basal area.

Different distribution patterns were observed for the species. The relative basal area of *P. densiflora* was higher in microsite types ST, RP, RO and NS (Table 2. 2; see Table 2. 1 for abbreviations of microsite types). *Alnus pendula* was present in all microsite types, although the relative basal area was very small. Deciduous broad-leaved species occurred ubiquitously in the plot, while most of evergreen broad-leaved species occurred only at lower slope positions near the stream.

Table 2. 2 Species composition of the nine microsite types. The relative number of stems (RN) and relative basal area (RBA) of each species (%) is shown. For abbreviations of microsite type, see Table 2.1

	LS		ST		RP		RO		TR		MS		US		RG		NS	
	RN	RBA	RN	RBA	RN	RBA	RN	RBA	RN	RBA	RN	RBA	RN	RBA	RN	RBA	RN	RBA
Coniferous species																		
Pinus thunbergii Parl.	30	81	3	38	0	3	7	41	19	75	31	94	29	86	24	84	1	11
Pinus densiflora Sieb. et Zucc.	1	9	3	24	7	77	16	25	3	12	-	-	2	6	7	7	8	32
Other 3 species	-	-	1	1	-	-	0	0	-	-	-	-	-	-	-	-	2	5
Evergreen broad-leaved species																		
Eurya japonica Thunb.	11	1	5	1	12	2	15	3	3	0	3	0	1	3	-	-	2	1
Ilex crenata Thunb.	3	0	14	4	12	3	3	1	0	0	-	-	-	-	-	-	-	-
Ilex pedunculosa Miq.	-	-	7	13	2	3	-	-	3	0	-	-	-	-	-	-	3	8
Camellia japonica L.	1	0	3	2	1	0	-	-	-	-	-	-	-	-	-	-	-	-
Other 4 species	1	0	-	-	-	-	-	-	2	0	1	0	-	-	-	-	-	1
Deciduous broad-leaved species																		
Clethra barbinervis Sieb. et Zucc.	16	1	14	7	14	7	27	23	20	5	15	1	44	4	36	5	27	22
Rhododendron reticulatum D. Don	2	0	36	2	46	4	26	3	12	1	1	0	3	0	22	2	48	11
Alnus pendula Matsum.	9	1	8	4	0	0	1	1	36	6	47	4	20	3	4	3	3	6
Lyonia ovalifolia Wall.	2	0	-	-	1	0	1	0	1	0	-	-	1	0	0	0	2	1
Fraxinus sieboldiana Blume	1	1	1	2	2	-	0	1	-	-	2	-	-	1	0	-	2	1
Quercus serrata Thunb.	1	1	3	3	1	1	1	0	-	-	2	0	1	0	4	1	0	1
Other 21 species	20	5	3	3	1	1	4	0	0	0	2	0	1	0	1	0	3	1

- indicates no trees in the microsite type. 0 indicates smaller than 0.5%.

Grouping of microsite types

The nine microsite types can be grouped into the following three groups based on the basal area of *P. thunbergii* and all trees (Fig.2. 2):

Group 1 (LS, TR, MS, US, RG). The planted *P. thunbergii* saplings grew successfully. The proportion of other species to the total basal area was very small. The total basal area did not differ significantly between five microsite types, although the basal area in TR was slightly smaller than those of the other four microsite types.

Fig. 2. 2. Basal area of *Pinus thunbergii* trees and trees of other species larger than 1cm DBH in each microsite type.

Group 2 (ST, RO, NS). In this group, the afforestation of *P. thunbergii* had failed. Naturally regenerated trees such as *P. densiflora, C. barbinervis* and *R. reticulatum* covered the microsite types. Basal areas in this group were smaller than those of Group 1.

Group 3 (RP). The basal area in RP was much larger than those of other microsite types. The larger basal area in RP was due to the presence of large *P. densiflora* trees. These trees were present before the planting of *P. thunbergii* and had grown larger with fertilization.

In this study, the author mainly focused on the five microsite types of Group 1 to evaluate interactions between soil properties and *P. thunbergii* along the slope.

Species diversity

The largest value of H' was observed in LS, and smallest values in MS and US (Fig. 2. 3). For the five microsite types of Group 1, the species diversity index decreased upslope, although RG showed a slightly larger value of H' than MS and US. The value of H' was large at ST, while the total basal area in ST was very small. Species diversity was moderate in RP where total basal area was largest.
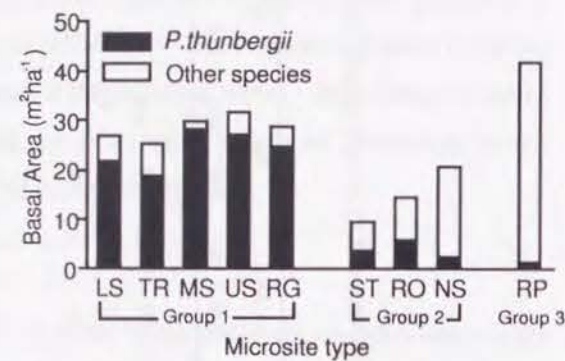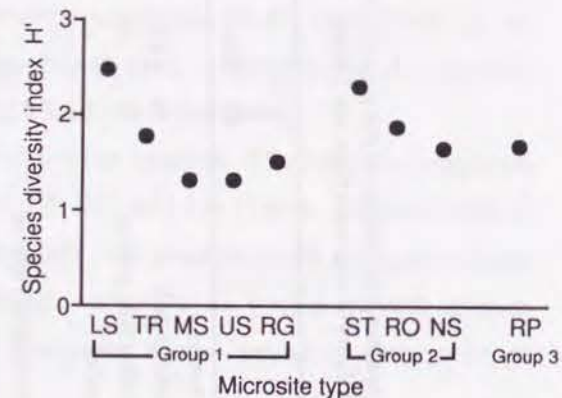

Fig. 2. 3. Comparison of Shannon-Wiener's species diversity index H' between the nine microsite types.

Soil thickness and texture

Variation in soil thickness was observed for the nine microsite types (Fig. 2. 4a). The soil thickness in the three microsite types at lower slope positions (LS, ST and RP) was greater ($P < 0.01$) than in the six microsite types at upper slope positions. For these six microsite types the mean soil thickness ranged between 25 and 35 cm and did not differ between the microsite types. The mean fine soil content in the mineral soil layer 0-5 cm deep was largest in LS (Fig. 2. 4b). The smallest value was observed in RO and TR. Similar topographic variation was observed for fine soil content in the mineral soil 5-10 cm deep. The mean value of the fine soil content of the 5-10 cm mineral soil layer was not significantly different from that of the 0-5 cm mineral soil layer in each microsite type. Soil thickness showed larger spatial heterogeneity than fine soil content. The coefficient of variance for the 94 points was 105% for soil thickness and 36% for fine soil content.

Fig. 2. 4. Soil thickness on the bedrock (a) and fine soil content of surface soil 0-5 cm deep (b) in each microsite type (mean ± 1 SE). Bars denoted by the same letter are not significantly different from each other at *P*< 0.05 (Tukey's HSD test).

Soil moisture content

Moisture content in the L-layer was highest around the stream and decreased upslope (Fig. 2. 5). The moisture contents of the FH-layer and the 0-5 cm mineral soil layer also decreased upslope. The moisture content of the 5-10 cm mineral soil layer was almost constant for the nine microsite types. The coefficients of variance for the 94 points were 86%, 61%, 52% and 25% in the L-, FH-, 0-5 cm and 5-10 cm mineral soil layers, respectively. Spatial heterogeneity in soil moisture content decreased with soil depth.
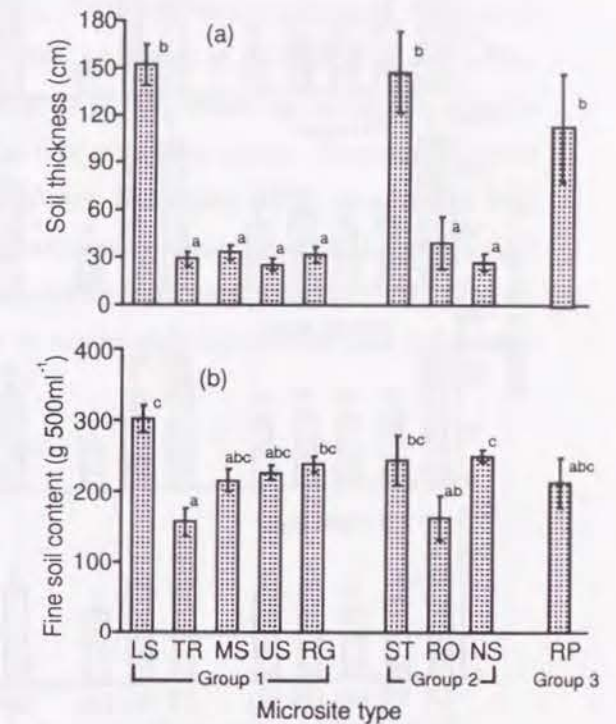
Soil carbon accumulation

The amount of accumulated carbon in the L-, FH-, and 0-5 cm and 5-10 cm mineral soil layers was 5.58 ± 2.69, 9.29 ± 7.59, 3.46 ± 1.70 and 1.35 ± 1.11 ton ha-1 (mean $\pm$ 1 SD), respectively. The amount of accumulated carbon in the forest floor (L-layer + FH-layer) was much larger than that in the mineral soil. The carbon concentration of mineral soil ($1.26 \pm 0.99\%$, mean $\pm$ 1 SD) was lower than those of other temperate forests (Vogt *et al.* 1986).

The total amount of soil carbon was smaller at lower slope positions and tended to increase upslope (Fig. 2. 6). Variation in the amount of accumulated carbon in the FH-layer caused the variation in total amount across the microsite types. The amount of the FH-layer was larger at middle and upper slope positions. The amount of accumulated carbon in the

L-layer did not differ between the nine microsite types. The amount of carbon in the mineral soil was slightly larger at the lower slope position.

Aboveground stand structure

Development of the aboveground structure of *P. thunbergii* was compared between the five microsite types in Group 1. Basal area, mean DBH, tree height and stem volume of *P. thunbergii* of the five microsite types were plotted against tree density (Fig. 2. 7). The tree density of *P. thunbergii* represents the degree of self-thinning at each microsite types, as initial tree density was constant for the five microsite types. Tree density was largest at RG and decreased downslope. In contrast, the mean DBH, tree height and stem volume increased downslope. The basal area was almost constant for the five microsite types. These changes in stand structure indicated that growth rate of aboveground parts of *P. thunbergii* was higher at lower slope positions and decreased upslope.

Fig. 2. 5. Moisture contents of the four soil layers of each microsite type (mean $\pm$ 1 SE). Bars denoted by the same letter are not significantly different from each other at $P < 0.05$ (Tukey's HSD test). Moisture content = 100 X (fresh weight - dry weight) / dry weight.
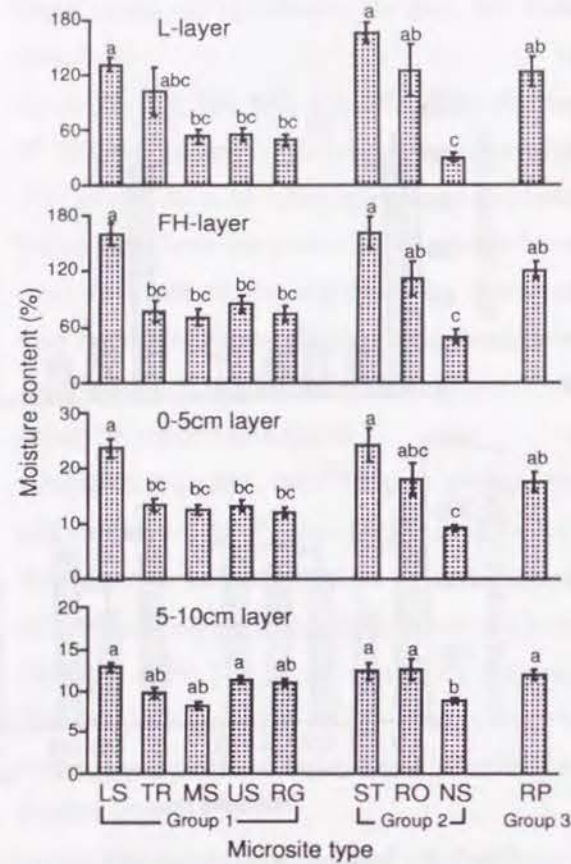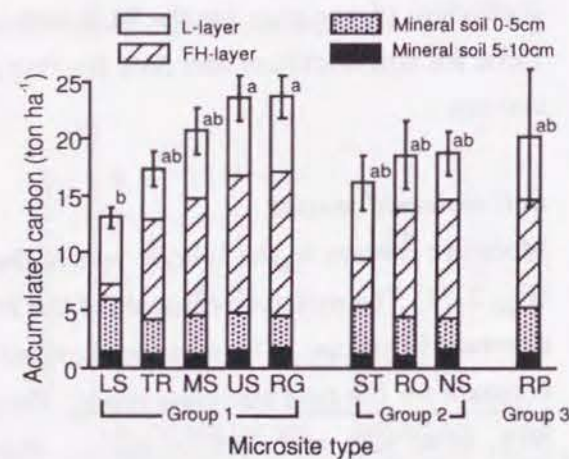

Fig. 2. 6. Amount of accumulated carbon in each soil layer (mean $\pm$ 1 SE). The total amounts denoted by the same letter are not significantly different from each other at $P < 0.05$ (Tukey's HSD test).
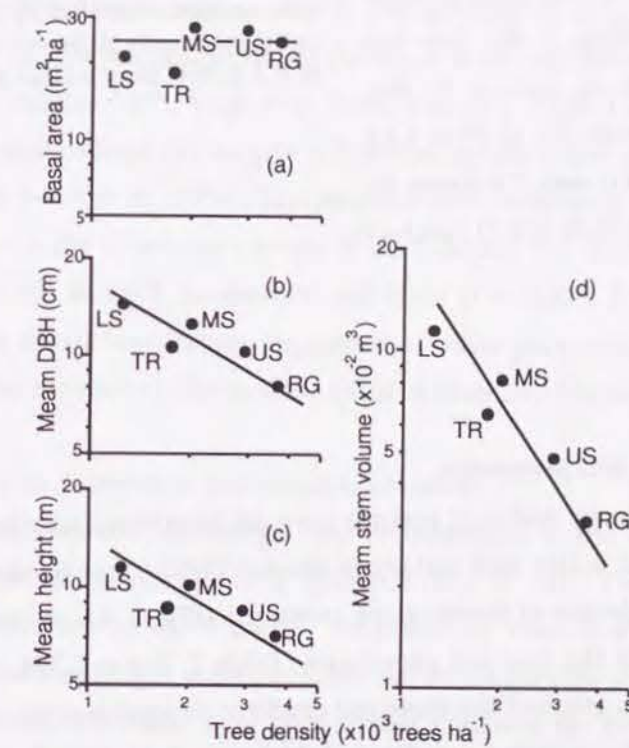

Fig. 2. 7. The relationships between (a) basal area, (b) mean DBH, (c) mean stem height and (d) mean stem volume and tree density of *Pinus thunbergii*. Gradients of lines are 0, -1/2, -1/2 and -3/2 in (a), (b), (c) and (d), respectively.

Fine root biomass

The amount of fine roots in the FH-, and 0-5 cm and 5-10 cm mineral soil layers was 0.21 ± 0.29, 1.22 ± 1.00 and 0.33 ± 0.37 ton ha^{-1} (mean $\pm$ 1 SD for the 94 points), respectively. The proportion of fine root biomass in the FH-, and 0-5 cm and 5-10 cm mineral soil layers to the total fine root biomass was 12%, 69% and 19%, respectively. Fine roots were concentrated in the soil surface. According to our field observation, fine roots were very rare in soil below 10 cm in depth.

The total amount of fine roots tended to increase upslope (Fig. 2. 8). For the five microsite types in Group 1, the amount of fine roots in RG (2.97 ± 1.13 ton ha^{-1}, mean $\pm$ 1 SD) was 7.6 times as larger than that in LS (0.39 ± 0.21 ton ha^{-1}).

Fig. 2. 8. Amount of fine root (< 2 mm in diameter) in each layer (mean $\pm$ 1 SE). The total amounts denoted by the same letter are not significantly different from each other at $P < 0.05$ (Tukey's HSD test).

DISCUSSION

Correlations between soil properties

Soil thickness on bedrock and soil texture play an important role in determining the soil's capacity to hold water and nutrients (Burke 1989). Soil thickness and fine soil content tended to be larger at lower slope positions (Fig. 2. 4). A positive correlation was observed between the two soil properties (Table 2. 3, $r = 0.354$, $P < 0.001$). Both physical soil properties affected the moisture gradient along the slope. The soil moisture content showed a higher correlation with soil thickness ($r = 0.580$, $P < 0.001$) rather than with fine soil content ($r = 0.219$, $P < 0.05$). Downslope movement of soils and their deposition determine the physical soil properties and moisture gradient along the slope (Brubaker et al. 1993, 1994).
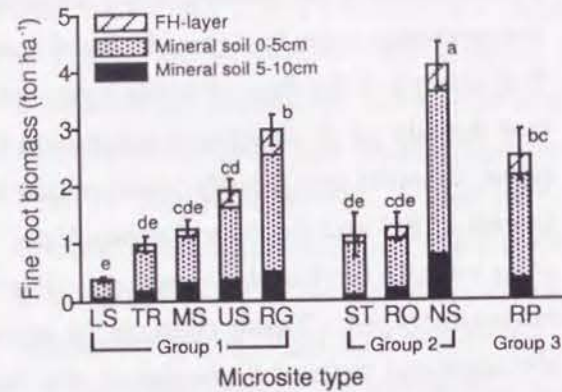
Table 2. 3 Correlation coefficients between soil properties ($n = 94$)

	Soil thickness	Fine soil content	Moisture content			Amount of carbon		
		0-5 cm	L-layer	FH-layer	0-5 cm	L-layer	FH-layer	0-5 cm
Soil thickness		***	***	***	***		***	
Fine soil content in 0-5 cm layer	0.354			**			*	
Moisture content in L-layer	0.614	0.155		***	***	*	*	***
Moisture content in FH-layer	0.530	0.309	0.736		***	*	*	***
Moisture content in 0-5 cm layer	0.580	0.219	0.613	0.584		*	***	***
Amount of carbon in L-layer	0.135	0.083	0.258	0.263	0.241			
Amount of carbon in FH-layer	-0.359	-0.234	-0.259	-0.220	-0.378	0.088		
Amount of carbon in 0-5 cm layer	0.308	0.223	0.346	0.457	0.688	0.156	-0.052	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

The amount of accumulated carbon in the forest floor increased upslope. The increase was mostly due to an increase in the amount of accumulated carbon in the FH-layer (Fig. 2. 6). Development of the FH-layer is an indication of slow rates of litter decomposition (Nakane 1975; Vogt et al. 1986; Katagiri 1988; Takeda & Kaneko 1988). Decomposition rates of litter are largely influenced by the water and nutrient conditions (Gosz et al. 1976; Swift et al. 1979). The amount of accumulated carbon in the FH-layer was correlated with the moisture content of the L-layer ($r = -0.259$, $P < 0.05$), FH-layer ($r = -0.220$, $P < 0.05$) and 0-5 cm mineral soil layer ($r = -0.378$, $P < 0.001$). These rather small correlation coefficient values suggest that other properties such as the nutrient content of litterfall may also influence the rates of litter decomposition.

Development of stand structure and forest succession

The mean stem volume of P. thunbergii was proportional to the -3/2 power of the tree density for the five microsite types of Group 1 (Fig. 2. 7d). This relationship agreed with 'the 3/2 power law of self-thinning' proposed by Yoda et al. (1963). Furthermore, the mean DBH and tree height were proportional to the inverse of square root of the tree density. In contrast, the basal area was almost constant for the five microsite types (Fig. 2. 7a). These relationships agreed with 'the 3/2 power law system' proposed by Yamakura (1985). This suggested that the development pattern of aboveground stand structure of P. thunbergii did not differ between the slope positions.

The aboveground structure of P. thunbergii was most developed in LS. Correspondingly, many tree species naturally regenerated in LS (Table 2. 2). The species

diversity index was highest in LS (Fig. 2. 3). The index was very small in MS, US and RG. Tobita *et al.* (1993) studied the limiting factors on the distribution of naturally regenerated trees in this plot. They reported that dry soil conditions and development of the FH-layer prevented the natural regeneration in the middle and upper slope position. Therefore, it was suggested that the topographic variations of the soil properties result in spatial heterogeneity in forest succession.

Morphological plasticity of P. thunbergii

The changes in the aboveground structure of *P. thunbergii* along the slope followed the 3/2 power law of self-thinning. This indicated that the aboveground biomass of *P. thunbergii* was largest at LS and decreased upslope. However, the fine root biomass was smallest in LS and increased upslope (Fig. 2. 8). The fine root biomass was plotted against the tree height of *P. thunbergii* for the four microsite types in Group 1 (Fig. 2. 9a). Of the five microsite types in Group 1, TR was excluded in Fig. 2. 9a, as tree growth might be reduced by the rocky soil conditions in TR and the values of aboveground
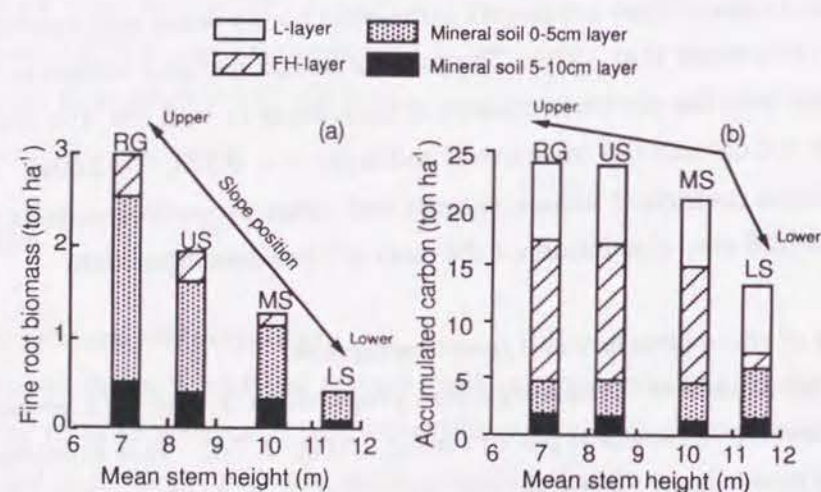

Fig. 2. 9. (a) Morphological plasticity in above- and belowground allocation of *Pinus thunbergii* along the slope. Fine root biomass was plotted against the mean stem height of *P. thunbergii* in the four microsite types of Group 1. (b) Relationship between carbon accumulation in the forest floor and mineral soil and the development of the aboveground forest structure along the slope. Accumulation of soil carbon was plotted against the mean stem height of *P. thunbergii*

stand structure were smaller for its slope position (Fig. 2. 7). Stem height was represented as an index of the aboveground biomass.

The amount of fine root increased upslope with decreasing tree height (Fig. 2. 9a). This inverse relationship between fine root biomass and tree height indicated that root/shoot ratio of *P. thunbergii* was modified in response to a topographic gradient along the slope. Root/shoot ratio decreases with increases in site fertility and aboveground productivity (Keyes & Grier 1981; Santantonio & Hermann 1985; Cameau & Kimmins 1989). The variation in forest structure was caused by the morphological plasticity of *P. thunbergii* in response to environmental heterogeneity along the slope.

Accumulation pattern of organic matter in plants and soil

The total amount of soil carbon was smallest in LS and increased upslope with decreasing mean tree height of *P. thunbergii* (Fig. 2. 9b). The larger amount of accumulated carbon in the FH-layer suggested slower litter decomposition and lower availability of water and/or nutrients. The development of the FH-layer accounted for the increase in the amount of soil carbon. Aboveground biomass was negatively correlated with amount of soil carbon. In contrast, fine root biomass was positively correlated with amount of soil carbon (Fig. 2. 9). This is also a result of the morphological plasticity of *P. thunbergii* in response to the environmental gradient. Soil-plant interactions in the stand, combined with topographic variation, resulted in spatial heterogeneity of the accumulation pattern of organic matter in plants and the soil.

The small correlation coefficient value between the amount of accumulated carbon in the FH-layer and soil moisture content (Table 2. 3) suggested that nutrient content of litterfall might also affect decomposition rates. The nutrient content of litterfall has been shown to decrease from lower to upper slope positions (e.g. Welbourn *et al.* 1981; Tsutsumi *et al.* 1983; Katagiri 1988). Changes in nutrient use of *P. thunbergii* in response to environmental gradients may also affect the litter decomposition and accumulation pattern of soil carbon.

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Chapter 3

Nutrient-Uptake and -Use Efficiency of *Pinus thunbergii* Parl. along a Topographical Gradient of Soil Nutrient Availability

INTRODUCTION

Plants vary widely in their efficiency of nutrient uptake and nutrient use in response to nutrient availability (Chapin 1980). Previous studies indicated that as nutrient availability increased, the proportion of available nutrients taken up by plants would decrease (Chapin *et al*. 1982; Gray & Schlesinger 1983; Shaver & Melillo 1984) and the amount of biomass produced per unit nutrient uptake would decrease (Vitousek 1982, 1984; Pastor *et al*. 1984; Silver 1994). These plant responses to the nutrient availability, such as changes in tissue and litter chemical compositions, have significant effects on ecosystem processes such as accumulation of soil organic matter and nutrient cycling (Melillo *et al*. 1982; Pastor *et al*. 1984; Vitousek *et al*. 1987; Berendse *et al*. 1989; Matson 1990; Binkley & Valentine 1991; Vinton & Burke 1995).

Topography is known to play a critical role in changing the soil nutrient availability (Schimel *et al*. 1985; Burke 1989; Zak *et al*. 1991; Brubaker 1993, 1994). Several authors have shown the topographic variations in nutrient cycling in forest ecosystems (Tsutsumi *et al*. 1984; Pastor *et al*. 1984; Garten *et al*. 1994).

The purpose of present study is to investigate the changes in nutrient uptake and nutrient use of *Pinus thunbergii* Parl. along a topographical gradient of nutrient availability. To evaluate the nutrient uptake and nutrient use of plants in response to the soil nutrient availability, three efficiency indices were used as proposed by Bridgham *et al*. (1995): (1) nutrient-response efficiency (production per unit nutrient availability); (2) nutrient-use efficiency (production per unit nutrient uptake); (3) nutrient-uptake efficiency (nutrient uptake per unit nutrient availability). Nutrient-response efficiency of a plant (PR/R_{av}) is determined by the product of its nutrient use efficiency (PR/R_{ac}) and its nutrient uptake efficiency (R_{ac}/R_{av}):

$PR/R_{av} = PR/R_{ac} \times R_{ac}/R_{av}$.

where PR is production, R_{ac} is the amount of nutrient acquired, and R_{av} is nutrient availability. These indices can distinguish the ability of a species to acquire nutrients

and its ability to use them in growth once acquired. An exact accounting of nutrient-use efficiency requires accurate belowground estimates of production, but this time-consuming to measure (Vitousek 1982). Bridgham *et al.* (1995) substituted litterfall production for aboveground production (*PR*) as Vitousek (1982) proposed, and they used nutrient return in litterfall as an index of the amount of a nutrient acquired for production (R_{ac}).

In this study, we examined nitrogen and phosphorus because these nutrients are cycled in forest ecosystems largely in litterfall (Vitousek 1982) and they are often limiting nutrients for plant growth in forest ecosystems (Waring & Schlesinger 1985).

We addressed two major questions: (1) Does nutrient-response efficiency increase with decreasing soil nutrient availability? (2) If nutrient-response efficiency is higher at lower levels of soil nutrient availability, do nutrient-uptake and/or its use efficiencies increase with decreasing soil nutrient availability?

METHODS

Study site

The study was carried out in a *P. thunbergii* plantation on Mt. Tanakami, Shiga Prefecture, Japan. In this area, the bedrock was granite which had been much weathered. The soil was sandy. The mean annual temperature was 12.4°C and annual precipitation was 1411 mm during the years between 1976 and 1980 (Iwatsubo *et al.* 1982). A study plot of 64 m x 40 m (Fig. 2. 1) was set up in a *P. thunbergii* plantation which had been established in 1971 (34°55' N, 135°58'E, 420 m above sea level). The direction of the plot was S55°E. The plot covered a steep ridge and an underground stream. Details of the study plot were provided in Chapter 2.

Topographic classification

The plot was divided into 160 subplots of 4 m x 4 m. To evaluate the smaller scale topographical variation, the elevation of every intersection of the 4 m x 4 m grids was measured. On the basis of slope position (relative position from ridge top to valley floor along a slope), slope direction, and amount of exposed rocks, the 160 subplots were categorized into nine microsite types (Fig. 2. 1 and Table 2. 2).

LS: Lower slope site near the stream.

ST: Stream site at which the water was usually undercurrent.

RP: Riparian terrace site between bared rocks and the stream.

RO: Rocky site on the lower slope.

TR: Transitional site from middle slope site to the rocky site.

MS: Middle slope site.

US: Upper slope site on the south side.

RG: Ridge site.

NS: Upper slope site on the north side.

Fig. 3. 1. Basal area of trees larger than 1 cm in DBH (Diameter at breast height) in each microsite type.

The nine microsite types were grouped into the following three groups based on the basal area of *P. thunbergii* and all trees (Fig. 3. 1). Group 1 (LS, TR, MS, US, RG); The planted *P. thunbergii* saplings successfully grew and predominated. Group 2 (ST, RO, NS); The planting of *P. thunbergii* had failed. Group 3 (RP); *Pinus densiflora* Sieb. et Zucc. had already existed before the planting of *P. thunbergii*.

In this study, the author mainly focused on the five microsite types of Group 1 in evaluating the response of *P. thunbergii* to the nutrient gradient along the slope.

Soil sampling

Soil samples were collected at the 94 points (at the every other corner of subplots, Fig. 2. 1) in the plot in July (for extractable phosphorus) and September (for nitrogen mineralization rate), 1991 by removing a core (11.3 cm in diameter and 5 cm deep). The soil sampling was conducted a few days after the rain. The soil samples were collected from the mineral soil surface (0-5 cm), because fine roots were concentrated in the soil surface (Chapter 2). The proportions of fine root biomass in FH-, mineral soil 0-5 cm and 5-10 cm layers to the total fine root biomass were 12%, 69% and 19 %, respectively. According to our field observation, fine roots were very rare in the soil below 10 cm in depth. The fresh weight of the soil sample was measured. The soil samples were divided into litter, fine root (< 2 mm in diameter), coarse root (≥ 2 mm), fine soil (< 2 mm) and gravel (≥ 2 mm). The fine soil was used for the analysis of nutrient availability in the soil. The air-dried weight of each fraction was measured. Five grams of each fraction was oven-dried at 105°C and weighed to obtain dry ratios.
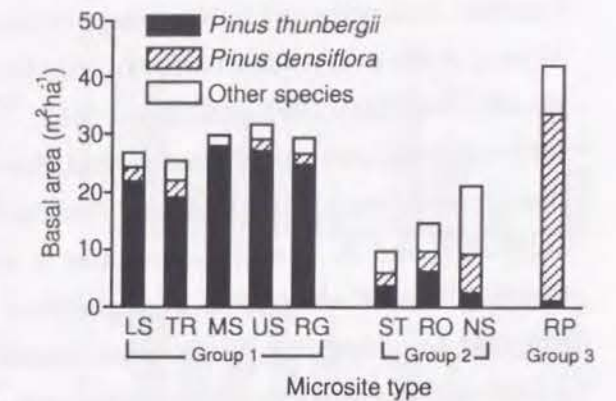
Litterfall collection

Litterfall was collected in litter traps of area 0.25 m². Ninety-four such litter traps were located at the every other corner of subplots (Fig. 2. 1). The litterfall was collected every month from May 1991 until April 1992. Litter samples were air-dried and separated into following parts; pine needle, seed, flower, branch, bark and corn, other species leaf, flower, seed, branch and bark, and fine particle. Pine needle contained the needles of *P. thunbergii* and *P. densiflora*, because it was difficult to distinguish the litter of *P. thunbergii* and *P. densiflora*. Five grams of each fraction was oven-dried at 105℃ and weighed to obtain dry ratios. Pine needle and the other litterfall components were milled, and prepared for chemical analysis.

Chemical analysis

Nitrogen mineralization rate was determined in a 30 day aerobic incubation. The initial amounts of nitrate and ammonium were determined by extracting from 5 g of soil with 50 ml of 2 N KCl solution (Keeney & Nelson 1982). Subsamples (5 g soil) were incubated in a controlled-environmental cabinet at 30℃. Soil moisture was maintained initial value of each subsample. After 30 days each subsample was extracted in KCl solution as described above. Net mineralization rate was calculated as the change in the amounts of nitrate plus ammonium over the incubation period. Available phosphorus was extracted from 1 g of soil with 7 ml of 0.03 N NH₄F and 0.025 N HCl solution (Olsen & Sommers 1982).

Total carbon and nitrogen contents were determined using a CN analyzer (Yanaco MT-600). Litterfall samples for the analysis of phosphorus were digested with perchloric acid and nitric acid. Nitrate and ammonium contents in the soil sample and phosphorus content were analyzed with a spectrophotometer (Hitachi U-1000).

Statistical analysis

Analysis of variance (SYSTAT 1992) was used to determine differences among mean values in each microsite type. The Tukey's HSD (Honestly significant difference) test was used for multiple comparisons. The mean values in each microsite type were calculated by averaging the values from sampling points within each microsite type and on its borders.

RESULTS

Nutrient availability in soil

Nitrogen mineralization rate and amount of extractable phosphorus were substituted for nitrogen and phosphorus availabilities in soil, respectively (nitrogen mineralization rate is more indicative to estimate the nitrogen availability than the amount of inorganic nitrogen). Nitrogen mineralization rate was largest around the stream and tended to decrease upslope (Fig. 3. 2). Among the five microsite types of Group 1, the nitrogen mineralization rate decreased upslope, though TR had smaller value for its slope position. Amount of extractable phosphorus was smallest in NS and there was no significant difference among the other eight microsite types. Among the five microsite types of Group 1, the amount of extractable phosphorus tended to decrease upslope.

Fig. 3. 2. Nitrogen mineralization rate and amount of extractable phosphorus in each microsite type (mean ± 1 SE). Bars denoted by the same letter are not significantly different from each other at $P < 0.05$ (Tukey's HSD test).

Litterfall production

The mean annual litterfall in the whole plot was 6.15 ± 1.76 ton ha⁻¹ yr⁻¹ (mean ± 1 SD). The mean values of pine needle, other organs of pine, and the others were 3.56 ± 1.29, 1.33 ± 0.55, and 1.22 ± 0.34 ton ha⁻¹ yr⁻¹ (mean ± 1 SD), respectively. Pine needle and whole pine organs composed 57.9% and 79.7% of total amount of litterfall, respectively.

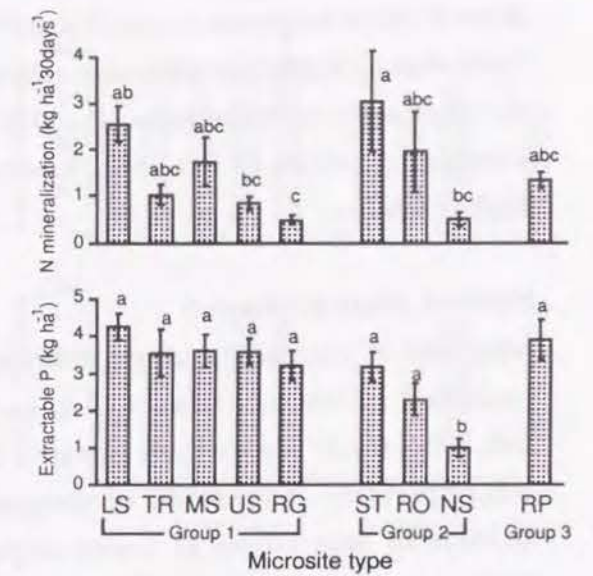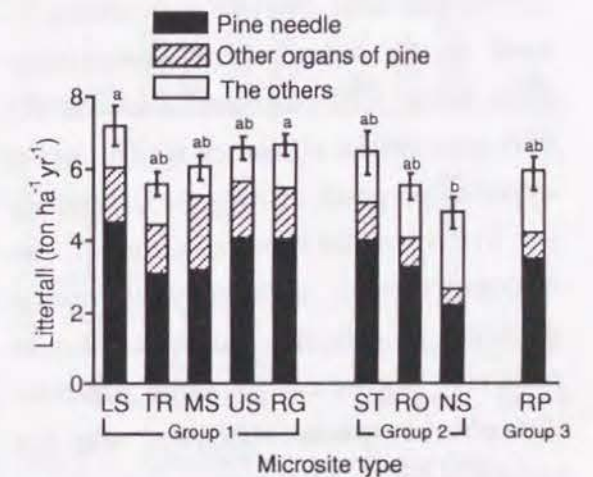The mean annual litterfall was largest in LS and smallest in NS (Fig. 3. 3). The

Fig. 3. 3. Amount of litterfall in each microsite type(mean ± 1 SE). The total amount denoted same letter are not significantly different at $P < 0.05$ (Tukey's HSD test).

value in NS was significantly smaller than those in other microsite types ($P < 0.05$). There was no significant difference among the other eight microsite types ($P < 0.05$), though the values in RO and TR were slightly smaller.

Nutrient return in litterfall

Amounts of nitrogen and phosphorus contained in litterfall were 43.5 ± 18.3 and 3.25 ± 1.29 kg ha^{-1} yr^{-1} (mean $\pm$ 1 SD), respectively. The amount of nitrogen in litterfall was larger at lower slope positions and decreased upslope (Fig. 3. 4). The amount of phosphorus in litterfall was also larger at lower positions and decreased upslope.

Fig. 3. 4. Nutrient return in litterfall in each microsite type (mean ± 1 SE). Bars denoted the same letter are not significantly different at $P < 0.05$ (Tukey's HSD test).

Nutrient-uptake efficiency

The nutrient return in litterfall / soil nutrient availability ratio, or nutrient uptake per unit nutrient availability, is used as an index of nutrient-uptake efficiency (Bridgham et al. 1995). Nitrogen-uptake efficiency was higher at upper slope positions (Fig. 3. 5). Among the five microsite types of Group 1, the nutrient-uptake efficiency increased upslope, though the value in TR was relatively higher for its slope position. Phosphorus-uptake efficiency was far highest in NS, and there was no significant difference among the other eight microsite types.
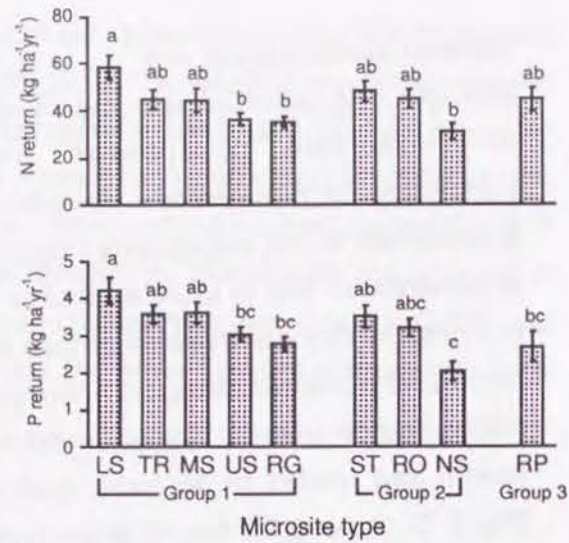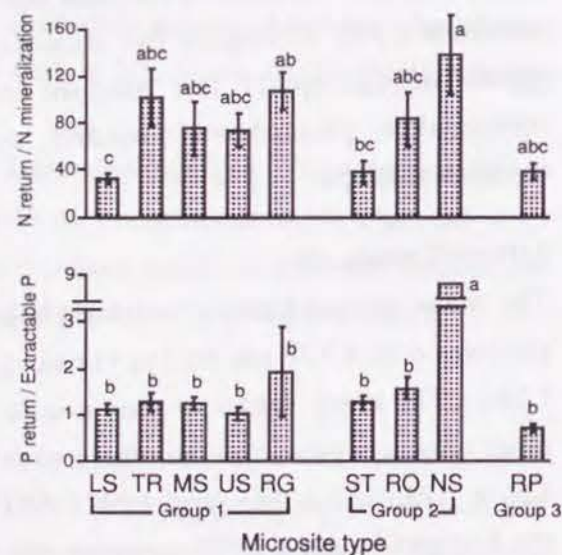

Fig. 3. 5. Nutrient return in litterfall / soil nutrient availability ratio in each microsite type (mean ± 1 SE). Bars denoted the same letter are not significantly different at $P < 0.05$ (Tukey's HSD test).

Nutrient-use efficiency

The mass / nutrient return ratio of litterfall, or litterfall production per unit nutrient uptake, is used as an index of nutrient-use efficiency (Vitousek 1982). Nitrogen-use efficiency was smallest in LS and increased upslope (Fig. 3. 6). Phosphorus-use efficiency increased upslope from lower to upper slope positions.

Nutrient-response efficiency

The ratio of litterfall mass / soil nutrient availability, or litterfall production per unit nutrient availability, is used as an index of nutrient-response efficiency (Bridgham et al. 1995). Nitrogen-response efficiency increased upslope, though TR had higher value for its slope position (Fig. 3. 7). Phosphorus-response efficiency was far highest in NS, and there was no significant difference among the other eight microsite types.

DISCUSSION

Soil nutrient availability tended to be lower at upper slope positions (Fig. 3. 2). Nutrient-uptake, its use and its response efficiencies tended to be higher at upper slope positions (Fig 3. 5, 3. 6, and 3. 7). These patterns implied that plants might increase the three efficiencies in response to the lower soil nutrient availability. To elucidate the response of P. thunbergii to
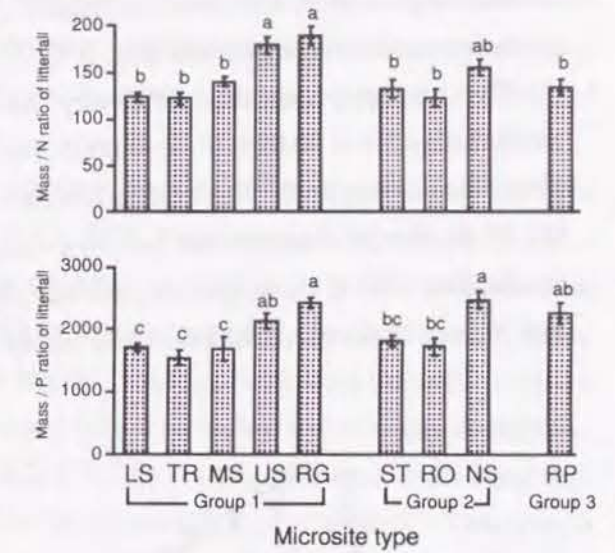

Fig. 3. 6. Mass / nutrient return ratio of litterfall in each microsite type(mean ± 1 SE). Bars denoted the same letter are not significantly different at $P < 0.05$ (Tukey's HSD test).
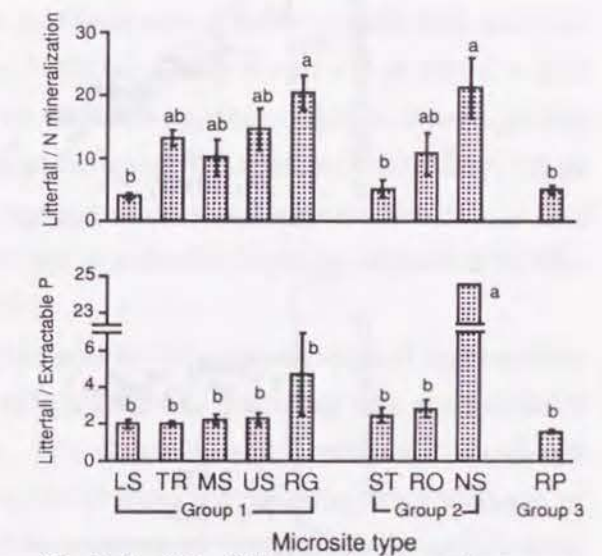

Fig. 3. 7. Litterfall mass / soil nutrient availability ratio in each microsite type (mean ± 1 SE). Bars denoted the same letter are not different at $P < 0.05$ (Tukey's HSD test).

the soil nutrient availability, the relationships between the three efficiencies and nutrient availability within the five microsite types of Group 1 in which *P. thunbergii* predominated were examined (Fig. 3. 8).

The nutrient-response efficiency was negatively correlated with soil nutrient availability ($r = -0.929$, $P < 0.0005$ for nitrogen and $r = -0.700$, $P < 0.0005$ for phosphorus, Fig. 3. 8). The author has two explanations for these negative correlations. (1) *P. thunbergii* changes the nutrient-response efficiency in response to the nutrient availability. (2) If these correlations simply resulted from autocorrelations between Y and X axes, these correlations would imply that litterfall production is not related to the
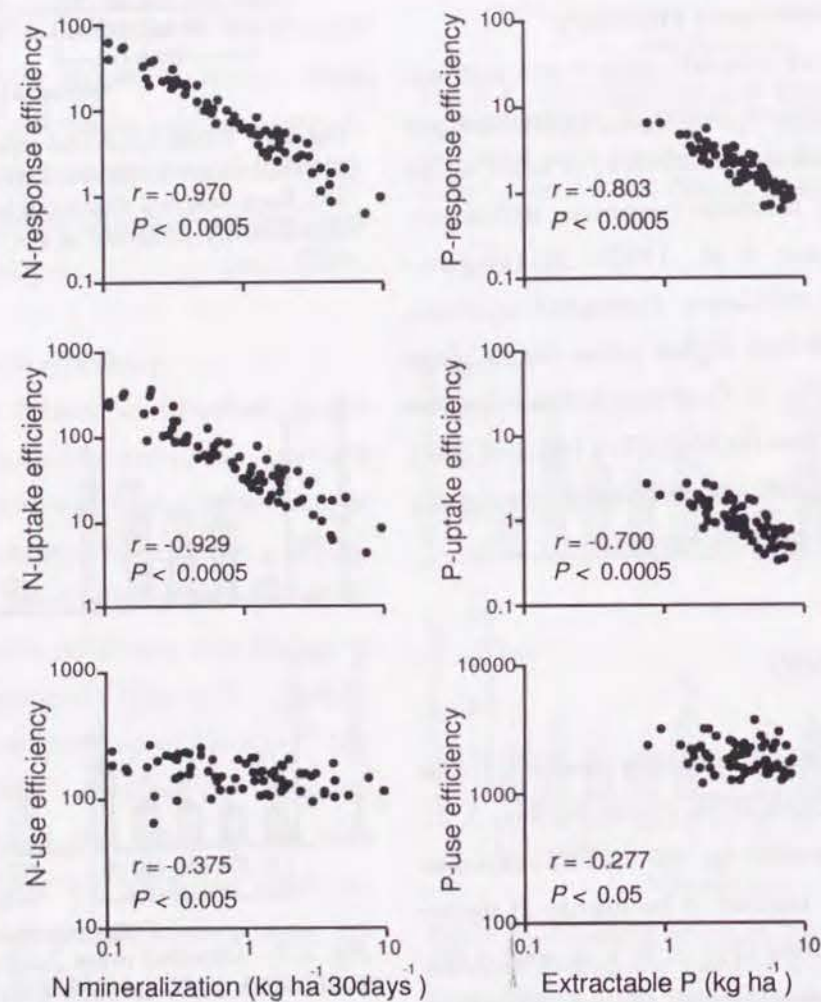

Fig. 3. 8. Relationships between nutrient-response, its uptake and its use efficiencies, and soil nutrient availability within the Group 1.

soil nutrient availability. Nutrient-response efficiency is determined by the product of its nutrient-uptake and its nutrient-use efficiencies. To explain what mechanism could account for these negative correlations between nutrient-response efficiency and soil nutrient availability, the relationships between nutrient-uptake and its use efficiencies and soil nutrient availability are examined.

The correlation coefficients between nutrient-uptake efficiency and soil nutrient availability were significant ($r = -0.970$, $P < 0.0005$ for nitrogen and $r = -0.803$, $P < 0.0005$ for phosphorus, Fig. 3. 8). These negative correlations would indicate that increase in nutrient-uptake efficiency might be a response of *P. thunbergii* to the lower soil nutrient availability. This suggestion is logical if nutrient uptake is limited. Nutrient return in litterfall, or nutrient uptake, decreased with decreasing soil nutrient availability ($r = 0.308$, $P < 0.01$ for nitrogen and $r = 0.272$, $P < 0.05$ for phosphorus), indicating that nutrient uptake was limited at lower levels of nutrient availability. This result supported the suggestion which is consistent with previous studies showing that nutrient-uptake efficiency increased with decreasing nutrient availability (Chapin *et al.* 1982; Gray & Schlesinger 1983; Shaver & Melillo 1984). The increase in nutrient-uptake efficiency was thought to be achieved by the increase in fine root biomass (Chapter 2). The high root / shoot biomass ratio is the response of low nutrient availability and increase nutrient uptake (Chapin 1980).

The correlation coefficients between nutrient-use efficiency and soil nutrient availability were significant ($r = -0.375$, $P < 0.005$ for nitrogen and $r = -0.277$, $P < 0.05$ for phosphorus, Fig. 3. 8). These negative correlations suggested that *P. thunbergii* also increased nutrient-use efficiency in response to the lower soil nutrient availability. These results were consistent with the previous researches on forest ecosystems (Pastor *et al* 1984; Silver 1994) and with experimental studies of individual species (Shaver & Melillo 1984; Birk & Vitousek 1986; Tanner *et al.* 1992).

The relationships between nutrient-uptake and its use efficiencies, and soil nutrient availability expressed that the change in nutrient-response efficiency was a response of *P. thunbergii* to the soil nutrient availability. The author thus inferred that *P. thunbergii* increased litterfall production per unit nutrient availability resulting from increase in both nutrient-uptake and its use efficiencies in response to the decrease in soil nutrient availability.

Nutrient-use efficiency had smaller correlation coefficients with the soil nutrient availability than nutrient-uptake efficiency did. The nutrient-use efficiency, however, varied widely from 65.9 to 263.1 for nitrogen and from 1152 to 3771 for phosphorus

(Nutrient concentrations in litterfall were 0.38% - 1.52% for nitrogen, and 0.027% - 0.086% for phosphorus). These variations in nutrient-use efficiency along a topographic gradient would have effects on the accumulation of organic matter and nutrient cycling in the forest ecosystem. High nutrient-use efficiency under low nutrient availability drives infertile ecosystems toward even greater nutrient deficiency (Shaver & Melillo 1984), because low litter nutrient content reduces decomposition rate and subsequent release of available nutrient (Gosz *et al*. 1973; Melillo *et al*. 1982 ; Gholz *et al*. 1985). These positive feedback loops could promote the accumulation of organic matters at upper slope positions (Chapter 2). On the other hand, at lower slope positions, the turnover of organic matter in the forest floor was very fast. Thus the physiological plasticity of a plant species in response to the nutrient gradient could enhance the spatial variation in nutrient cycling.

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Nutrient Resorption from *Pinus thunbergii* Parl. needles along a Topographic Gradient

INTRODUCTION

Nutrient resorption from senescing leaves is an important adaptation to infertile soils, since it reduces nutrient loss (Chapin 1980) and increases the plant's nutrient-use efficiency (Vitousek 1982). Though many studies have attempted to correlate nutrient resorption efficiency with soil nutrient availability, many details of resorption ecology remain to be resolved. In some studies resorption was considered to be more efficient in trees growing on infertile soil (Small 1972; Flanagan & Van Cleve 1983; Boerner 1984; Chapin & Moilanen 1991; Dalla-Tea & Jokela 1994). In other studies plants growing on more fertile soil have higher proportional resorption (Chapin & Kedrowski 1983; Lajtha 1987; Nambiar & Fife 1987). In still other cases the efficiency of resorption is not influenced by soil nutrient availability (Birk & Vitousek 1986; Aerts & Caluwe 1989; Lajtha & Klein 1989; Schlesinger *et al.* 1989; Chapin & Moilanen 1991).

A reason of these inconsistent results is the ways of these studies which have made it difficult to differentiate between phenotypic and genotypic responses to soil fertility (Pugnaire & Chapin 1993).

In Chapter 3, increase in nutrient-use efficiency with decreasing soil nutrient availability from lower to upper slope positions within an even-aged *Pinus thunbergii* Parl. plantation were observed. It was pointed out that the increase in nutrient-use efficiency was a phenotypic response of *P. thunbergii* trees to low nutrient availability. In the present study, the author focused on the phenotypic response of *P. thunbergii* trees to the nutrient gradient in the plantation.

The aims of this study are to examine the differences in nutrient contents in green and senescent needles, and nutrient resorption efficiency among different slope positions, and to evaluate the mechanisms which could account for the increase in nutrient-use efficiency with decreasing soil nutrient availability. In addition, the relationship between resorption efficiency and other factors that could control nutrient resorption such as plant nutrient status (Chapin & Kedrowski 1983; Lajtha 1987) and needle mass (Helmisaari 1992) were also discussed. In this study, the author addressed

three major questions:

(1) Do *P. thunbergii* trees growing on low nutrient availability soils have smaller nutrient content in green and senescent needles?

(2) Do *P. thunbergii* trees growing on low nutrient availability soils have higher proportional resorption than do trees growing on more fertile soils?

(3) Is nutrient resorption efficiency positively correlated with nutrient content and/or mass of green needle?

METHODS

Study site

The study was carried out in a *P. thunbergii* plantation on Mt. Tanakami, Shiga Prefecture, Japan. In this area, the bedrock was granite which has been weathered deeply. Soil materials were sandy. The mean annual temperature was 12.4°C and annual precipitation was 1411 mm during the years between 1976 and1980 (Iwatsubo *et al.* 1982). A study plot of 64 m x 40 m was set up in a *P. thunbergii* plantation which had been established in 1971 (34°55' N, 135°58'E, 420 m above sea level). The direction of the plot was S55°E. The plot was laid across a steep ridge and an underground stream. Details of the study plot have been reported in Chapter 2.

The plot was divided into 160 subplots of 4 m x 4 m. To evaluate the smaller scale topographical variation, the elevation of every intersection of the 4 m x 4 m grids was measured. On the basis of slope position, direction, and amount of exposed rocks, the 160 subplots were categorized into nine microsite types (Chapter 2.). In this study, the author chose four microsite types (LS; lower slope, MS; middle slope, US; upper slope and RG; ridge) to evaluate the effects of slope positions on the response of *P. thunbergii* to the nutrient availability. Some characteristics of vegetation in each microsite type were shown in Table 4. 1. Total basal area was almost constant around 30m² ha⁻¹. Tree density was smallest in LS and increased upslope. Mean stem height of *P. thunbergii* was highest in LS and decreased upslope.

Nutrient availability

To examine the soil nutrient availability, nitrogen mineralization rate and amount of extractable phosphorus in each microsite type were shown in Table 4. 2. Nitrogen mineralization rate decreased upslope from 2.56 kg ha⁻¹ 30days⁻¹ in LS to 0.46 kg ha⁻¹

Table 4. 1 Some characteristics of vegetation in each microsite type.

	Microsite	type		
	LS	MS	US	RG
Total basal area (m²ha⁻¹)	26.8	29.8	31.6	29.3
Basal area of *P. thunbergii* (m²ha⁻¹)	21.8	28.1	27.1	24.7
Number of *P. thunbergii* (ha⁻¹)	1228	1979	2913	3624
Mean height of *P. thunbergii* (m)	12.3	10.2	8.6	7.1

Table 4. 2 Nitrogen mineralization rate and amount of extractable phosphorus in each microsite type (mean ± 1 SD).

	Microsite	type		
	LS	MS	US	RG
N mineralization (kg ha⁻¹30days⁻¹)	2.56±1.61a	1.73±2.09ab	0.84±0.62bc	0.48±0.40c
Extractable P (kg ha⁻¹)	4.25±1.46a	3.61±1.72a	3.58±1.39a	3.21±1.67a

Means denoted by same letter are not different at $P < 0.05$ in Tukey's HSD test.

30days⁻¹ in RG. The amount of extractable phosphorus tended to decrease upslope from 4.25 kg ha⁻¹ in LS to 3.21 kg ha⁻¹ in RG, though there was no significant difference among the microsite types.

Green needle sampling

Green needles of *P. thunbergii* were collected from 6 trees in each microsite type after needle maturation in the beginning of October. A first-order branch containing 4 age classes (0-, 1-, 2-, 3-year) were collected from the uppercrown of each tree. Plant material was taken immediately to the laboratory. Green needles were separated into the 4 age classes. The needles belonging to the same age class within each tree were combined for analysis.

Senescent needle collection

Senescent needle was collected in 94 litter traps of area 0.25m² in the study plot (Chapter 3). The senescent needle was collected every month from May 1991 until April 1992. The collected needles (over 1year) were air dried, pooled, milled and prepared for

chemical analysis.

Laboratory analysis

The length and weight of green needle were measured (100 needles of each age class) for determination of the needle mass per unit length. The mass per unit length of senescent needle was also determined. Subsamples of the needles were dried at 105°C for 2 days to determine the dry ratio. Needle samples for the analysis of phosphorus were digested with perchloric acid and nitric acid. Total carbon and nitrogen content in needle were analyzed using a CN analyzer (Yanaco MT-600). Phosphorus content in needle was analyzed by the molybdenum blue procedure using a spectrophotometer (Hitachi U-1000).

Data processing

Resorption efficiency (%) was calculated as:

Resorption efficiency (%) = (Cg - Cs) / Cg x 100,

where Cg is nutrient content in green needle per unit length (g cm^{-1}), Cs is nutrient content in senescent needle per unit length (g cm^{-1}). Cg was calculated by averaging the values of all age classes in each tree, since nitrogen and phosphorus content per unit length in green needle did not differ between the needle age class. Cs was calculated by averaging the values in litter traps within each microsite type and on its borders. Therefore, error terms for resorption efficiency among trees could not given.

This approach does not account for leaching of nutrients from green and senescent needles. Leaching of nitrogen and phosphorus is usually very little (Parker 1983).

Statistical analysis

Analysis of variance (SYSTAT 1992) was used to determine differences among mean values in each microsite type. The Tukey's HSD (Honestly significant difference) test was used for multiple comparisons.

RESULTS

Nutrient concentration in needle

Nutrient concentration decreased greatly during senescence (Fig. 4. 1). The differences in nutrient concentration between green and senescent needles were 0.40% - 0.46% for nitrogen and 0.026% - 0.038% for phosphorus.

Nitrogen concentration in green needle in LS was higher ($P < 0.05$) than those in the other microsite types which were at upper slope positions. Among the other three microsite types the nitrogen concentration in green needle did not differ significantly. The mean nitrogen concentration in senescent needle was higher in LS and decreased upslope.

Phosphorus concentration in green needle tended to be higher at lower slope positions, though there was no significant difference among the microsite types ($P < 0.05$). Phosphorus concentration in senescent needle was larger ($P < 0.05$) at lower slope positions (LS and MS) and smaller at higher slope positions (US and RG).

Dry weight of needle per unit length

Dry weight of needle per unit length also decreased during senescence (Fig. 4. 2). The differences in dry weight of needle per unit length between green and senescent needles were 0.09 - 1.78 mg cm^{-1}.

Dry weight of green needle per unit length increased upslope from 3.6 mg cm^{-1} in LS to 4.6 mg cm^{-1} in RG. Dry weight of senescent needle decreased upslope from 3.5 mg cm^{-1} in LS to 2.8 mg cm^{-1} in RG.

Nutrient content in needle per unit length

Nitrogen content in green needle per unit length did not differ significantly among the
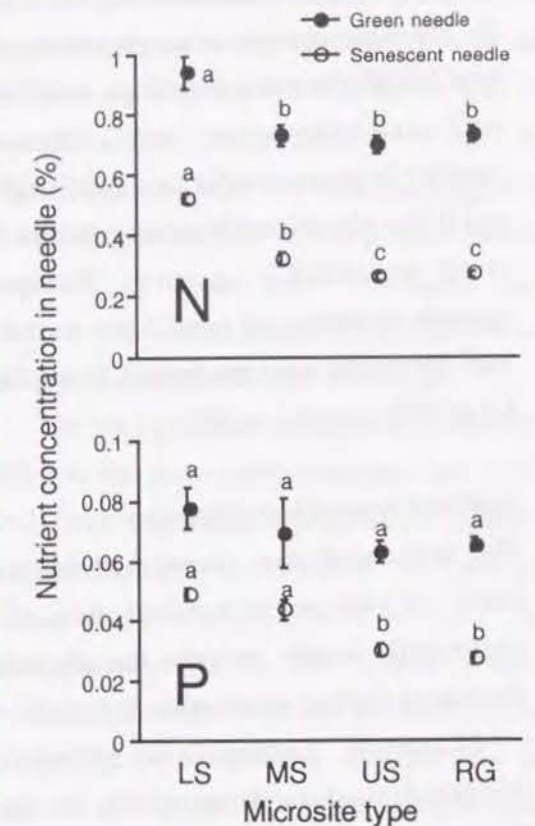

Fig. 4. 1. Nutrient concentration in green and senescent needles in each microsite type (mean ± 1 SE). Means denoted the same letter are not significantly different at $P < 0.05$ (Tukey's HSD test).
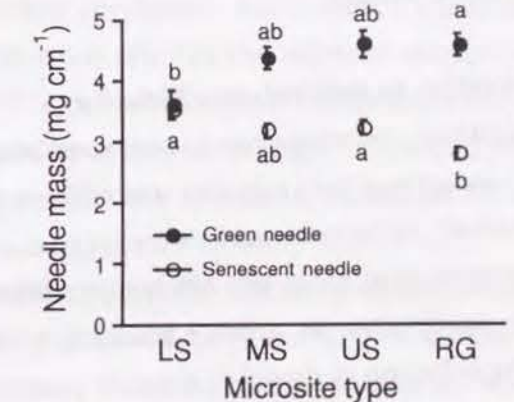

Fig, 4. 2. Dry mass per unit length of green and senescent needles (mean ± 1 SE). Means denoted by the same letter are not significantly different at $P < 0.05$ (Tukey's HSD test).

microsite types around 30 µg cm⁻¹ (Fig. 4. 3). Nitrogen content in senescent needle per unit length decreased upslope from 18.3 µg cm⁻¹ in LS to 7.6 µg cm⁻¹ in RG. Phosphorus content in green needle per unit length did not differ significantly among the microsite types around 2.5 µg cm⁻¹. Phosphorus content in senescent needle per unit length had decreased upslope from 1.73 µg cm⁻¹ in LS to 0.74 µg cm⁻¹ in RG.

Nutrient resorption efficiency

We calculated the resorption efficiency based on changes in nutrient contents per unit needle length, because the dry weight decreased during senescence (Fig. 4. 2).

Nitrogen resorption efficiencies increased upslope from 42.6% in LS to 76.5% in RG (Fig. 4. 4). Phosphorus resorption efficiency also increased upslope from 27.8% in LS to 72.1% in RG.

Fig. 4. 3. Nutrient content in green and senescent needles per unit length in each microsite type (mean ± 1 SE). Means denoted the same letter are not significantly different at $P < 0.05$ (Tukey's HSD test).

DISCUSSION

Relation to nutrient-use efficiency

Nutrient concentrations in senescent needle was lower at upper slope positions (Fig. 4. 1) indicating that nutrient-use efficiency of needle production (needle mass per unit nutrient, or inverse nutrient concentration in needle) was higher at upper slope positions. Increase in nutrient-use efficiency of litter production in low nutrient sites is thought to be partly due to greater biomass production per unit of nutrient (low nutrient concentration in tissue) in nutrient poor sites and partly due to more effective resorption of nutrient in such sites (Vitousek 1982, 1984).

The decrease in tissue nutrient concentrations with low nutrient availability was shown in some previous studies (e.g., Chapin 1980). In this study, the nitrogen and
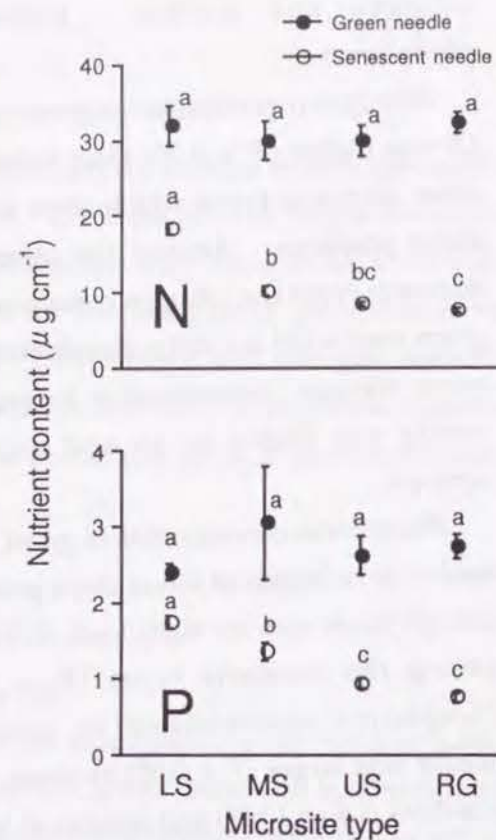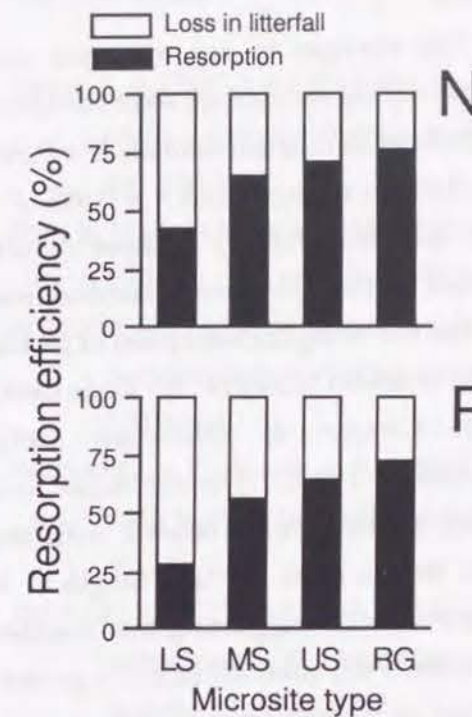

Fig. 4. 4. Nitrogen and phosphorus resorption efficiency in each microsite type.

phosphorus concentrations in green needle were not significantly correlated with soil nutrient availability $r = 0.818$, $P > 0.17$ for nitrogen and $r = 0.858$, $P > 0.13$ for phosphorus). These correlations suggested that the contribution of the greater needle production per unit nitrogen and phosphorus to the increase in nutrient-use efficiency of *P. thunbergii* was small.

The nitrogen and phosphorus resorption efficiencies increased upslope (Fig. 4. 4), and inversely related to the soil nutrient availability ($r = -0.952$, $P < 0.05$ for nitrogen, $r = -0.980$, $P < 0.02$ for phosphorus, Fig. 4. 5). These results indicated that the increase in nutrient-use efficiency is controlled by increase in nutrient resorption efficiency. The increase in nutrient resorption efficiency with decreasing nutrient availability agreed with Pugnaire & Chapin (1993) who showed that a high nutrient resorption is a phenotypic response to low nutrient availability.

Factors affecting resorption

Though some factors that could control nutrient resorption have been examined, consistent results were not seen. Plant nutrient status affected the nutrient resorption efficiency (Chapin & Kedrowski 1983; Lajtha 1987) and some did not (Schlesinger 1989; Chapin & Moilanen 1991). In other studies, carbohydrate flux strongly influenced the nutrient resorption efficiency (Chapin & Kedrowski 1983; Chapin & Moilanen 1991; Hermisaari 1992).

In this study, the correlations between nutrient resorption efficiency and nutrient content in green needle per unit length was not significant ($r = -0.271$, $P > 0.73$ for nitrogen and $r = -0.525$, $P > 0.47$ for phosphorus). These correlations revealed that nutrient resorption efficiency was not controlled by the nutrient status in green needle. These results was consistent with Lajtha and Klein (1988) and Chapin & Moilanen (1991) who found no relations between nutrient resorption efficiency and plant nutrient
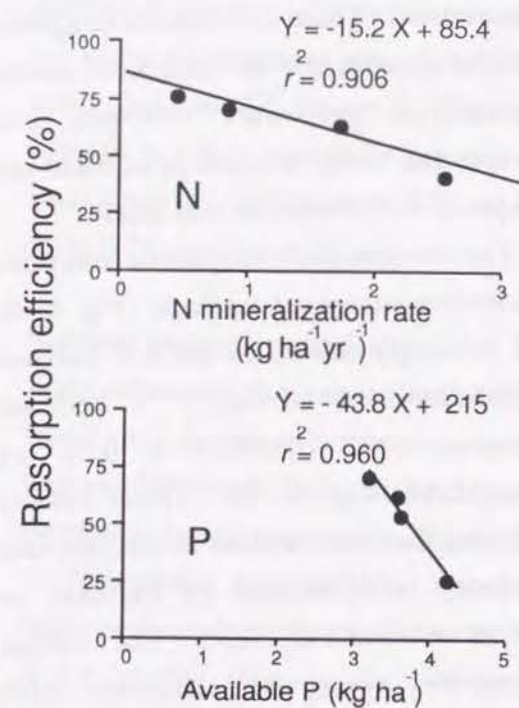
status.

The changes in dry mass per unit length during senescence were correlated with those in nutrient content ($r = 0.994$, $P < 0.01$ for nitrogen and $r = 0.995$, $P < 0.01$ for phosphorus). These results implied that nutrients were resorbed from needles following the resorption of mobile carbohydrate (Chapin & Kedrowski 1983; Chapin & Moilanen 1991; Helmisaari 1992). Needle mass loss during senescence correlated with the green needle mass per unit length ($r = 0.969$, $P < 0.03$), suggesting that needles with greater dry mass contained a greater portion of carbohydrates (Hermisaari 1992).

The dry mass of green needle per unit length increased with decreasing soil nutrient availability ($r = -0.951$, $P < 0.05$ for nitrogen, $r = -0.962$, $P < 0.04$ for phosphorus). Mooney & Gulmon (1992) showed the inverse relationship between leaf weight per unit leaf area and the

nutrient availability as a response of plants to nutrient gradient. The increase in needle dry mass per unit length with decreasing nutrient availability suggested that *P. thunbergii* altered the needle structure in response to low nutrient availability.

In conclusion, the increase in nutrient resorption is a phenotypic response of *P. thunbergii* to low nutrient availability. The changes in nutrient resorption efficiency should control the change in nutrient-use efficiency. The nutrient resorption efficiency is more closely related to needle dry mass per unit length than nutrient content in foliar needle. The nutrient resorption efficiency could be facilitated by an increase in dry mass per unit length in green needle with a decrease in the soil nutrient availability.

Fig. 4. 5. Relationship between nutrient resorption efficiency and soil nutrient availability.

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Effects of Nitrogen Concentration and Environmental Condition on Decomposition Rates of Pine Needle Litter

INTRODUCTION

The decomposition of plant litter is an important factor controlling the nutrient cycling in forest ecosystems. The decomposition rate determines the rate at which nutrients become available for uptake by plants, and plays an important role in determining ecosystem productivity. Decomposition rates of litters are regulated by the interaction between litter quality, environmental conditions and soil organisms (Swift *et al.* 1979).

The litter quality changes greatly with the nutrient-use of plants (Vitousek 1982, 1984). In general, plants create positive feedbacks between litter quality and decomposition rate (Pastor *et al.* 1984; Hobbie 1992). Plants that occur in low nutrient habitats grow slowly, use nutrients conservatively and produce poor quality litter that decompose slowly. The feedbacks between litter characteristics and soil nutrient levels have important implications for forest species dynamics and ecosystem development through time (Pastor & Post 1988).

The effects of litter quality on decomposition have been demonstrated in studies mainly focusing the effects of nitrogen and lignin (Berg & Staaf 1980; Berg *et al.* 1982; Melillo *et al.* 1982; McClaugherty & Berg 1987; Berg & Ekbohm 1991).

The purpose of this study is to examine the influence of environmental conditions and nitrogen concentration of litter on the decomposition rates and patterns of chemical changes in litter during the decomposition processes. The author also discussed its implications in nutrient cycling.

It is often difficult, however, to separate the above-mentioned effects in nature, because litter quality is dependent on the site conditions and individual features of litter are dependent on each other. In the previous study (Chapter 3 and 4), *Pinus thunbergii* Parl. needle litter with different chemical compositions was collected in an even aged plantation which was laid across a steep ridge and valley bottom. In the present study, the author placed these needles with different nitrogen concentrations on different topographic positions. Therefore the effects of nitrogen concentration of litter and topographic positions can be evaluated excluding the effects of species.

METHODS

Study site

The study was carried out in a *P. thunbergii* plantation on Mt. Tanakami, Shiga Prefecture, Japan. In this area, the bedrock was granite which has been weathered deeply. The soil was sandy. The mean annual temperature was 12.4°C and annual precipitation was 1411 mm during the years between 1976 and 1980 (Iwatsubo *et al.* 1982). A study plot of 64 m x 40 m was set up in a *P. thunbergii* plantation which had been established in 1971 (34°55' N, 135°58'E, 420 m above sea level). The direction of the plot was S55°E. The plot covered a steep ridge and an underground stream. Details of the study plot have been reported in the previous chapters.

Litter bag methods

Decomposition processes of pine needle litter were studied using the nylon mesh bag technique. Needle litter of *P. thunbergii* tree were collected in 94 litter traps as described in Chapter 3. Nitrogen concentration of needle litter in each litter trap was measured (Chapter 4). Needle litters in some litter traps were combined for preparing three types of samples with different nitrogen concentrations (type L, type M and type H). Initial nitrogen concentrations of type L, M and H were 0.40 ± 0.02%, 0.61 ± 0.03% and 0.80 ± 0.05% (mean ± 1 SD), respectively. Five grams of air dried needle litters were placed into litter bags (each 15 cm X 15 cm in area with mesh size 3 mm).

The three types of litter bags were placed at lower and upper slope positions in the plot. At each slope position, 10 sampling plots of 1 m X 1 m were established to contain 10 litter bags of each type. After the removal of newly fallen litter, the litter bags were fastened to the forest floor by metal pins to prevent and to ensure a good contact between litter bags and the organic layers.

Litter bags were collected every 3 months from March 1992 to February 1993. On each sampling occasion, 10 litter bags of each type and position were collected (i.e. one litter bag of each type was collected from each sampling plot).

Laboratory analysis

Samples of initial and decomposing needles were milled, and prepared for chemical analysis. Subsamples of needles were oven-dried at 105°C and weighed to obtain dry weight ratios. Total carbon and nitrogen contents were determined using a CN analyzer (Yanaco MT-600).

The decomposition rate of needle litter was estimated using the exponential decay model of Olson (1963):

$$DM / DM_0 = \exp(-kt)$$

where k is the decay constant, t is the month, DM_0 = original mass of dry matter, DM = mass of dry matter after given period.

Statistical analysis

Analysis of variance (SYSTAT 1992) was used to determine differences among mean values in each microsite type. The Tukey's HSD (Honestly significant difference) test was used for multiple comparisons.

RESULTS

Changes in litter weights and water content

About 60% of the original mass remained at the end of the experiment (Fig. 5. 1). The decomposition rate of litter was always higher at lower slope position (Fig. 5. 2 and Table 5. 1). The differences in remaining weight between the slope position increased with exposed time, and the differences were significant after 9 months, though the difference for type L was not significant.

In the first 3 months there were no significant differences in decomposition rates among the needle types (Fig. 5. 2). At 6 month, the remaining weight of type L was larger than those of the others at both upper and lower slope positions (*P* < 0.05). After 9 months, there were no significant differences in remaining weight among the needle types.

Water content of litter was always significantly larger at lower slope position (*P*
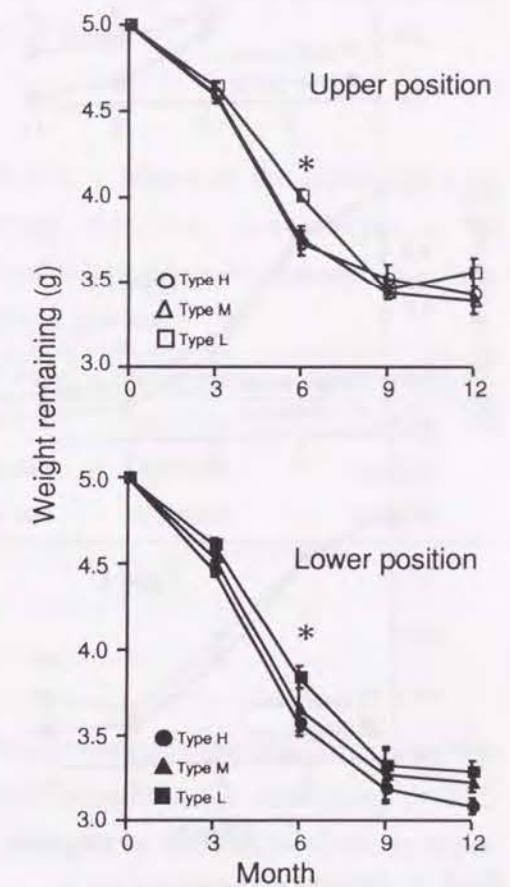

Fig. 5. 1. Changes in weight of *Pinus thunbergii* needles enclosed in litter bags (mean ± 1 SE). * Significant differences between the sample type at *P* < 0.05 (Tukey's HSD test).

Table 5. 1.   Decomposition rates for *Pinus thunbergii* needle

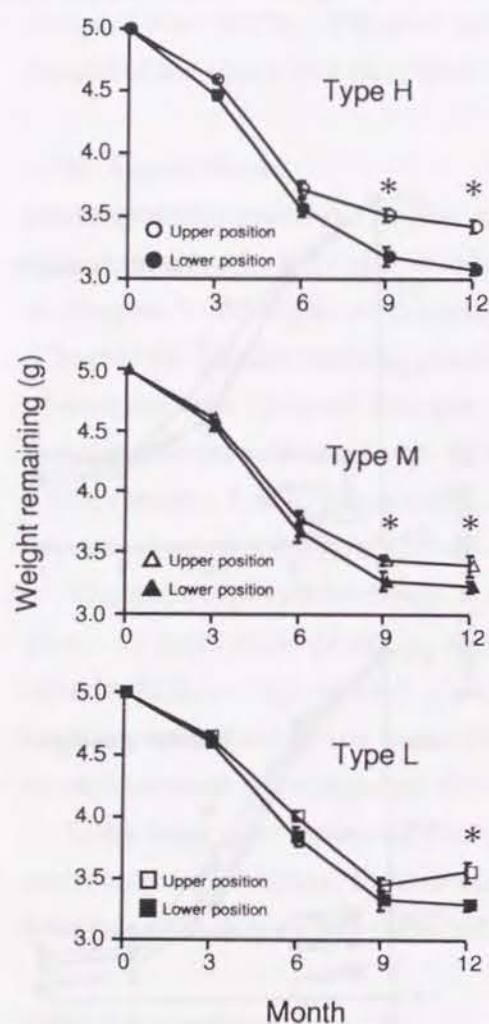| During	Lower position			Upper position		
	Type L	Type M	Type H	Type L	Type M	Type H
0 - 3 months	0.027	0.032	0.037	0.024	0.028	0.029
3 - 6 months	0.060	0.072	0.075	0.049	0.067	0.069
6 - 9 months	0.048	0.038	0.039	0.050	0.030	0.030
9 -12 months	0.004	0.005	0.011	0.001	0.005	0.005

Fig. 5. 2. Changes in weight of *Pinus thunbergii* needles enclosed in litter bags (mean ± 1 SE). * Significant differences between the slope position at $P < 0.05$ (Tukey's HSD test).

< 0.05, Fig. 5. 3). There were no significant differences in water content among the needle types.
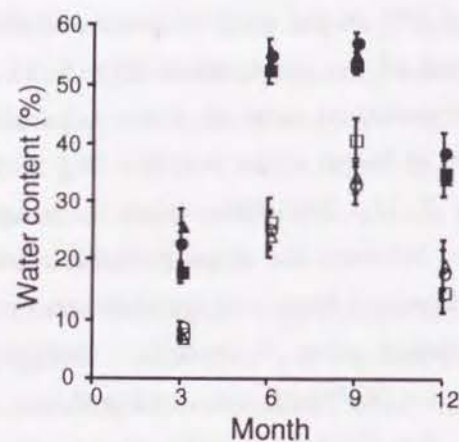

Fig. 5. 3. Changes in water content of *Pinus thunbergii* needle litter (mean ± 1 SE). See Fig. 5. 1 and Fig. 5. 2 for symbols.

Changes in nitrogen concentration

Changes in nitrogen concentration during decomposition was related to accumulated litter mass loss (Fig. 5. 4 and Table 5. 2). Nitrogen concentration increased linearly
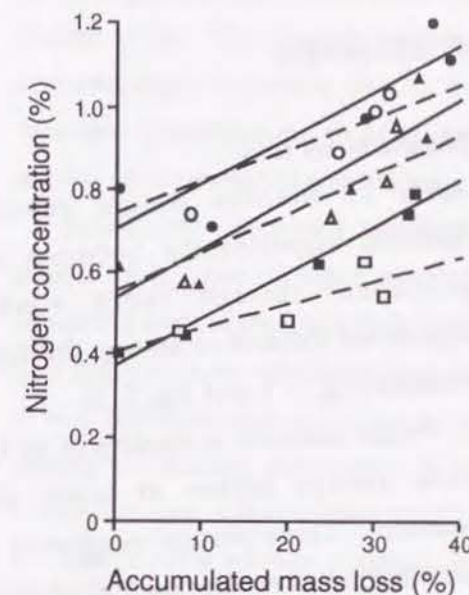

Fig. 5. 4. Changes in nitrogen concentration in relation to accumulated litter mass loss for Pinus thunbergii needle litter. See Fig. 5. 1 and Fig. 5.2 for symbols.

with accumulated mass loss in all types of needle at both slope positions. To compare relative rates of concentration increases the author used the slope coefficient. High coefficient values reflect high increase rates and vice versa. The slopes of the regression lines for all types of needle were larger at upper slope position ($P < 0.05$). The slopes of the regression lines relating nitrogen concentration to accumulated mass loss did not differ significantly among the three types of needle.

Table 5. 2   Slopes of the regression lines relating nitrogen concentrations to accumulated mass loss for decomposing *Pinus thunbergii* needles.

Needle type	Lower position	Upper position
Type L	0.01119	0.00060
Type M	0.01204	0.00095
Type H	0.01094	0.00077

Changes in nitrogen mass

Remaining nitrogen in needle of type H and type M decreased in the first 3 months (Fig. 5. 5). Remaining nitrogen of type L slightly increased throughout the observation period. After 3 months, the differences in the remaining nitrogen of needles in all three types were decreasing as compared to the initial values. However, after 3 months, in the upper slope position, the remaining nitrogen was almost constant. At lower position, the remaining nitrogen increased gradually. The differences in remaining nitrogen of needles among the three types did not change greatly at both upper and lower slope
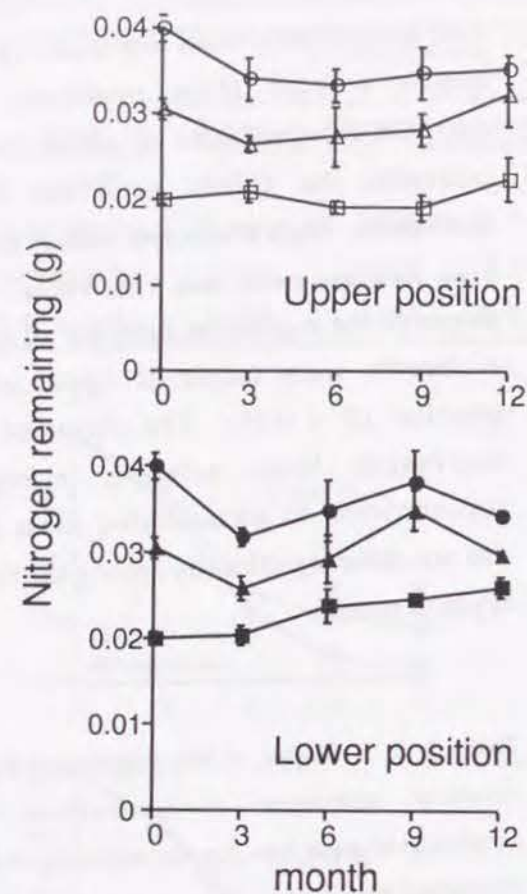
Fig. 5. 5. Changes in amounts of nitrogen in *Pinus thunbergii* needle litter (mean ± 1 SE). See Fig. 5. 1 and Fig. 5. 2 for symbols.

positions after 3 months.

DISCUSSION

Needle mass loss

After 12 months weight remaining differed significantly between slope positions, though there were no significant difference among the type of needles (Fig. 5. 1 and Fig. 5. 2).

Water contents in needles of all types were always higher at lower slope position. These results suggested that contribution of environmental conditions to the decomposition rates was larger than that of litter chemical composition.

Berg & Staaf (1980) proposed a two-phase decomposition model in which the former phase was regulated by the litter nutrient concentrations and the latter phase by the lignin concentration. In the later stage, the decomposition rates were inversely related to nutrient concentration (Berg & Ekbohm1991). In the present study, the decomposition rate of needle with higher nitrogen concentrations were faster than those with lower nitrogen concentrations during 3 - 6 month period (Table 5. 1). On the other hand, the decomposition rate of needle with higher nitrogen concentrations were slower than those with lower nitrogen concentrations during 6 - 9 month period. These results supported the model of Berg & Staaf (1980), and agreed with Berg & Ekbohm (1991).

Nitrogen dynamics

Nitrogen concentrations of needle litter increased linearly with the accumulated mass loss. The slope for nitrogen increase was steeper at lower slope position (Fig. 5. 4). Nitrogen mineralization rate at lower slope positions was higher than that at upper positions in this plot (Chapter 2). These results indicated that decomposing microorganisms uptake available nitrogen at higher rate at lower slope positions (Berg & Tamm 1994). The slope for nitrogen increase did not differ regardless of the nitrogen concentration in needle (Fig. 5. 5 and 5. 4). These results suggested that increase in nitrogen concentration in litter was not affected by the substrate but by the biotic and abiotic environmental conditions.

Remaining nitrogen in needle decreased in the first 3 months, though the nitrogen in needle with lower nitrogen concentration increased slightly (Fig. 5. 5). The nitrogen loss of needle with higher nitrogen was larger than those with lower nitrogen concentration. The nitrogen loss was thought to be caused by leaching of easily soluble materials. The lower nitrogen concentration of needle litter was achieved by higher proportion of resorption during senescence (Chapter 4). Easily soluble nitrogen in the needle with lower nitrogen concentration might had been resorbed during senescence.

The smaller release of nitrogen from the needle with lower nitrogen concentration could feedback through the lower nitrogen availability in soil to lower nitrogen concentration in litter.

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General Discussion

In this chapter, 1) the patterns of soil properties and stand structure along a topographic gradient, and 2) the topographic variations in interactions between plants and the soil will be discussed in view of the results presented in the preceding chapters. Figure 6. 1 and Table 6.1 show the differences in nutrient cycling caused by the variations in the interactions between plants and the soil along a slope.
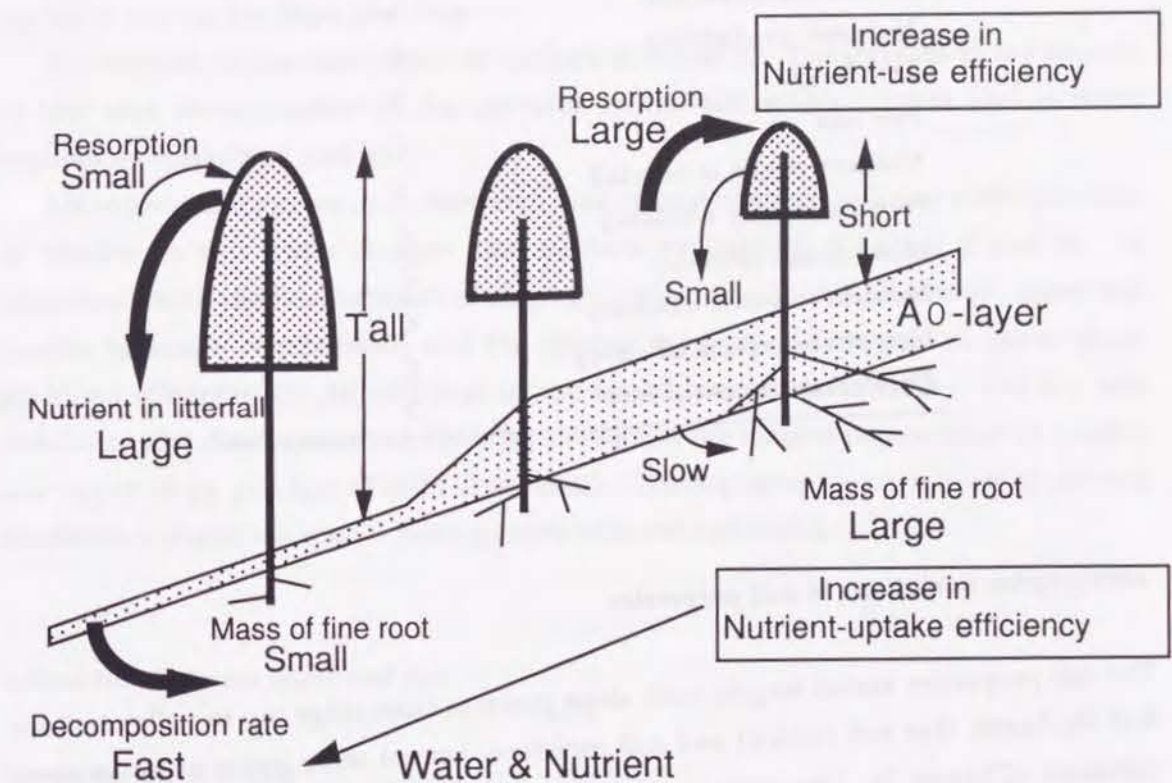

Fig. 6. 1. Nutrient cycling and nutrient use of plants along a slope. Some of nutrient flows are indicated by arrows.

Table 6.1 Comparison of nutrient cycling and nutrient use of
plants in a *Pinus thunbergii* plantation along a slope.

	Slope position	
	Lower	Upper
Soil depth	>	
Fine soil content	>	
Moisture content in soil	>	
Carbon in forest floor	<	
Carbon in mineral soil	>	
Nutrient availability	>	
Tree height	>	
Fine root	<	
Nutrient return in litterfall	>	
Nutrient-uptake efficiency	<	
Nutrient-use efficiency	<	
Nutrient-response efficiency	<	
Nutrient resorption efficiency	<	
Decomposition rate of litter	>	

Topographic variations in soil properties

The soil properties varied largely with slope position from ridge top to valley bottom.
Soil thickness, fine soil content and soil moisture content were larger at lower slope
positions (Chapter 2). The patterns observed were thought to be caused by water and
material movement from upper to lower position. The influence of topography on the
movement of water and soil can influence or control the type and intensity of soil
processes (Huggett 1975; Pennock *et al*. 1994). The amount of accumulated carbon in
the forest floor increased upslope, while the amount of accumulated carbon in
mineral soil layer decreased upslope. The nutrient availability in the soil decreased
upslope for nitrogen and phosphorus (Chapter 3).

   At upper slope positions, downslope runoff and lateral flows of water within the
soil, led to water deficiency. As a consequence of lower water content in the soil, the

lower decomposition rate of organic matter (Chapter 5) and lower nutrient availability
occurred at upper slope positions.

Topographic variations in stand structure

The mean stem diameter, height and volume of *P. thunbergii* increased downslope with
decreasing tree density (Chapter 2). The changes in the aboveground structure of *P.
thunbergii* along the slope followed the 3/2 power law of self-thinning (Yoda *et al.* 1963),
suggesting that development pattern of aboveground stand structure of *P. thunbergii* did
not differ among the slope positions.

   The amount of fine root increased upslope (Chapter 2). The increase in the amount
of fine root corresponded to the decrease in the soil water content and nutrient
availability (Chapter 2 and 3).

   Aboveground structure of *P. thunbergii* was more developed at lower slope positions
in relation to soil water content and nutrient availability (Chapter 2 and 3). In
accordance with the development of aboveground structure of *P. thunbergii*, many tree
species naturally regenerated, and the species diversity was higher at lower slope
positions (Chapter 2). In addition to the lower nutrient availability, the dry soil
conditions and development of FH-layer prevented the natural regeneration at middle
and upper slope position (Tobita *et al*. 1993). The topographic variations of the soil
properties induced the spatial heterogeneity in forest succession.

Interaction between plant and soil

Morphological plasticity
Aboveground biomass of *P. thunbergii* decreased upslope, while the amount of fine root
increased upslope with the decrease in soil water content and nutrient availability
(Chapter 2 and 3). The inverse relationship between fine root biomass and aboveground
biomass indicated that root/shoot ratio of *P. thunbergii* was modified in response to a
topographical gradient of water and nutrient availability. At upper slope positions in
which water and nutrient availabilities were lower, *P. thunbergii* had higher root/shoot
ratio to acquire more water and nutrient. Gross allocation to below-ground, however, is
not known in this study, and few studies have been conducted on gross allocation of

production to below-ground in forests (Keyes & Grier 1981; Santantonio & Hermann 1985; Cameau & Kimmins 1989). Further investigation of below-ground including root turnover and mycorrhizal colonization is needed.

Effect of plant morphological response on soil

The responses of plants to heterogeneous soil environments have important consequences for community structure (Tilman 1988). In this study, the morphological plasticity of *P. thunbergii* in response to environmental heterogeneity along the slope was observed. The trade-off in allocation of captured resources between above- and below-ground caused the variation of forest structure along the slope. Aboveground structure of *P. thunbergii* was more developed and many tree species naturally regenerated at lower slope positions. The regeneration of other broad-leaved species has also important implications for decomposition processes. The leaves of broad-leaved species were more easily decomposable than those of pine trees (Berg & Staaf 1980). The higher decomposition rate of litter could feedback into the higher nutrient availability (Pastor *et al.* 1984; Shaver & Melillo 1984).

Physiological plasticity

To evaluate the response of *P. thunbergii* to the nutrient gradient, nutrient-response efficiency (production per unit nutrient availability), nutrient-uptake efficiency (nutrient uptake per unit nutrient availability), and nutrient-use efficiency (production per unit nutrient uptake) were examined along the topographical gradient of nutrient availability (Bridgham *et al.* 1995. Chapter 3).

All three efficiencies increased upslope with decreasing soil nutrient availability. The increase in nutrient-response efficiency was achieved by both increases in nutrient-uptake and nutrient-use efficiencies. At lower levels of nutrient availability, *P. thunbergii* increased litterfall production per unit nutrient availability by increasing in both the ability to acquire nutrients and ability to use them in growth once acquired.

The increase in nutrient-uptake efficiency is thought to be achieved by the increase in fine root biomass and nutrient uptake per unit root mass (Chapin 1980). In the present study, the increase in fine root biomass contributed to the increase in nutrient-uptake efficiency of *P. thunbergii*, though it is not shown whether nutrient uptake per unit root mass decreases as the nutrient availability decreases (Chapin 1980; Gray & Schlesinger 1983).

The increase in nutrient-use efficiency of litter production in low nutrient sites is

deduced to be partly due to greater biomass production per unit of nutrient (low nutrient concentration in tissue) in nutrient poor sites and partly due to more effective resorption of nutrient from senescing leaf in such sites (Vitousek 1982, 1984). In the present study, the increase in nutrient-use efficiency of *P. thunbergii* was achieved by the increase in nutrient resorption efficiency (Chapter 4). The contribution of greater needle production per unit nutrient to higher nutrient-use efficiency was small.

In previous studies, though the relationships between resorption efficiency and some factors that could control nutrient resorption such as plant nutrient status (Chapin & Kedrowski 1983, Lajtha 1987) and needle mass (Helmisaari 1992) were examined, consistent results were absent. In this study, the nutrient resorption efficiency was not controlled by the nutrient status in green needle. Nutrients were resorbed from needles following the resorption of mobile carbohydrate. The nutrient resorption efficiency could be facilitated by the increase in dry mass of green needle per unit length (containing a greater portion of carbohydrates) in response to low nutrient availability.

Effect of plant physiological response on soil

The response of plant to nutrient availability along the slope position may exert important ecosystem processes. Nutrient uptake by plants plays an important role in promoting tight nutrient cycling (Borman *et al.* 1977). Nutrient-uptake efficiency was higher at upper slope positions with lower nutrient availability. Increase in nutrient-uptake efficiency can increase the proportion of available nutrient acquired by plant within an ecosystem. Then nutrient losses from an ecosystem would decrease.

The nutrient use-efficiency of plants increase upslope. High nutrient-use efficiency under low nutrient availability drives infertile systems toward even greater nutrient deficiency (Shaver & Melillo 1984), because low litter nutrient content reduces decomposition rate and subsequent release of available nutrient (Gosz *et al.* 1973; Melillo *et al.* 1982 ; Gholz *et al.* 1985). These positive feedback loop leads to tight nutrient cycle system which holds nutrient in the forest floor and decreases the loss of nutrients from ecosystem to outside (Millar *et al.* 1979).

To test the positive feedback loop, the effects of initial nitrogen concentration of litter on the decomposition process were examined (Chapter 5). The decomposition rate of needle litter over 12 months did not differ regardless of the initial nitrogen concentration in needle, though the decomposition process differed. However, about 60% of the original mass remained at the end of the experiment. The effects of initial nitrogen concentration on the decomposition process in later stage was unknown. The

influence of litter quality such as lignin and cellulose on the process of the concomitant mineralization and humus formation in FH-layer should be studied.

The nitrogen release from needle with higher nitrogen concentration was larger than those with lower nitrogen concentration in the first 3 months. The smaller release of nitrogen from the needle with lower nitrogen concentration led to the lower nitrogen availability. The lower nitrogen concentration of needle litter was achieved by higher proportion of resorption during senescence. These results suggested that the higher nutrient resorption efficiency could feedback to the lower nutrient availability.

The downslope movement of water and materials along a slope caused the topographic variations in the soil properties and nutrient availability. In response to the variable environmental condition, plants alter their resource use in morphological and physiological ways. These responses of plants feedback to the environmental conditions. The differences in the interaction between plant and soil along a topographic gradient made the topographic variations of nutrient cycling in a forest ecosystem.

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SUMMARY

Chapter 1

Forest ecosystem is a result of interactions between plants and soil. Topography plays
an important role in constituting the spatial variation in the forest ecosystem. In this
study, focusing on the interactions between plants and soil, the topographic variations
in stand structure and nutrient cycling were revealed in a *Pinus thunbergii* Parl.
plantation on Mt. Tanakami, Shiga, Japan.

Chapter 2

Soil properties and above- and belowground forest structure were examined. The soil
properties and stand structure varied greatly with slope position from ridge top to
valley floor. Soil thickness, fine soil content and soil moisture content were greater in
lower slope positions. The amount of organic carbon in the forest floor was greater in
upper slope positions. The organic carbon content in the mineral soil was slightly
greater in lower slope positions. These changes in soil properties suggested an upslope
decrease in decomposition rate and water and/or nutrient availability. The
aboveground structure of *P. thunbergii* was more developed at lower slope positions.
The mean stem diameter, height and volume of *P. thunbergii* increased downslope with
decreasing tree density. However, fine root biomass increased greatly upslope. This
inverse relationship between tree height and fine root biomass indicated morphological
plasticity of *P. thunbergii* in exploiting environmental heterogeneity. Variations in
soil-plant interactions in the stand along various topographies caused spatial
heterogeneity in the accumulation pattern of organic matter in plants and the soil.

Chapter 3

To examine responses of plants to nutrient availability, the author investigated changes
in soil nutrient availability, litterfall production and nutrient content in litterfall along a
topographic gradient in a *Pinus thunbergii* Parl. plantation. Responses were evaluated in
terms of three efficiency indices: (1) nutrient-uptake efficiency (the ratio of nutrient
return in litterfall / soil nutrient availability); (2) nutrient-use efficiency (the mass /
nutrient return ratio of litterfall); (3) nutrient-response efficiency (the ratio of litterfall

mass / soil nutrient availability). These indices can distinguish the ability of a species to acquire nutrients and its ability to use them in litterfall production. Nitrogen and phosphorus availabilities in soil were lower at upper slope positions. The three efficiencies were higher at upper slope positions and negatively correlated with soil nutrient availability for both nitrogen and phosphorus. The increase in nutrient-response efficiency was achieved by both increases in nutrient-uptake and nutrient-use efficiencies.

Chapter 4

Nitrogen and phosphorus resorption from needles of *Pinus thunbergii* Parl. trees planted on four different slope positions (LS; lower slope, MS; middle slope, US; upper slope and RG; ridge) were examined in relation to soil nutrient availability. Nitrogen concentration in green needle was greater at LS. Phosphorus concentration in green needle did not differ between the slope positions. Both nitrogen and phosphorus concentrations in senescent needle decreased from lower to upper slope positions. Nutrient resorption efficiencies (resorbed nutrient / nutrient content in green needle) increased from lower to upper slope position (42.6 - 76.5% for nitrogen and 27.8 - 72.1% for phosphorus) with decreasing soil nutrient availability. Nutrient resorption efficiency was found to be related to the needle dry mass per unit length. There was no clear correlation between nutrient resorption efficiency and the nutrient content in green needle.

Chapter 5

To test the feedbacks between litter quality and nutrient availability, the effects of initial nitrogen concentration of litter on the decomposition process were examined by an experimental study using litterbags. After 12 months, weight remaining of litter was smaller at the lower slope position, while the weight remaining of litter did not differ regardless of the initial nitrogen concentration in litter. Water contents in litter were always higher at lower slope position. The decomposition process was different according to the the type of litter. At the 6th month, the remaining weight of lower nitrogen litter was larger than those of the others. After 9 months, there were no significant differences in remaining weight among the needle types. Nitrogen concentration increased linearly with accumulated mass loss. The increase in nitrogen

concentration and decrease in remaining weight was greater at lower slope position. The increase in nitrogen concentration in litter did not differ regardless of the initial nitrogen concentration in litter. The nitrogen release from litter with higher nitrogen concentration was larger than those with lower nitrogen concentration.

Chapter 6

The topographic variations in the soil properties, stand structure, and interactions between plants and soil were discussed on the basis of the preceding chapters. The downslope movement of water and materials along a slope caused the topographic variations in the soil properties and nutrient availability. In response to the variable environment, plants alter their resource use in morphological and physiological ways. These responses of plants feedback to the environmental conditions. The differences in the interaction between plants and the soil along a topographic gradient made the topographic variations of nutrient cycling in a forest ecosystem.