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論　文（Original article）

Aboveground production and nitrogen utilization in nitrogen-saturated coniferous plantation forests on the periphery of the Kanto Plain

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Abstract

The Tsukuba Forest Experimental Watershed on the periphery of the Kanto Plain receives high nitrogen deposition and has high nitrogen loss in stream water, indicating a nitrogen saturated condition. We investigated the soil properties, aboveground production and nitrogen utilization in hinoki cypress and Japanese cedar plantation forests located in the watershed. There was a low accumulation of organic horizon in the both forests, indicating rapid decomposition and nitrogen release from the organic horizon. Nitrogen input by litter fall was similar to the rate of annual soil nitrogen mineralization. Although the aboveground net primary production was relatively high in both forests, the Japanese cedar forest had a higher proportion of pollen cones. In addition, taller trees in the Japanese cedar forest had lower leaf biomass as indicated by the lower ratio of crown depth to tree height. The stem growth of these taller trees was lower than that of smaller trees. These results suggest a symptom of decline for taller trees in the Japanese cedar forest. Previously, the decline of Japanese cedar was mainly observed within the Kanto Plain at lower altitudes but the results of this study suggest the presence of declining Japanese cedar on the periphery of the Kanto Plain. Further study is required on the spatial distribution of declining Japanese cedar forests in order to determine the mechanism.

Key words : Japanese cedar, hinoki cypress, nitrogen saturation, aboveground production, nitrogen utilization

1. Introduction

Recently nitrogen deposition to forest ecosystems is increasing due to human activities. When the supply of ammonium and nitrate exceeds the plant and microbial demand, excess nitrogen may result in higher soil nitrification rate, soil acidification, higher nitrogen loss in stream water and the decline of forest productivity. These conditions are considered to constitute nitrogen saturation and many studies have been carried out in Europe and North America (Aber et al. 1989, Gundersen et al. 2006). In Japan, several studies have reported high nitrogen loss by stream water at forests along the periphery of the Kanto Plain, indicating symptoms of nitrogen saturation (Ohrui et al. 1997, Mitchell et al.1997, Yoh et al.2001, Itoh et al.2004, Fujimaki et al.2009; Mitchell 2011, Yoshinaga et al. 2012).

Because nitrogen often limits the productivity of temperate forest ecosystems (Vitousek and Howarth 1991, LeBauer and Treseder 2008), adding it generally boosts forest productivity (LeBauer and Treseder 2008). However, if nitrogen is added still further, forest productivity would not rise further due to an imbalance of soil nutrient and soil acidification (Magill et al. 2004, Wallance et al. 2007). The effects of nitrogen deposition on forest systems can vary according to the development stage of the forest and tree species (Magill et al.2004; Bedison and McNeil 2009). Nitrogen deposition may also increase the production of reproductive organs, i.e. seeds and flowers, and the biomass allocation to leaves, stems and reproductive organs (Townsend et al. 2003; Callahan et al. 2008). Pollen cone production of hinoki cypress forests was related with soil C/N ratio (Nakanishi et al. 2008) and nitrogen deposition may promote pollen cone production.

Several studies have reported the decline of Japanese cedar at lower altitudes on the Kanto Plain (Nashimoto and Takahashi 1991, Sakata 1996, Matsumoto et al. 2002), with particularly pronounced

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decline for larger trees (Nashimoto and Takahashi 1991). The decline of these forests was related to many factors such as water stress (Sakata 1996), acid deposition (Nashimoto and Takahashi 1991), and high bulk density of the surface soil (Ito et al. 2002). When evaluating nitrogen saturation in Japanese cedar forests we must therefore consider the decline of Japanese cedar at lower altitudes.

In this study, we investigated the soil properties, forest productivity and nitrogen utilization in a hinoki cypress and Japanese cedar plantation at Tsukuba Forest Experimental Watershed on the periphery of the Kanto Plain. Kobayashi et al. (2011) showed that the area receives high nitrogen deposition and high nitrogen loss by stream water, indicating a nitrogen saturated condition. We compared nitrogen dynamics in the forests in Tsukuba and other forests in Japan and discussed the possible effects of nitrogen deposition in the area.

2. Material and Method

2.1 Study site

The study site is located at the Tsukuba Forest Experimental Watershed of the Forestry and Forest Products Research Institute, Ibaraki prefecture on the periphery of the Kanto Plain (N36°10’, E140°10’, 320-390 m in altitude). The mean annual precipitation is about 1400 mm, and the mean annual temperature is 13.1 °C. A watershed with an area of 3.8 ha was established (Fig. 1). The soil parent material is volcanic ash over biotite gneiss. According to a survey near the study area, soil was classified as Eutric Fulvudand (Soil Survey Staff 2010) and was rich in free oxide of aluminum and iron (Imaya et al. 2007, Imaya A personal communication). According to the Forest Soil Classification (Forest Soil Division 1976), soil on the ridges was classified into dry subtypes of moist brown forest soil (BD(d) type) while that on the slopes was moist brown forest soil (BD type) (Ohnuki and Yoshinaga 1995).

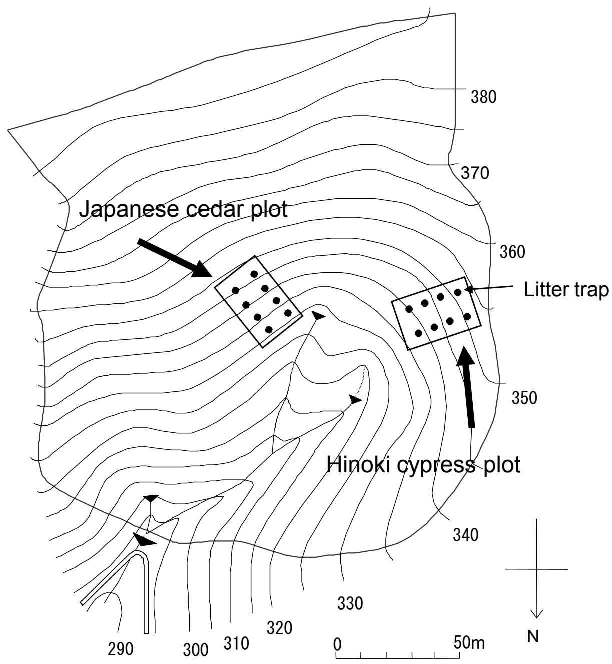

Fig. 1. Location of the study plots

A 20 × 30 m plot was established in the hinoki cypress and Japanese cedar forests for a tree census (Fig. 1) on the north-east and north-west facing slopes, respectively, separated by a valley. The hinoki cypress and Japanese cedar trees were planted in 1968 and 1953 and the stand ages in 2007 were 39 and 54 years, respectively (Table 1). Nitrogen input, as measured by bulk precipitation in 2008, was 7.2 kg N ha^{-1} yr^{-1} while that by through fall in the hinoki cypress and Japanese cedar forests was 22.4 and 11.4 kg N ha^{-1} yr^{-1}, respectively (Kobayashi et al. 2011). Nitrogen loss by stream water of the same year was 11.3 kg N ha^{-1} yr^{-1} (Kobayashi et al. 2011). Previous studies have reported that nitrogen loss from Japanese cedar forests ranged from 0.6-28.0 kg N ha^{-1} yr^{-1} (Mitchell et al. 1997) and the nitrogen loss of the Tsukuba area was relatively high and comparable to the value in nitrogen saturated forests on the periphery of the Kanto Plain (12.7-16.1 kg N ha^{-1} yr^{-1}, Mitchell et al. 1997).

2.2 Soil

Soil samples were collected from depths of 0-10, 10-20, 20-30, 30-40, 40-50 cm from a soil profile in the hinoki cypress and Japanese cedar forests. The collected samples were then sieved to pass 2 mm, whereupon the fine soil obtained was analyzed for

Table 1. Stand characteristics in 2007

		Hinoki cypress	Japanese cedar
Age	(yr)	39	54
Density	(trees ha^{-1})	2417	1500
Ry index*		0.91	0.86
DBH	(cm)	18.6	23.3
Height	(m)	15.4	18.8
Stem biomass	(Mg ha^{-1})	221.3	213.4

*Relative yield index (Ando 1968)

carbon and nitrogen content by an NC analyzer (NC 22F; Sumika Analytical Center, Osaka). The soil pH was also determined for the soil–water suspension (1:2.5 w/w) using a pH meter (HM30V; DKK-TOA, Tokyo).

Litter in the organic horizon was collected from an area 0.5 × 0.5m at 6 locations in each plot in April 2008. The collected samples were divided into twigs and other materials, whereupon the dry weight of each of these samples was measured. The samples were ground and measured for nitrogen and carbon concentration by an NC analyzer. The mean residence time of mass, carbon and nitrogen in the organic horizon were calculated as follows, assuming constant input and accumulation at a steady state.

Mean residence time (yr) =
Accumulation (Mg ha^{-1}) / Input by litterfall (Mg ha^{-1} yr^{-1})

2.3 Stem growth

Tree height and diameter at breast height (DBH) was measured for trees exceeding 5 cm in DBH at the end of the growing season from 2007 to 2011. In 2011, the height of the lowest live branch was also measured (Hb). Stem volume was calculated from the tree height and DBH by using the equation for hinoki cypress and Japanese cedar for the area (Forest Agency 1970). Stem biomass was calculated by the stem volume multiplied by the base bulk density from the reported value (hinoki cypress 407 Mg m^{-3}, Japanese cedar 314 Mg m^{-3}, Fujiwara 2004). The annual DBH growth rate and stem growth rate were also calculated and the stem growth of dominant trees was evaluated. Trees were arranged from larger stem volume and the cumulative stem volume was calculated. The larger individuals up to 50% of total stem volume were considered dominant trees. In the hinoki cypress and Japanese cedar plots, 33 and 28% of trees were considered dominant, respectively. The relationship between tree height in 2007 and subsequent stem growth from 2008 to 11 was analyzed, as well as that between tree height in 2007 and the ratio of crown depth to the tree height.

2.4 Litterfall

Eight litter traps with an area of 0.5 m^2 were placed in the hinoki cypress and Japanese cedar plots in September 2007 (Fig. 1). Litterfall was collected at 1-2 month intervals from September 2007 to July 2011. In this study, we defined a leaf-fall year as running from July through to June the following year, because the leaf fall rate of the hinoki cypress is lowest in July (Inagaki et al. 2010). We did not collect litterfall from July to September in 2007, but we considered the underestimation for annual content relatively small because the amount of litterfall from July to September was low in other years (less than 8% of the annual litterfall). The collected litterfall from 8 traps was combined into a single sample. The samples were then divided into conifer leaves, other leaves, pollen cones, seed cones, conifer branches and others, and their dry weight at 75 ºC was measured. Because conifer leaves and pollen cones are very small and difficult to separate, part of the samples (about 30 g, 5-100% of the total sample) was divided for these organs. The nitrogen and carbon concentration of the sorted samples were measured using an NC analyzer. The nitrogen concentration of conifer leaves was measured for every collection but that for other organs were measured for the combined sample from July to June the following year.

2.5 Biomass and nitrogen allocation

Biomass allocation into leaves, stem, branches and reproductive organs were calculated. The pollen cones in the litterfall do not include pollen and the ratio of the weight of pollen-laden pollen cones to that of those without is 2.5 and 2.0 for the hinoki cypress and Japanese cedar, respectively（Kiyono et al. 2003, Saito and Takeoka, 1983）. The production of pollen cones was calculated as the fallen pollen cones multiplied the above ratio. Nitrogen allocation to different organs was also calculated. The nitrogen concentration of stems was also determined for recently fallen trees in the area. The preliminary study in Kochi and Kyoto prefectures (Inagaki et al. unpublished data) suggests that the nitrogen concentration of pollen is similar to fallen pollen cones, i.e. the mean (SD) of the ratio of nitrogen concentration in pollen to that in fallen pollen cones was 1.0 (0.05) for the hinoki cypress (n=4) and 1.1 (0.20) for the Japanese cedar (n=7). Therefore we considered the nitrogen concentration of pollen was same as that of fallen pollen cones.

The nitrogen use efficiency of conifer leaves (NUE_{leaf}) was calculated as the ratio of mass to the nitrogen content of conifer leaves by the definition of Vitousek (1982). The nitrogen use efficiency of aboveground (NUE_{ag}) was calculated as the ratio of aboveground production to nitrogen utilized for the aboveground biomass production.

3. Results

3.1 Soil properties

The masses in the organic horizon were 8.25 and 14.38 Mg ha^{-1} in the hinoki cypress and Japanese cedar forests, respectively (Table 2). The carbon contents in the organic horizon were 4.12 and 7.17 Mg ha^{-1} while the nitrogen contents were 73.1 and 126.2 kg ha^{-1} in the hinoki cypress and Japanese cedar plots, respectively. C/N ratio in the organic horizon was higher for branch than non-branch material but was similar between hinoki cypress and Japanese cedar forests.

In the hinoki cypress forest, although the soil pH was low in the surface soil (0-10 cm depth), it gradually increased with depth (Fig. 2). In the Japanese cedar forest, conversely, the soil pH was low (4.4) and relatively constant in the soil profile. Soil carbon and nitrogen concentration were higher at the surface soil and gradually decreased with depth. The C/N ratio in the surface soil was about 16 and decreased to 12-13.

3.2 Stem growth

At the end of the growing season in 2007, the hinoki cypress forest had a higher stand density, lower mean DBH and lower mean tree height than the Japanese cedar forest (Table 1). The stem volume of the two forests was similar. The relative yield indices defined by Ando (1968) were 0.91 and 0.86 in the hinoki cypress and Japanese cedar forests, suggesting that the hinoki cypress forest was very crowded. The mean annual DBH growth rates were 0.26 and 0.24 cm for the hinoki cypress and Japanese cedar forests, showing no difference between them (Table 3). The mean annual stem growth was higher in the hinoki cypress forest (11.4 Mg ha^{-1} yr^{-1}) than in the Japanese cedar forest (8.6 Mg ha^{-1} yr^{-1}). The mortality rate was higher but net annual stem production was higher in the hinoki cypress forest than the Japanese cedar forest.

In the Japanese cedar forest, taller trees in 2007 had a lower ratio of crown depth to tree height in 2011; suggesting taller trees have fewer leaves due to the higher lowest live branch (Fig. 3a). The ratio of crown depth to tree height in 2011 in the hinoki cypress forest was greater for taller trees (Fig. 3b), which is the opposite trend to Japanese cedar forests. In the Japanese cedar forest, the annual stem growth of dominant trees for 4 years was lower for taller trees in 2007 (Fig. 3c). Conversely, in the hinoki cypress forest, the annual stem growth of dominant trees was higher for taller trees in 2007 (Fig. 3d).

Table 2. Accumulation and mean residence time (MRT) of organic matter, carbon and nitrogen in the organic horizon

	Hinoki cypress			Japanese cedar		
	Non-branch	branch	total	Non-branch	branch	total
Mass						
Organic horizon (Mg ha^{-1}) (a)	5.61	2.64	8.25	11.29	3.09	14.38
Litterfall (Mg ha^{-1}yr^{-1}) (b)	5.22	0.73	5.95	6.44	0.48	6.92
MRT (yr) (a/b)	1.07	3.64	1.39	1.75	6.49	2.08
Carbon						
Organic horizon (Mg ha^{-1}) (a)	2.76	1.36	4.12	5.60	1.57	7.17
Litterfall (Mg ha^{-1}yr^{-1}) (b)	2.78	0.36	3.14	3.38	0.24	3.62
MRT (yr) (a/b)	0.99	3.72	1.31	1.65	6.60	1.98
Nitrogen						
Organic horizon (kg ha^{-1}) (a)	59.6	13.5	73.1	112.4	13.8	126.2
Litterfall (kg ha^{-1}yr^{-1}) (b)	44.8	3.9	48.7	61.9	1.9	63.7
MRT (yr) (a/b)	1.33	3.42	1.50	1.82	7.44	1.98
C/N ratio						
Organic horizon	46	101	56	50	114	57
Litterfall	62	93	65	55	129	57

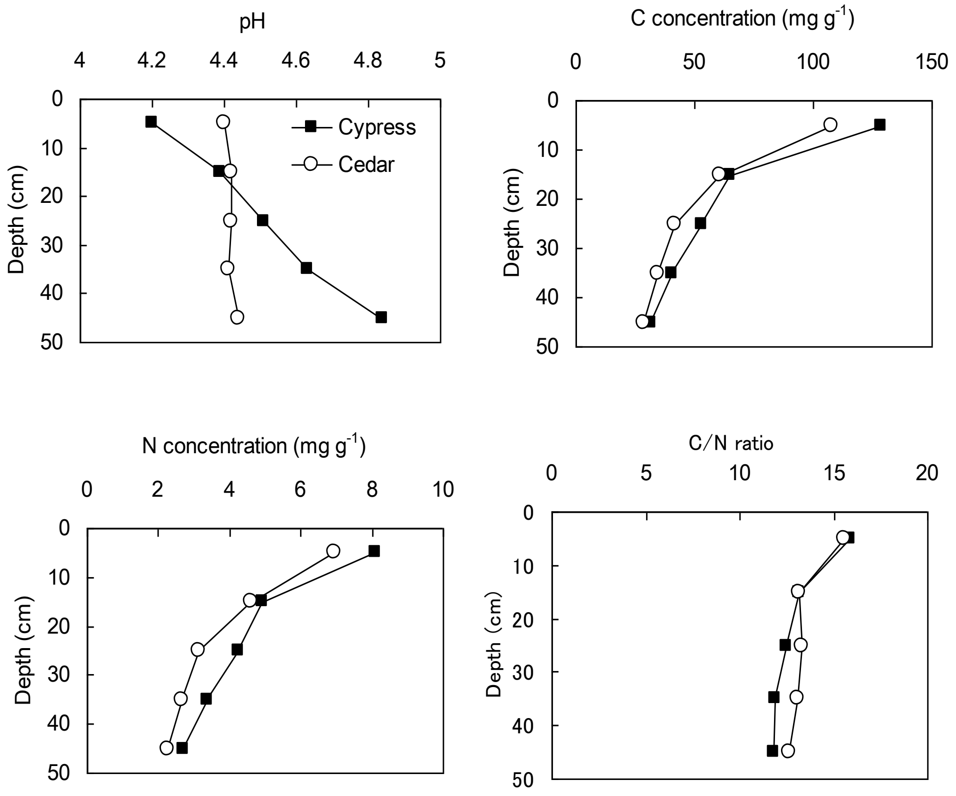

Fig. 2. pH, total C and N concentration in the soil profile

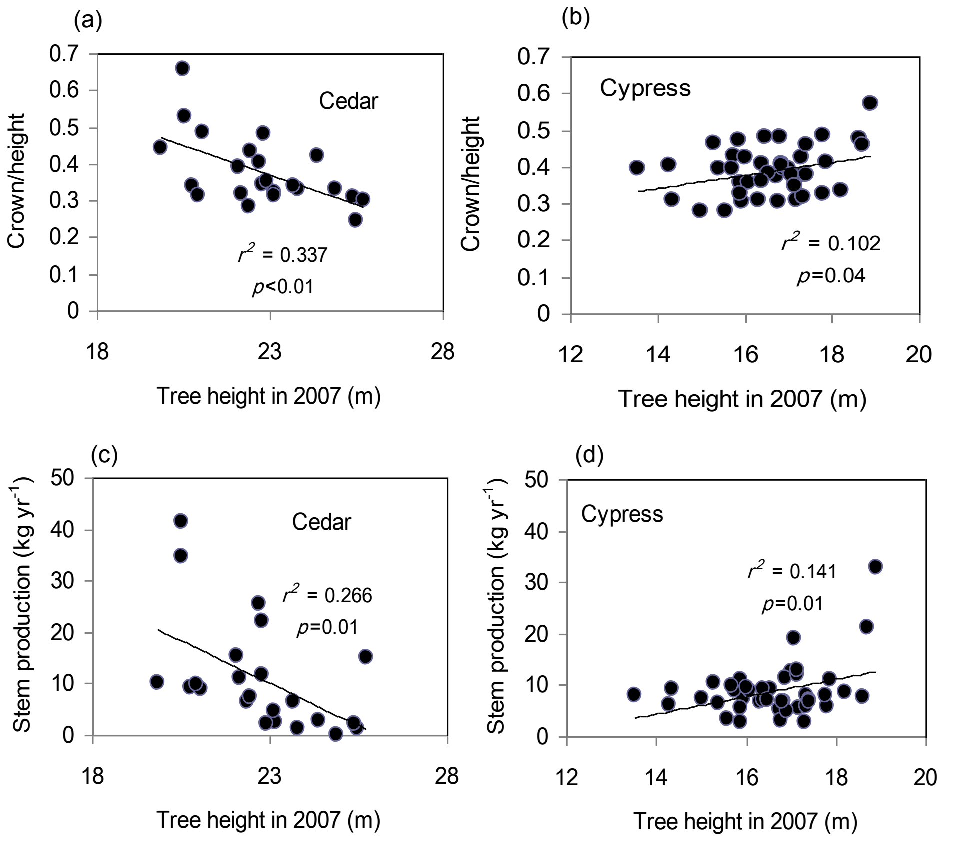

Fig. 3. Relationship between tree height in 2007 and the ratio of crown depth to tree height in 2011 or stem growth from 2007 to 2011

Table 3. Stem growth in hinoki cypress and Japanese cedar plantation

	Density (trees ha^{-1})	Diameter growth (cm yr^{-1})	Stem increment (Mg ha^{-1} yr^{-1})	Mortality rate (Mg ha^{-1} yr^{-1})	Net stem increment (Mg ha^{-1} yr^{-1})
Hinoki cypress					
2008	2417	0.25	9.7	0.0	
2009	2317	0.22	16.0	3.3	
2010	2183	0.17	6.1	4.6	
2011	2167	0.31	13.8	0.6	
Mean		0.24	11.4	2.1	9.3
Japanese cedar					
2008	1500	0.24	6.1	0.0	
2009	1383	0.32	12.4	5.6	
2010	1367	0.22	8.8	0.5	
2011	1367	0.26	7.0	0.0	
Mean		0.26	8.6	1.5	7.1

3.3 Litterfall

The mean annual litter produced in 2007-2011 was 5.95 and 6.92 Mg ha^{-1} yr^{-1} in the hinoki cypress and Japanese cedar forests, respectively (Table 4). The mean production of conifer leaves were 4.75 and 4.38 Mg ha^{-1} yr^{-1} in the hinoki cypress and Japanese cedar forests, respectively. The proportion of conifer leaves to total litterfall was greater in the Japanese cedar forest. Many green conifer leaves fell in 2009-10 for the hinoki cypress forest, and 2007-8 for the Japanese cedar forest. The percentage of green coniferous leaf relative to coniferous leaves was greater in the Japanese cedar (22%) than in the hinoki cypress forest (17%). Many pollen cones also fell in the Japanese cedar forest. In the mast year of 2010-11, 1.7 Mg ha^{-1} yr^{-1} of pollen cones was recorded as falling, which was equivalent to 3.4 Mg ha^{-1} yr^{-1} of pollen cones with pollen.

The mean annual nitrogen inputs by litterfall for 4 years were 48.7 and 63.0 kg N ha^{-1} yr^{-1} in the hinoki cypress and Japanese cedar forests, respectively. The nitrogen concentrations of conifer leaves were 8.51 and 8.05 mg N g^{-1}, and those of total litterfall were 8.23 and 9.24 mg N g^{-1} for the hinoki cypress and Japanese cedar forests, respectively (Table 5). The inter-annual variation of reproductive organs was considerable and nitrogen concentration of pollen cones high in the Japanese cedar forest. These conditions should lead to a greater variation in the total-litter nitrogen concentration.

When we compare the annual production rate of conifer leaves with previous studies (Table 6), the value for hinoki cypress in this study was relatively high while that in the Japanese cedar forest was higher than the average. The annual nitrogen input of conifer leaves showed a similar trend. The nitrogen concentration of conifer leaves of the hinoki cypress forest exceeded the average but that in the Japanese cedar forest was similar to the average.

3.4 Mean residence time of the organic horizon

The mean residence times of non-branch material in the organic horizon were 1.07 and 1.75 years and those of branch were 3.64 and 6.49 years in the hinoki cypress and Japanese cedar forests, respectively (Table 2). The mean residence times of total mass in the organic horizon were 1.39 and 2.08 years in the hinoki cypress and Japanese cedar forests, respectively. The mean residence time of carbon and nitrogen content showed a similar trend to that of mass.

3.5 Allocation

The results of biomass allocation were compared with those in the 38-year-old Japanese cedar forests at the Katsura experimental forest with low nitrogen deposition in Ibaraki prefecture (Inagaki et al. 2011) (Table 7). Biomass allocation to leaves was similar between the three forests (27.2-29.7%), although biomass allocation to stems was lower in the Tsukuba Japanese cedar forest (54.7%) than the other two forests (63.3-63.9%) while that to pollen cones was higher in the Tsukuba Japanese cedar forest (10.4%) than the other two forests (0.7-2.6%). Nitrogen allocation to stems was similar between the three forests (13.2-15.7%). In the Tsukuba Japanese cedar forest, nitrogen allocation to pollen cones was higher and that to leaves was lower than the other two forests.

For the hinoki cypress and Japanese cedar forests in Tsukuba, the nitrogen use efficiency of conifer leaves (NUE_{leaf}) was similar between the two forests (119-120). The nitrogen use efficiency of aboveground (NUE_{ag}) in the Japanese cedar forest (227) was lower than that in the hinoki cypress forest (322).

4. Discussion

4.1 Soil properties

The mean values of carbon contents in the organic horizon were 5.15 and 5.25 Mg C ha^{-1} for hinoki cypress and Japanese cedar forests in Japan (Takahashi et al. 2010). Carbon content in this study was slightly

Table 4. Litter mass and litter nitrogen input in the hinoki cypress and Japanese cedar forests

Year	Conifer leaves			Branch	Pollen cones	Seed cones	Other leaves	Others	Total
	Brown	Green	Total						
Litter mass (Mg ha^{-1} yr^{-1})									
Hinoki cypress									
2007-8	3.45	0.65	4.10	0.86	0.02	0.05	0.01	0.15	5.19
2008-9	3.05	0.52	3.57	0.53	0.06	0.21	0.01	0.24	4.62
2009-10	3.40	1.40	4.80	1.02	0.00	0.28	0.04	0.28	6.42
2010-11	5.87	0.63	6.51	0.48	0.13	0.17	0.01	0.24	7.55
Mean	3.95	0.80	4.75	0.73	0.05	0.18	0.02	0.23	5.95
Japanese cedar									
2007-8	3.75	2.01	5.76	0.66	1.01	0.66	0.16	0.24	8.49
2008-9	2.53	0.62	3.15	0.33	0.30	0.48	0.28	0.45	4.99
2009-10	3.63	0.73	4.37	0.41	0.23	0.68	0.31	0.41	6.40
2010-11	3.77	0.49	4.26	0.51	1.70	0.66	0.22	0.44	7.79
Mean	3.42	0.96	4.38	0.48	0.81	0.62	0.24	0.38	6.92
Litter nitrogen input (kg N ha^{-1} yr^{-1})									
Hinoki cypress									
2007-8	26.8	8.4	35.2	5.0	0.2	0.3	0.1	1.4	42.2
2008-9	24.4	6.9	31.3	3.2	0.5	1.3	0.1	3.1	39.5
2009-10	26.7	16.3	43.1	4.9	0.0	1.9	0.7	3.7	54.3
2010-11	41.7	8.8	50.5	2.6	1.4	1.1	0.2	3.1	58.9
Mean	29.9	10.1	40.0	3.9	0.5	1.2	0.3	2.8	48.7
Japanese cedar									
2007-8	33.7	18.3	52.0	2.6	10.5	5.6	2.7	3.8	77.2
2008-9	17.4	6.3	23.7	1.1	3.1	4.8	5.1	7.6	45.3
2009-10	28.3	7.3	35.6	1.5	2.4	6.8	6.2	7.3	59.7
2010-11	30.6	4.4	35.0	2.2	17.9	6.6	3.9	7.1	72.7
Mean	27.5	9.1	36.6	1.9	8.5	5.9	4.5	6.5	63.7

Table 5. Nitrogen concentration of litterfall (mg N g^{-1})

Year	Conifer leaves			Branch	Pollen cones	Seed cones	Other leaves	Others	Total
	Brown	Green	Total						
Hinoki cypress									
2007-8	7.77	12.82	8.57	5.79	11.87	6.85	14.97	8.95	8.12
2008-9	7.99	13.32	8.76	5.99	9.00	6.22	12.23	12.67	8.54
2009-10	7.86	11.65	8.96	4.81	13.67	6.93	17.80	13.17	8.45
2010-11	7.10	13.85	7.76	5.45	10.69	6.33	16.98	12.74	7.80
Mean	7.68	12.91	8.51	5.51	11.31	6.58	15.50	11.88	8.23
Japanese cedar									
2007-8	6.86	10.16	7.51	3.32	10.16	9.90	18.43	17.03	9.09
2008-9	7.79	9.90	8.15	3.60	10.42	9.93	20.14	18.01	9.33
2009-10	8.12	8.95	8.21	4.38	10.50	9.98	17.62	16.32	9.33
2010-11	8.03	9.42	8.34	3.89	10.41	9.57	18.49	16.92	9.21
Mean	7.70	9.61	8.05	3.80	10.37	9.85	18.67	17.07	9.24

Table 6. Mass and nitrogen content of litterfall in the hinoki cypress and Japanese cedar forests in previous studies

	Mass ($Mg\ ha^{-1}\ yr^{-1}$)		Nitrogen content ($kg\ N\ ha^{-1}\ yr^{-1}$)		N concentration ($mg\ N\ g^{-1}$)	
	Conifer leaves	Total litter	Conifer leaves	Total litter	Conifer leaves	Total litter
Hinoki cypress (n=24)						
Mean	2.89	4.32	23.7	35.3	8.1	8.0
Minmum	1.60	2.00	9.9	14.9	5.7	5.9
Maxmum	4.80	6.41	48.0	68.0	10.9	10.6
SD	0.88	1.25	9.2	14.0	1.5	1.5
Japanese cedar (n=14)						
Mean	3.05	4.68	25.4	40.0	8.1	8.6
Minmum	1.04	1.60	7.7	17.4	5.3	6.2
Maxmum	5.90	7.40	58.4	71.5	12.7	11.4
SD	1.45	1.63	15.9	16.3	2.1	1.7

Data is from Fukushima et al (2011),Haibara and Aiba (1982), Ichikawa (2008), Inagaki et al (2004, 2005, 2010),Oura (2010), Toda et al (1991), Tsutsumi et al (1983)

Table 7. Biomass and nitrogen allocation in the hinoki cypress and Japanese cedar forests. Values in parentheses indicate percentage to the total amount.

	Tsukuba Hinoki cypress (this study)		Tsukuba Japanese cedar (this study)		Katsura Japanese cedar (Inagaki et al 2011)	
Biomass allocation ($Mg\ ha^{-1}\ yr^{-1}$)						
Stem	10.2	(63.9)	8.6	(54.7)	8.2	(63.3)
Branch	0.7	(4.5)	0.5	(3.0)	0.4	(3.2)
Leaf	4.7	(29.7)	4.4	(27.9)	3.5	(27.2)
Pollen cones	0.1	(0.7)	1.6	(10.4)	0.3	(2.6)
Seed cones	0.2	(1.1)	0.6	(3.9)	0.5	(3.7)
Total	16.0	(100.0)	15.7	(100.0)	13.0	(100.0)
Nitrogen allocation ($kg\ ha^{-1}\ y^{-1}$)						
Stem	7.1	(13.2)	11.4	(15.7)		
Branch	3.9	(7.4)	1.9	(2.6)		
Leaf	40.0	(75.0)	36.6	(50.3)		
Pollen cones	1.2	(2.2)	16.9	(23.3)		
Seed cones	1.2	(2.2)	5.9	(8.2)		
Total	53.4	(100.0)	72.7	(100.0)		
NUE_{leaf}	119		120			
NUE_{ag}	322		227			

higher in the Japanese cedar forest (7.17 Mg C ha^{-1}) but lower in the hinoki cypress forest (4.12 Mg C ha^{-1}, Table 2). The reported mean residence times of mass in the organic horizon were 1.3-5.1 years for hinoki cypress and 3.0-4.4 years for Japanese cedar forests (Ichikawa et al. 2003). Vogt et al. (1986) summarized the mean residence time of the organic horizon from global forest ecosystems and the mean value for temperate coniferous forests was 4.6 years. Compared with these studies, the mean residence time of this study was short, suggesting rapid decomposition of the organic horizon, as was the mean residence time of nitrogen content in this study. During the decomposition processes, the C/N ratio generally decreases (Takeda 1994) and the mean residence time of nitrogen should exceed that of mass. The short mean residence time of nitrogen in this study suggests that immobilization of nitrogen is limited and nitrogen in the organic horizon should be released as fast as organic matter decomposes.

When compared to the study conducted in the Kanto and Chubu districts of Japan (Imaya et al. 2005), soil pH of the Japanese cedar forest in this study is very low, especially in deeper soil (Fig.2). Previous studies showed that soil pH decreased after application of nitrogen fertilizer (Inoue 1982, Nagakura et al. 2006) thereby suggesting that the addition of nitrogen lowers soil pH in Japanese cedar forests. A relatively large loss of nitrogen in this study is noted between Japanese forests (Kobayashi et al. 2011), and high nitrogen deposition in the area would partially explain low soil pH in the Japanese cedar forest. Soil pH is determined by many factors other than nitrogen deposition (van Breemen et al. 1983) and the relative importance of nitrogen deposition should be investigated in the future.

Soil nitrogen mineralization (0-50 cm depth) in the study area was previously determined by the resin core method over two years, from 2008 to 2009 (Inagaki et al. 2012, Table 8).The annual nitrogen mineralization rate of soil was 75.0 and 51.0 kg N ha^{-1} yr^{-1} in the hinoki cypress and Japanese cedar forests, respectively. In the Oyasan area, where nitrogen deposition was high, the annual nitrogen mineralization rate for soil at a depth of 0-20 cm was 51.5 kg N ha^{-1} yr^{-1} (Oyanagi et al. 2004). In the Katsura area, with lower nitrogen deposition, the annual nitrogen mineralization rate was 105.1 kg N ha^{-1} yr^{-1} (Hirai et al. 2007). Takebayashi et al. (2010) showed that nitrogen mineralization was not high in forests with higher nitrogen deposition. These findings suggest that the relationship between nitrogen deposition and soil nitrogen mineralization is unclear.

4.2 Biomass production and nitrogen utilization

Mean stem production in the Japanese cedar forest was lower than that in the hinoki cypress forest (Table 3). Taller trees in the Japanese cedar forest have fewer leaves, as indicated by the lower ratio of crown depth to tree height indicating a symptom of decline (Fig. 3a). In addition, the growth of taller trees in the Japanese cedar forest was lower than smaller trees (Fig. 3c) and is limited due to lower amount of leaves. At the lower altitude of the Kanto Plain, many studies reported the decline of the Japanese cedar (Nashimoto and Takahashi 1991, Sakata 1996, Matsumoto et al. 2002）which was particularly pronounced for larger trees (Nashimoto and Takahashi 1991). Previously, the decline of the Japanese cedar was mainly distributed in lower areas and not observed in mountainous areas on the periphery of the Kanto Plain (Matsumoto et al. 2002). However the result of this study suggest the presence of the declining Japanese cedar and the maximum tree height are limited in the mountain area.

Nagakura et al. (2008) revealed that adding of nitrogen to Japanese cedar trees increases transpiration. Nagakura et al. (2006) also noted a drier soil water condition when nitrogen was added to a Japanese cedar plantation. In contrast, Sase et al. (1998) have shown that lower wax content in leaves affected by an acid aerosol should increase transpiration. These findings suggest that increased transpiration by certain factors should be important but the mechanism of declines in Japanese cedar forests is complex. The mechanism of the decline of taller trees in this study is not clearly known and further study is required in mountainous areas as well as in urban areas.

Although aboveground production was similar between the hinoki cypress and Japanese cedar forests, their allocation differed (Table 7). In the Japanese cedar forest, allocation to reproductive organs was considerable but that to stems was low. When compared with Japanese cedar forests in the Katsura area with low nitrogen deposition (Inagaki et al. 2011) the Japanese cedar forest in Tsukuba also had high allocation to reproductive organs. The mean annual production of pollen cones was 1.6 Mg $ha^{-1}yr^{-1}$, while that in a mast year was very high (3.4 Mg $ha^{-1}yr^{-1}$, Table 7). This value exceeds the reported values in Katsura area (0.2-0.5 Mg $ha^{-1}yr^{-1}$; Inagaki et al. 2011). As far as the authors know, the largest reported pollen cone production was 4.2 Mg $ha^{-1}yr^{-1}$ in Okayama prefecture (Hashizume and Suo 1996) and the value of this study is relatively high. These findings suggest that the Japanese cedar has the potential to produce pollen cones and the Japanese cedar forest in this study has a high production of pollen cones. The production of pollen cones in the hinoki cypress forest was low (0.1 Mg $ha^{-1}yr^{-1}$, Table 7). Reported values of the annual production of pollen cones for the hinoki cypress forests ranged from 0.0-0.3 Mg ha^{-1} yr^{-1} (Nakanishi et al. 2008) and the production of pollen cones in this study was modest. We concluded that the production of pollen cones was lower in the hinoki cypress than the Japanese cedar and the production was likely to differ due to the species' characteristics.

Nitrogen input by litterfall of this study was relatively large when compared with previous studies (Table 7) and was similar to the rate of annual soil nitrogen mineralization (Table 8). The nitrogen concentrations of conifer leaves in nitrogen saturated forests were 9.3 and 8.9 mg N g^{-1} in the hinoki cypress and Japanese cedar forests in the Oyasan area, and 10.2-10.6 mg N g^{-1} in the Tama area (Haibara and Aiba 1982, Toda et al. 1991, Oura 2010). The nitrogen concentration of conifer leaves in this study was lower than that in these forests and close to the mean value for Japanese forests (Table 6). These results suggest that the nitrogen concentration of conifers in the study site is approximately average. However, the nitrogen allocation to reproductive organs was very large in the Japanese cedar forest of this study. The nitrogen concentration of pollen cones was also relatively high and high allocation to pollen cones may lead to lower aboveground nitrogen use efficiency (NUE_{ag}) (Table 7). Based on these findings, we concluded that a larger nitrogen allocation to reproductive organs should lead to lower nitrogen use efficiency in the Japanese cedar forest and that the pattern of nitrogen allocation was an important component to determine nitrogen utilization in forest ecosystems.

Table 8. Annual net soil nitrogen mineralization rate (kg N ha^{-1}) in the two plots over 2 years (data from Inagaki et al 2012)

Soil depth (cm)	Hinoki cypress	Japanese cedar
0-10cm	52.7	31.2
10-20cm	15.0	10.8
20-30cm	4.7	4.8
30-40cm	2.3	2.3
40-50cm	0.2	1.8
0-50 cm total	75.0	51.0

5. Conclusion

The nitrogen cycling in the hinoki cypress and Japanese cedar forests in the Tsukuba Forest Experimental Watershed was summarized as acidified soil, rapid turnover of mass and nitrogen in the organic horizon, and soil nitrogen mineralization at a moderate rate. The aboveground production and nitrogen uptake by trees were relatively large but taller trees in the Japanese cedar forest had fewer leaves and lower growth rate. These results suggest a symptom of decline for taller trees in the Japanese cedar forest. The Japanese cedar was allocated a large biomass and nitrogen to pollen cones. Previously, the decline of the Japanese cedar was mainly observed within the Kanto Plain at lower altitudes but the results of this study suggest the presence of the Japanese cedar in decline on the periphery of the Kanto Plain. Further study on the spatial distribution of Japanese cedar forests is required to understand the mechanism of the decline of the Japanese cedar.

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関東平野周辺の窒素飽和状態の針葉樹人工林における地上部生産と窒素利用様式

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要 旨

筑波共同試験地は、関東周辺の山間部に位置しており、森林に負荷される窒素量が多く、渓流水からの窒素流亡も大きい窒素飽和状態の森林流域である。この林分のスギ林とヒノキ林において、土壌の性質と地上部生産、器官への乾物生産の分配、窒素の分配を調査した。有機物層の現存量は小さく、有機物は速やかに分解され、窒素を放出した。リターフォールによる窒素供給量は、土壌の窒素無機化速度とほぼ同じであった。ヒノキ林、スギ林では地上部一次生産は高く維持されているものの、スギ林では雄花の分配率が大きく、地上部の窒素利用効率が低下した。スギ林では、樹高の高い個体で樹冠長が小さく葉量が少ない傾向が認められた。樹高の高い個体は低い個体よりも幹成長が小さい傾向が認められた。これらの結果は、スギ林の樹高の高い個体で衰退の兆候が認められることを示す。これまで山間部のスギ林は、関東平野部に比べて衰退の程度が小さいと考えられてきたが、本研究の結果より、衰退の兆候を示す林分が存在することが明らかになった。今後窒素負荷の影響を考慮しながら都市近郊のスギ林の健全性を評価することが重要である。

キーワード：スギ、ヒノキ、窒素飽和、地上部生産、分配

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