J For Res (2003) 8:247–252
DOI 10.1007/s10310-003-0033-3

ORIGINAL ARTICLE

Hiromi Tanabe · Takashi Nakano · Manami Mimura
Yoshiko Abe · Shigeru Mariko

Biomass and net primary production of a *Pinus densiflora* forest established on a lava flow of Mt. Fuji in central Japan

Received: April 13, 2002 / Accepted: March 7, 2003

Abstract We assessed the above- and below-ground biomass and net primary production (NPP) in a mature (85-year-old) *Pinus densiflora* forest established on a lava surface of Mt. Fuji in central Japan. The nitrogen (N) concentration of the forest soil was low (1.25%), and the mean soil carbon/nitrogen (C/N) ratio was 34.2; therefore, both plants and microorganisms would compete for N in our research forest. The total biomass was 192.62 Mg ha^{-1}, of which 67.28% was in the stems and 25.71% was in the roots. The fine-root biomass was 1.12% of the total biomass. The total NPP of the forest reached 11.89 Mg ha^{-1} year^{-1}, which fell within the values reported for other cool temperate *P. densiflora* forests established on non-volcanic-related substrata. The below-ground production was about 39% of the total NPP; the value was relatively small under the conditions of low total N concentration and high soil C/N ratio. Our study suggested that *P. densiflora* could recruit and grow on geologically new substrata without increasing the allocation of its annual carbon budget to below-ground organs (i.e., roots).

Key words Japanese red pine · Lava surface · Nitrogen-poor stand · C/N ratio

Introduction

The amounts of nutrients, particularly nitrogen (N), that are available in the soil, affect the biomass allocation and total primary production of plants, and forest growth is generally limited under nutrient-poor conditions (Gower et al. 1992). When the N supply is limited, the annual carbon investment in fine roots increases, and consequently the growth of above-ground parts decreases (Keyes and Grier 1981). In contrast, N fertilization has been shown to increase the total foliage mass and leaf area at the stand level (Gower et al. 1992).

Under soils formed on new substrata, such as a tephra layer, lava, or bare ground that developed after volcanic eruptions or a glacial recession, trees generally suffer from low N availability (Vitousek et al. 1989). N and phosphorus are both important for plant growth; N is the factor limiting production at an early stage in soil development, while low phosphorus is the factor limiting production at a later stage (Vitousek et al. 1993). Forest tree species can recruit on these new substrata only after N-fixing plants have increased available N. For example, Bormann and Sidle (1990) reported that soil N increased rapidly after glacial recession when a nitrogen-fixing shrub (*Alnus sinuata*) dominated, leading to the establishment of spruce trees (*Picea sitchensis*).

Pine species, however, can grow even on new substrata and occupy sites in the early stages of primary succession. The ability of pines to become established on N-poor sites may be determined by N_2 fixation in the rhizosphere of pine trees (Bormann et al. 1993). However, other studies have found very low levels of non-symbiotic N_2 fixation in pines (Hendrickson 1990; Limmer and Drake 1996; Barkmann and Schwinter 1998), and they have concluded that the regeneration success of pines in N-deficient soils was not attributable to N_2 fixation. Thus, it is still unclear how pines can regenerate on geologically new substrata.

Pinus densiflora Sieb. et Zucc. is widespread in Japan and can occupy sites consisting of new substrata in the early stages of primary succession. Previous studies of *P.*

H. Tanabe (✉)
Department of Primary Education, Tsuru University, 3-8-1 Tahara, Tsuru 402-0054, Japan
Tel. +81-554-43-4341 (ext 617); Fax +81-554-43-4347
e-mail: htanabe@mbd.nifty.com

T. Nakano · M. Mimura[1] · Y. Abe · S. Mariko[2]
Yamanashi Institute of Environmental Sciences, Fujiyoshida, Japan

Present addresses:
[1] Nakakoma-gun, Yamanashi, Japan
[2] Institute of Biological Sciences, University of Tsukuba, Tsukuba, Japan

densiflora have dealt mostly with the biomass and productivity of above-ground parts (Hachiya et al. 1989) or of forests established on non-volcanic-related substrata (Karizumi 1974). The variation in nutrient status can explain the variation in both root net primary production (NPP) and total biomass, although root NPP does not solely correlate with nutrient availability for many pine species (Vogt et al. 1996). Information on biomass and productivity of below-ground parts of forests established on volcanic surfaces is needed to understand the mechanisms of the establishment and growth of pine on new substrata. In the present study, we quantified the above- and below-ground biomass and the NPP in relation to the soil N condition of a mature *P. densiflora* forest established on a volcanic surface (i.e., lava flow) of Mt. Fuji. We also compared the biomass allocation and ecosystem productivity of the *P. densiflora* forest with those of other cool temperate *P. densiflora* forests established on non-volcanic-related substrata.

Methods

Study site

The study was carried out in a cool temperate *P. densiflora* forest (85 years old) on the north-facing slope (35°27′N, 138°45′E; 1043 m above sea level) of Mt. Fuji in Yamanashi Prefecture, located about 5 km south of Fujiyoshida City, central Japan. The study site was located on a lava flow called Kenmarubi, approximately 650–1500 m in width. The flow occurred at 890 ± 90 y.B.P. (Gak-633) (Miyaji 1988). The bedrock is basalt (Miyaji 1988). The pine forest was established without any human management. No charcoal was observed within the soil profile, suggesting that the forest developed without fire disturbances. According to a 90-year-old local resident (K. Kobayashi, personal communication), the study site was wasteland before the establishment of the forest. This information indicates that the forest is younger than 90 years. Organic soils have not yet developed; only a little humus (about 20 cm in depth) has accumulated in the solidified lava.

The mean annual air temperature is 10.1°C, and the mean annual precipitation is 1436 mm based on the records collected from 1961 to 1990 at Kawaguchiko Meteorological Station. Precipitation is concentrated in the summer season. Several typhoons approach this area almost every year, and some standing dead trees and living trees are knocked down by strong winds.

A 30-ha plot was established in 1993 within the pine forest, and a census of canopy tree species was made. The tree layer was dominated by *P. densiflora* (98.1% of the total basal area), followed by *Larix kaempferi* (Lamb.) Carriere (0.8%). In 1998, a 20 × 20 m plot was established within the 30-ha plot. Species, heights and diameters at 1.3 m above ground ($D_{1.3}$) of all trees ($D_{1.3} > 1$ cm) and subtree and shrub layers in the plot were recorded (Table 1). *Ilex pedunculosa* Miq. dominated in the sub-tree layer. "N-fixing plants", such as legumes and alder species, were not observed. The ages of these pine trees, determined from annual rings of nine sample trees (described below) at 30 cm above-ground, ranged from 65 to 83 years in 1998. The tree density of *P. densiflora* in this plot was 927 trees ha^{-1} as measured in early 1999 (825 trees per 0.89 ha^{-1}; Toshiyuki Ohtsuka, Yamanashi Institute of Environmental Sciences, Japan, unpublished data).

Table 1. Stand characteristics of the study site. Values are averaged over trees ($D_{1.3} > 1$ cm) within a 20 × 20 m plot

Species	Mean $D_{1.3}$ (cm)	Mean height (m)	Basal area	
			(m^2 ha^{-1})	(%)
Pinus densiflora	23.6	18.5	47.0	82.0
Ilex pedunculosa	5.5	6.1	4.2	7.3
Quercus crispula	5.8	6.6	1.3	2.2
Lyonia ovalifolia var. *elliptica*	3.9	5.2	1.3	2.2
Pieris japonica	3.8	3.6	1.1	1.8
Prunus jamasakura	8.6	10.5	0.5	0.8
Betula platyphylla var. *japonica*	14.7	11.5	0.4	0.7
Vaccinium oldhamii	2.6	3.6	0.4	0.7
Clethra barbinervis	4.3	6.1	0.4	0.7
Sorbus alnifolia	4.0	5.6	0.2	0.3
Juniperus rigida	8.1	8.8	0.1	0.2
Euonymus macropterus	2.8	5.6	0.1	0.2
Ilex macropoda	4.9	5.4	0.1	0.2
Tilia japonica	3.2	4.6	0.1	0.1
Abelia spathulata	1.6	2.8	0.1	0.1
Fraxinus lanuginosa	2.5	4.3	0.1	0.1
Hydrangea paniculata	3.0	3.9	0.1	0.1
Euonymus alatus	2.6	3.0	0.0	0.0
Corylus sieboldiana	1.7	1.7	0.0	0.0
Total	5.6	6.2	57.3	100.0

$D_{1.3}$ is the stem diameter at breast height (1.3 m above the ground)
Latin names follow Satake et al., (1989a, 1989b)

Soil and fine-root sampling

A 2.5 × 5 m rectangular quadrate was established at each of two separate sites in the 30-ha plot. Each rectangle was further divided into two 2.5 × 2.5 m squares.

In April 2000, prior to the fine-root sampling, the percentages of N and C (dry-mass base) of the soil samples were analyzed. Soil samples were taken from the same four 2.5 × 2.5 m quadrats that were used for fine-root analysis. Soil samples were air-dried and sieved through a 2-mm mesh sieve. Samples were oven-dried at 70°C for 7 days, weighed, and chemically analyzed using an NC analyzer (Sumigraph NC-900; Sumika, Tokyo, Japan).

In every month from May 2000 to May 2001, except February and March 2001 because of snow accumulation, after removal of the litter layer, soils (containing roots) were collected from one 15 × 15 cm square within each of the four larger (i.e., 2.5 × 2.5 m) squares; thus, four replicates were collected for each sampling time. Soil sampling positions were at least 50 cm apart from each other. Whole soil was sampled from the surface to the lava layer. When we excavated coarse roots, we confirmed that the fine roots were mostly concentrated above the lava layer (about 5–30 cm in depth). Soil samples were stored in a refrigerator until they were analyzed. Fine roots ($\leq$5 mm) were sorted into live and dead roots using forceps within 5 days after sampling and were oven-dried at 70°C for 7 days for measurement of dry mass.

Destructive sampling

Nine *P. densiflora* trees blown down by strong winds in 1998 and 1999 were chosen inside the 30-ha plot to estimate the allometric relationships between $D_{1.3}$ and biomass of each component. Their $D_{1.3}$ values ranged from 10.0 to 34.4 cm, with an average of 21.9 cm. The fresh masses of aboveground living components (stems, branches, and leaves) and coarse roots (>5 mm in diameter) of these sample trees were weighed separately in the field. The coarse roots were excavated carefully by hand and winch with minimal loss of fractions. The dry mass of each component was calculated using the corresponding dry/fresh mass ratio that was obtained from an oven-dried (70°C) sample. The allometric relationship between the $D_{1.3}$ and dry mass of each component was derived by the least-squares regression method.

From the *P. densiflora* sample trees, stem disks were taken at 1.3 m in height. Wood diameters of each sample tree in 1993 and 1996, were determined by measuring the outer diameters of the annual rings of these years. Bark thickness in these years was calculated by the assumption that the bark width proportionally increases year by year. $D_{1.3}$ was assumed to be the sum of the wood diameter and the bark thickness in these years.

Estimation of biomass

The forest biomass of each component was calculated by multiplying the mean biomass of that component in an individual *P. densiflora* tree by the tree density of *P. densiflora*. We have original census data from 1998 but not from 1996. To unify the calculation method of forest biomass with data from 1996 and 1998, we did not apply the classical allometry method by using each diameter-weight regression for the original census data directly. The biomass of each component (stems, branches, leaves and coarse roots) of the sample trees in 1997 was calculated from $D_{1.3}$ based on allometric relationships between $D_{1.3}$ and biomass. The density in 1997 was determined from aerial photographs taken just above the research forest. The center of the area was magnified 10 times and the numbers of *P. densiflora* canopies inside the four 50 × 50 m squares were counted. The densities in 1997 and 1999 were studied early in each of these years; the decrease in tree density during each winter season was ignored here.

The fine-root biomass was calculated as the mean living biomass during the period from May 2000 to May 2001 (four replicates × 11 sampling times). In April 2001, we collected additional soil samples outside each of the four square quadrates to test microsite differences in fine-root biomass.

Litterfall

Litterfall was collected monthly over a 570-day period from September 1, 1998, to March 23, 2000, using 0.64 m^2 frame traps ($n = 9$) placed within the 20 × 20 m plot. The collections were sorted into four fractions (leaf, twig, bark, and cones) by species, and masses were determined after drying at 70°C.

Estimation of net primary production

NPP was estimated by summing the annual biomass increment and detritus production (litterfall) according to the summation method (Kira and Shidei 1967). The loss of dry matter by grazing was ignored. We defined NPP as a half of the increment of woody parts (stem, branch, and coarse root) between 1996 and 1998.

Fine root production (P) was calculated according to the method of McClaugherty et al. (1982). In this method, $P = \Sigma Pi$ where i is the month and Pi is the monthly change in both live and dead fine-root biomass (ΔL and ΔD, respectively), subject to the following rules: when both ΔL and ΔD are positive, $Pi = \Delta L + \Delta D$; when ΔL is positive and ΔD is negative, $Pi = \Delta L$; when ΔL is negative, $Pi = 0$.

Results

Soil characteristics

Soil properties of the study forest are shown in Table 2. The soil total N% averaged 1.25%, ranging from 1.15% to 1.40%, and the total C% averaged 42.61%, ranging from 37.18% to 47.01%. Soil depth averaged about 20 cm, ranging from 7.5 to 29.0 cm.

Biomass and NPP

Prior to the biomass estimation, the variances of the $D_{1.3}$s of the sample trees in 1993 were compared with those of all the *P. densiflora* trees within the 30-ha plot (2 cm min, 54 cm max, and 20.07 cm mean) by the *F*-test. The variances of $D_{1.3}$s of the sample trees (42.634) and whole trees (38.462) within the plot were not significantly different ($P = 0.3536$), indicating that the sampled trees were representative of the whole stand. The dry mass of each component was positively correlated with $D_{1.3}$ for the *P. densiflora* sample trees (Fig. 1). The values of the coefficient of determination (r^2) in these regressions ranged from 0.72 to 0.97. The density of *P. densiflora* of the study forest in 1997 was 936 trees ha^{-1}.

The total biomass (above- and below-ground) of the *P. densiflora* forest was estimated to be 192.62 Mg ha^{-1} in 1998, of which about 67% was in the stems and 25% was in the coarse roots (Table 3). The fine-root biomass was only about 1.0% of the total biomass. The variance in fine-root biomass did not differ between the samples taken inside the plot ($n = 4$) and the same samples plus four additional samples taken outside the plot ($n = 8$) ($P = 0.7072$, *F*-test), suggesting that four replicates were sufficient to evaluate fine-root biomass for each sampling time. Consequently, about 26% of the total biomass was stored as below-ground components.

Table 2. Percentage N and organic C of dry mass of soil, the C/N ratio and soil depth of a *Pinus densiflora* forest established on a lava flow of Mt.Fuji

Parameter	Mean	SD
%N	1.25	0.11
%C	42.61	4.15
C/N	34.20	3.05
Mean depth (cm)	20.38	9.34

The soils (15 × 15 cm) were sampled in April in 2000; each value was an average of four soil samples

The NPP of the *P. densiflora* forest was 11.89 Mg ha^{-1} year^{-1} (Table 3). The total NPP consisted of short-lived components (litterfall production and fine-root production, 76.96%), mainly pine-needle litter (27.64%) and fine-root production (32.32%).

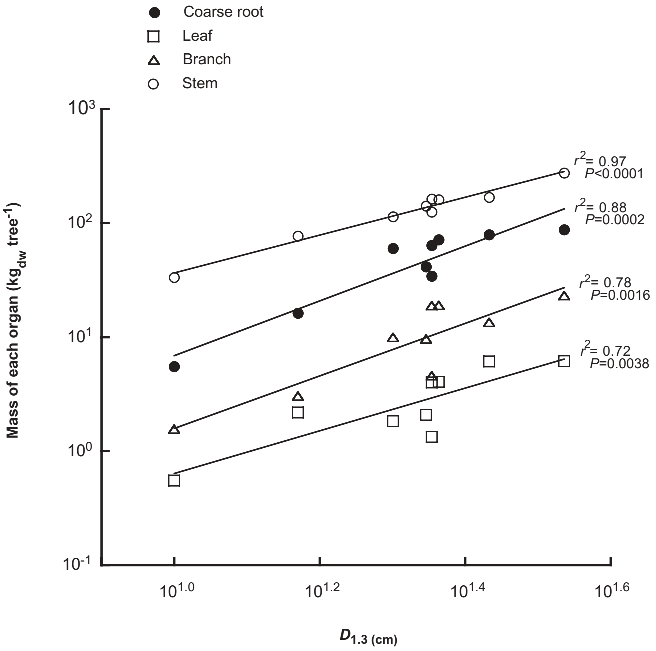

Fig. 1. Allometric relationships between the dry mass of different tree components (kg tree^{-1}) and tree diameters of *Pinus densiflora* trees growing on a lava flow of Mt. Fuji. Allometric relationships were approximated by the power-form equation, $y = ax^b$ (r^2 = square of adjusted correlation coefficient), where x is stem diameter at breast height ($D_{1.3}$). Coefficients a and b of each organ were as follows; coarse root: 0.0277, 2.3946; leaf: 0.0085, 1.8724; branch: 0.0078, 2.3023; stem: 0.8048, 11.6568. Nine sample trees of *P. densiflora* were employed for the approximation

Table 3. Above- and below-ground biomass and net primary production rates in an 85-year-old *Pinus densiflora* forest established on a lava flow of Mt.Fuji

Component	Biomass		Net production	
	(Mg ha^{-1})	(%)	(Mg ha^{-1}year^{-1})	(%)
Above-ground				
Stems	129.60	67.28	1.44	12.11
Branches	10.59	5.50	0.49	4.12
Needles	2.91	1.51		
Detritus				
P. densiflora needle			3.29	27.64
P. densiflora other[b]			2.02	17.00
Total detritus			5.31	44.64
Total above-ground	143.10	74.29	7.24	60.87
Below-ground				
Coarse roots (>5 mm)	47.36	24.59	0.81	6.81
Fine roots (≤5 mm)	2.16[a]	1.12	3.84[c]	32.32
Total below-ground	49.52	25.71	4.65	39.13
Ecosystem total	192.62	100.00	11.89	100.00

[a] Mean fine root biomass during May 2000 to May 2001
[b] Including cones, twigs and bark
[c] The data during May 2000 to May 2001 were calculated by McClaugherty et al. (1982)

Table 4. Biomass and productivity of other cool temperate *P. densiflora* forests established on mature substrata

Age (Years)	Soil type	Biomass			Biomass production		Production			BNPP/NPP (%)	Reference
		Above	Below (Mg ha^{-1})	Fine root	Below (%)	Fine root (%)	Above ANPP	Below BNPP (Mg ha^{-1} year^{-1})	Total NPP		
11	BlD(d)	66.0	16.0	1.3	19.5	1.5	19.0	5.9	24.8	23.6	
19	BlD(d)	98.6	23.5	1.4	19.3	1.1	18.4	6.0	24.4	24.6	Calculated by (Karizumi 1974)[a,b]
36	BlD(d)	124.1	29.1	1.4	19.0	0.9	14.6	4.9	19.5	25.0	
38	BlD(d)	177.0	43.4	1.0	19.7	0.5	10.0	3.5	13.5	25.7	
35	BlD(d)	104.6	27.0	1.0	20.5	0.7	7.7	3.0	10.7	27.8	
18	BA	112.1	24.8	5.7	18.1	4.1	26.8	11.4	38.2	29.9	
18	BA	67.1	16.0	2.1	19.3	2.6	17.9	6.4	24.3	26.5	
18	BA	26.7	7.5	1.1	21.9	3.3	6.7	3.6	10.3	34.5	
33	BA	91.1	21.7		19.2		13.7				Tadaki et al. (1979)

[a] Biomass and above-ground production of each plot were calculated by multiplying the mean biomass and annual growth of sample trees of the plot by the tree density

[b] Below-ground detritus production was estimated as the fine roots (≤5 mm in diameter) biomass

Discussion

We found that the total NPP of our research forest was relatively high despite the fact that the biomass and net production of the fine roots were relatively small in view of the low total soil N percentage and the high soil C/N ratio. These results are important for understanding how pine trees adapt to new substrata under N-poor conditions. It has been reported that N fertilization increases NPP of forests (Gower et al. 1994) and that carbon allocation into below-ground parts decreases with increasing soil-N availability (Haynes and Gower 1995). However, the forest in this study behaves differently from the forests studied by Gower and Haynes.

In our research forest, the soil C/N ratio was high (34.2) as a result of low total soil N. Kitayama et al. (1997) reported that the total N in topsoils in Hawaiian forests increased from 1.0% to 3.0% as the substrata age increased from 400 years to 4.1×10^6 years. The total N percentage of soil in our forest was similar to the values obtained for the four youngest sites investigated by Kitayama et al. (1997). The mean soil C/N ratio in our study was higher than the ratios in some boreal larch forests in Siberia (23.4–25.9) (Matsuura et al. 1997). The C/N ratio that is most favorable for microbial decomposition ranges between 10 and 30 (Larcher 1995). The high soil C concentration in our pine forest suggests that microbial litter decomposition was relatively slow, potentially resulting in highly immobilized N.

The productivity of our *P. densiflora* forest is comparable with the NPP values reported for other cool temperate *P. densiflora* forests established on non-volcanic-related substrata (Table 4), ranging from 10.3 to 38.2 Mg ha^{-1} year^{-1}. Because of the low N availability in our study site (Table 2), we expected that the NPP would be much lower than that of other forests. Moreover, the ratio of above-ground NPP to the total NPP in our research forest (74.29%; Table 3) lies within the range of ratios reported for *P. densiflora* forests established on non-volcanic-related substrata (65.5–76.4%; Table 4). The below-ground NPP in our study (4.65 Mg ha^{-1} year^{-1}) was similar to the values reported for these other *P. densiflora* forests, which ranged from 3.0 to 11.4 Mg ha^{-1} year^{-1} (23.6%–34.5% of total NPP; Table 4).

Allocation patterns generally shift to maximize total plant growth (Bazzaz 1997), and root proportion generally increases with decreasing N availability (Keyes and Grier 1981). The variation in nutrient status can explain the variation in both root NPP and total biomass, although root NPP does not depend solely on nutrient availability for many pine species (Vogt et al. 1996). The relatively low NPP of roots in our research forest supports this finding.

Mineral nutrients taken up by mycorrhizae appear to have a major role in the growth of *P. densiflora* trees in our forest. Many pine species require ectotrophic mycorrhizae (Schlesinger 1997), and nude *P. densiflora* lateral roots (i.e., non-associated roots with ectotrophic mycorrhizae) are rather rare under field conditions (Yamada 1996). Symbiotic mycorrhizal associations between tree roots and fungi are especially important in forests that have high soil C/N ratios because the fungi produce enzymes that enable nutrients, such as N, to be recycled from plant litter without mineralization (Smith and Read 1997). Several types of such ectotrophic mycorrhizae have been identified in our research forest (Akiyoshi Yamada, Shinshu University, Japan, personal communication). Thus, recruitment of *P. densiflora* and development of *P. densiflora* forests are likely to occur on geologically new substrata, such as lava flows, not by increasing the investment of carbon to fine-root production, but by symbiotic mycorrhizal associations that develop in N-poor soils.

Acknowledgments We are grateful to Dr. A. Yamada for his help in analyzing the mycorrhizal roots. We thank Drs. K. Miyazaki and M. Shibata of the Yamanashi Institute of Environmental Sciences (YIES) and Prof. S. Okitsu of Chiba University for valuable comments on an early version of the manuscript. We also thank Mr. T. Ogawa and Dr. N. Usui of the YIES and Dr. Y. Yamamura, Ms. M. Endo, and Ms. N. Isogai of Ibaraki University for their assistance during the field study. We gratefully acknowledge all the time-consuming work put in by the Yoshida Forestry Office of Yamanashi Prefecture in doing tree descriptions and a census of the 30-ha plot in 1993.

Literature cited

Barkmann J, Schwintzer CR (1998) Rapid N_2 fixation in pines? Results of a Maine field study. Ecology 79:1453–1457

Bazzaz AF (1997) Allocation of resources in plant: state of the science and critical questions. In: Bazzaz AF, Grace J (eds) Plant resource allocation. Academic Press, San Diego, pp 1–37

Bormann BT, Sidle RC (1990) Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. J Ecol 78:561–578

Bormann BT, Bormann FH, Bowden WB, Pierce RS, Hamburg SP, Wang D, Snyder MC, Li CY, Ingersoll RC (1993) Rapid N_2 fixation in pines, alder and locust: evidence from the sandbox ecosystem study. Ecology 74:583–589

Gower ST, Vogt KA, Grier CC (1992) Carbon dynamics of Rocky Mountain Douglas fir: influence of water and nutrient availability. Ecol Monogr 62:43–65

Gower ST, Gholz HL, Nakane K, Baldwin VC (1994) Production and carbon allocation patterns of pine forests. Ecol Bull 43:115–135

Hachiya K, Takeuchi I, Tochiaki K (1989) Productivity of high density stands in *Pinus densiflora* SIEB. et Zucc. Bull For For Prod Res Inst 354:39–97

Haynes BE, Gower ST (1995) Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiol 15:317–325

Hendrickson OQ (1990) Asymbiotic nitrogen fixation and soil metabolism in three Ontario forests. Soil Biol Biochem 22:967–971

Karizumi N (1974) The mechanism and function of tree root in the process of forest production. I. Method of investigation and estimation of the root biomass. Bull Gov For Exp Stn 259:1–99

Keyes MR, Grier CC (1981) Above- and belowground net production in 40-year-old Douglas fir stands on low and high productivity sites. Can J For Res 11:599–605

Kira T, Shidei T (1967) Primary production and turnover of organic matter in different forest ecosystems of the Western Pacific. Jpn J Ecol 17:70–87

Kitayama K, Schuur EAG, Drake DR, Dombois DM (1997) Fate of a wet montane forest during soil aging in Hawaii. J Ecol 85:669–679

Larcher W (1995) Physiological plant ecology. 3rd edn. Springer, Berlin Heidelberg New York

Limmer C, Drake HL (1996) Non-symbiotic N_2-fixation in acidic and pH-neutral forest soils: aerobic and anaerobic differentials. Soil Biol Biochem 28:177–183

Matsuura Y, Abaimov AP, Zyryanova OA, Isaev AP, Yefremov DP (1997) Carbon and nitrogen storage of mountain forest tundra soils in central and eastern Siberia. In: Inoue G, Takenaka A (eds) Proceedings of the fifth symposium on the joint Siberian permafrost studies between Japan and Russia in 1996. National Institute for Environmental Studies, Tsukuba, Japan, pp 95–99

McClaugherty CA, Aber JD, Melillo JM (1982) The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 63:1481–1490

Miyaji N (1988) History of younger Fuji volcano (in Japanese with English abstract). J Geol Soc Jpn 94:433–452

Satake Y, Hara H, Watari S, Tominari T (1989a) Wild flowers of Japan. Woody Plants I. Heibonsha, Tokyo

Satake Y, Hara H, Watari S, Tominari T (1989b) Wild flowers of Japan. Woody Plants II. Heibonsha, Tokyo

Schlesinger WH (1997) Biogeochemistry: an analysis of global change. 2nd edn. Academic Press, San Diego

Smith SE, Read DJ (1997) Mycorrhizal symbiosis. 2nd edn. Academic Press, San Diego

Tadaki Y, Takeuchi I, Kawahara T, Sato A, Hachiya K (1979) Growth analysis on the natural stands of Japanese red pine (*Pinus densiflora* Sieb. et Zucc.). III. Results of experiment. Bull For For Prod Res Inst 305:125–144

Vitousek PM, Matson PA, Cleve K (1989) Nitrogen availability and nitrification during succession: primary, secondary and old-field series. Plant Soil 115:229–239

Vitousek PM, Walker LR, Whiteaker LD, Matson PA (1993) Nutrient limitations to plant growth during primary succession in Hawaii Volcanoes National Park. Biogeochemistry 23:197–215

Vogt KA, Vogt DJ, Palmiotto PA, Boon P, O'Hara J, Asbjornsen H (1996) Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187:159–219

Yamada A (1996) The study of ecological community on ectomycorrhizal fungi in *Pinus densiflora* forests. PhD thesis, University of Tsukuba, Japan