



ELSEVIER

Forest Ecology and Management 163 (2002) 61–70

Forest Ecology
and
Management

www.elsevier.com/locate/foreco

Effects of dwarf bamboo (*Sasa* sp.) and forest floor microsites on conifer seedling recruitment in a subalpine forest, Japan

Y. Narukawa^{*}, S. Yamamoto

Laboratory of Forest Ecology and Physiology, Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya 464-8601, Japan

Received 27 December 2000; accepted 27 March 2001

Abstract

To clarify the effects of dwarf bamboo (*Sasa* sp.) and forest floor microsites on coniferous (*Abies mariesii*, *A. veitchii*, *Picea jezoensis* var. *hondoensis*, and *Tsuga diversifolia*) seedling recruitment, occurrence and survivorship of current and old (age ≥ 1 year old, height ≤ 15 cm) seedlings on soil and fallen logs were examined in quadrats (2 m \times 2 m) set systematically in a 1 ha permanent plot located in stands with or without *Sasa* understory of a subalpine forest, central Japan. Occurrence of old seedlings of *P. jezoensis* var. *hondoensis* and *T. diversifolia* was much greater in number on fallen logs than on soil, whereas old seedlings of *Abies* could occur with similar number on soil as well as fallen logs in the stand without *Sasa* understory. Whether old *Abies* seedlings occur on soil or on fallen logs varied largely with degree of *Sasa* coverage in the stand with *Sasa*, on the sites with *Sasa* cover $< 40\%$ in area, the old seedlings occurred more frequently on soil, but on the site with *Sasa* cover $\geq 40\%$ they occurred more frequently on fallen logs. The results indicate that the presence of *Sasa* raises the relative importance of fallen logs for the seedling recruitment of *Abies*. On the other hand, fallen logs are primarily important for the seedling recruitment of *P. jezoensis* var. *hondoensis* and *T. diversifolia* irrespective of the presence or absence of *Sasa*. The difference in occurrence of recruited seedlings between these two microsites was formed at some stages in seedling emergence and subsequent mortality process within a current year. The forest floor occupied by fallen logs was small in area, while soil covered large area of the forest floor. However, seedlings on fallen logs may not be affected by the suppression of understory vegetation, such as *Sasa* as those on soil. From this study, it is suggested that the difference of species life history traits (e.g. seed size), presence of various microsites, and their interactions with *Sasa* may be one of possible factors to maintain tree species coexistence in a subalpine old-growth coniferous forest. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: *Abies*; Fallen logs; Safe site; Subalpine old-growth forest; Tree species coexistence; Understory vegetation

1. Introduction

The forest floor is characterized by various microsites, such as soil, fallen logs, rotten stumps or root mounds (Orians, 1982; Putz, 1983; Beatty and Stone,

1986; Nakashizuka, 1989; Peterson and Pickett, 1990; Peterson et al., 1990; Lusk, 1995). Some of these microsites create safe sites for the seedling recruitment of plants (Harper, 1977; Christy and Mack, 1984). When different microsites can be used as recruitment sites by different species, the presence of various microsites has been considered to be one of important factors for the coexistence of tree species in forests (Grubb, 1977; Knapp and Smith, 1982;

^{*} Corresponding author. Tel.: +81-52-789-4050;

fax: +81-52-789-5014.

E-mail address: yona@mbox.media.nagoya-u.ac.jp (Y. Narukawa).

Duncan, 1993). In evergreen coniferous forests of the Pacific Northwest, the occurrence of tree seedlings is often restricted to fallen logs (Franklin and Dyness, 1973; Harmon and Franklin, 1989). For example, McKee et al. (1982) estimated that 88–97% of tree seedlings in *Picea sitchensis*–*Tsuga heterophylla* forests in Olympic National Park, Washington, grew on fallen logs. In Japan, occurrence of some conifer species on fallen logs has been reported for boreal and subalpine evergreen coniferous forests (Haruki, 1982; Suzuki et al., 1987; Nakamura, 1992; Kubota et al., 1994; Takahashi, 1994, 1997). However, comparative studies on the seedling recruitment of different tree species on fallen logs are very few.

The *Sasa* species, dwarf bamboos, are distributed widely from the warm temperate to the subfrigid zones in Asia, and often form dense undergrowth in forests (Shidei, 1974). *Sasa* flowers, then dies simultaneously in a wide area after rhizomatous vegetative reproduction during a long period (Campbell, 1985; Makita, 1992; Makita et al., 1993). Its presence has been considered to be one of the major factors impeding forest regeneration, because tree seedling recruitment is very difficult under the dense cover of *Sasa* (Nakashizuka and Numata, 1982a,b; Nakashizuka, 1987, 1988), like other understory bamboos in temperate regions, such as *Sinarundinaria* spp. in China (Taylor and Qin, 1988) and *Chusquea* spp. in Chile (Veblen, 1982). In some parts of subalpine forest of central Japan, a seedling-sapling bank of evergreen conifers is developed (Kohyama, 1984), while the understory of other parts is dominated by *Sasa*. In stands with *Sasa* understory, formation of seedling-sapling banks is strongly impeded by *Sasa* (Yamamoto, 1993, 1995), and if this situation is continued, this stand does not regenerate and may gradually change into an open stand with vigorous *Sasa* undergrowth. In this type of stand, elevated surfaces, such as fallen logs or root mounds are thought to be very important for the seedling recruitment of canopy trees.

To clarify the effects of *Sasa* and microsites on conifer seedling recruitment, we examined the conifer seedling occurrence and its early survival on different microsites in stands with or without *Sasa* understory in a subalpine old-growth forest of northern Yatsugatake mountains, central Japan. Specific questions are as follows:

1. What microsites are suitable for seedling recruitment of four major coniferous species (*Abies mariesii* Masters, *A. veitchii* Lindley, *P. jezoensis* var. *hondoensis* (Sieb. et Zucc.) Carriere, and *Tsuga diversifolia* (Maxim.) Masters) in a subalpine old-growth forest?
2. What are the effects of *Sasa* for the recruitment of conifer seedlings on various microsites, especially soil and fallen logs?

2. Methods

2.1. Study area

This study was conducted in the northern Yatsugatake mountains (36°00'N, 138°23'E, up to 2645 m a.s.l.) in central Japan (Fig. 1). These mountains are dead volcanoes and the surface in this region is composed of andesitic lavas, which originated in the Pleistocene or the Holocene (Tsuchida, 1991). The climatic and vegetational features were described by Oshima et al. (1958), Kimura (1963), and Franklin et al. (1979). The mean annual temperature is ca. 2 °C, and August (mean 21 °C) and February (mean –11 °C) are

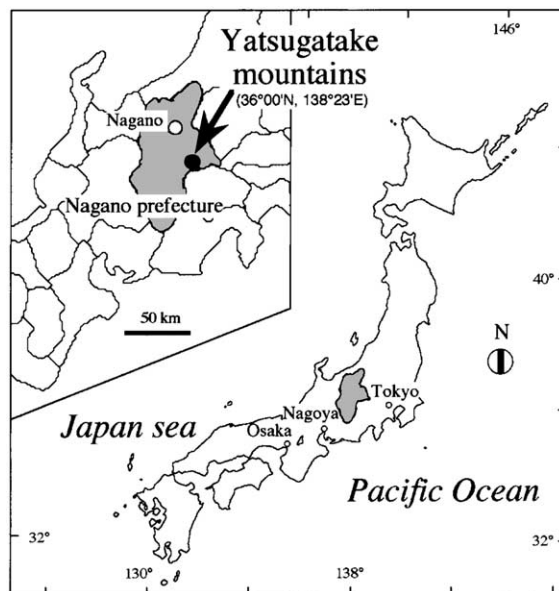


Fig. 1. The location of northern Yatsugatake mountains in central Japan.

the warmest and the coldest months, respectively. Annual precipitation is 1500–2000 mm. Subalpine coniferous forests grow between 1800–2500 m a.s.l.. Forests dominated by *A. mariesii* and *A. veitchii* cover a wide range of soil conditions and those dominated by *T. diversifolia* grow on very stony soils. Mosses or herbs usually cover the floors of most *Abies* forests, while *Sasa* sometimes grows on the floors of stands with deep, fine-textured volcanic-ash soils.

Two extensive (>20 ha), old-growth, unlogged stands (about 2200 m a.s.l.) were sampled near Shirakomaike pond in the northern Yatsugatake mountains. The stands are gently sloping topographies (mean inclination is 5°) and northwesterly aspects. One is covered by *Sasa hayatae* Makino understory (*Sasa* stand); the other is not (non-*Sasa* stand) and a seedling-sapling bank of conifers is developed. The number and basal area of stems ≥ 5 cm of DBH were not substantially different between the non-*Sasa* and the *Sasa* stands (Table 1; χ^2 -test, $P > 0.05$). Both stands were dominated by *T. diversifolia*, *A. mariesii*, and *P. jezoensis* var. *hondoensis*. In the *Sasa* stand, *Betula ermanii* was also important. The heights of the forest canopy were 25–30 m. Nomenclature follows Ohwi and Kitagawa (1983).

2.2. Plot setting and sampling

We established a 1 ha (100 m \times 100 m) permanent plot in a representative part of each stand. Quadrats (2 m \times 2 m) were systematically located within the

1 ha plot. Since two quadrats were in a small stream in the non-*Sasa* stand, they were omitted. Total area of quadrats were 132 m² (4 m² \times 33) and 124 m² (4 m² \times 31) in the *Sasa* stand and the non-*Sasa* stand, respectively. Each quadrat was divided into four 1 m \times 1 m subquadrats for convenient of investigation of seedlings, *Sasa*, and area of microsites. We recorded the percentage area occupied with microsites in each subquadrat as soil, fallen logs, stumps, buttresses, root mounds, or rocks. In the *Sasa* stand, we also recorded the coverage and the number of culms of *Sasa*, and measured the culm height in each subquadrat. The mean values of the four subquadrats were adopted as representative values of each 4 m² quadrat.

The quadrats were classified into three types according to the coverage of *Sasa*. Quadrats located in the non-*Sasa* stand, that is coverage of *Sasa* = 0%, were called N-quadrats. Quadrats in the *Sasa* stand were separated into Sn-quadrats (0% \leq coverage of *Sasa* < 40%) and Ss-quadrats (coverage of *Sasa* \geq 40%). Since 1997 was a mast year of seed production of *Abies* and *T. diversifolia*, many current seedlings were observed on the forest floor in 1998. In June 1998, current (individuals which emerged in 1998) and old (age ≥ 1 year old, height ≤ 15 cm) seedlings of all conifers within each quadrat were marked with small numbered flags, and the species name and rooting microsite of seedlings were recorded. When juvenile seedlings of *A. mariesii* and *A. veitchii* could not be identified, they were recorded together as *Abies*. Additional emergence

Table 1

Number (ha⁻¹), diameter at breast height (DBH mean \pm S.D., cm), and basal area (m² ha⁻¹) of stems (≥ 5 cm of DBH) in the 1 ha plot of stands without (non-*Sasa* stand) or with (*Sasa* stand) *Sasa* understory in a subalpine old-growth forest, central Japan^a

Species	Non- <i>Sasa</i> stand			<i>Sasa</i> stand		
	Number	DBH	Basal area	Number	DBH	Basal area
<i>A. mariesii</i>	258	17.5 \pm 13.9 (55.7)	6.18	257	15.7 \pm 11.5 (51.0)	4.99
<i>A. veitchii</i>	70	24.6 \pm 15.3 (69.7)	3.34	59	24.6 \pm 11.7 (47.8)	2.80
<i>P. jezoensis</i> var. <i>hondoensis</i>	20	53.5 \pm 16.2 (77.2)	4.49	24	40.4 \pm 11.6 (63.4)	3.07
<i>T. diversifolia</i>	217	37.1 \pm 14.7 (75.8)	23.47	248	33.4 \pm 12.6 (78.3)	21.68
<i>B. ermanii</i>	23	38.7 \pm 12.6 (57.3)	2.71	100	35.6 \pm 10.5 (59.4)	9.97
<i>B. corylifolia</i>	14	30.7 \pm 8.0 (54.1)	1.04	3	29.7 \pm 3.5 (33.1)	0.21
Total	602		41.21	691		42.73

^a The values of maximum DBH are given in parentheses. The data were derived from a total measure of the 1 ha plot.

and mortality were detected in censuses with about 1 month interval from June to September 1998.

2.3. Data analysis

To check whether the proportion of microsites on the forest floor is significantly different between the non-*Sasa* and the *Sasa* stands, we used a χ^2 -test. To check the difference between Sn- and Ss-quadrats, we used a *t*-test for the number and the culm height of *Sasa* and a Mann–Whitney *U*-test for the coverage of *Sasa*. Though, we recorded rooting microsites of seedlings by six types, we especially compared the occurrence and survival rate of seedlings on soil and fallen logs, because number of seedlings on other microsites, such as stumps, buttresses, root mounds, and rocks were not enough for statistical analysis. Because investigated areas of soil and fallen logs were different, we used the difference of observed values from expected values of seedlings, which were calculated from percentage occupied area of microsites, for the statistical analysis. The expected value of seedlings on each microsite = (total number of seedlings) \times (each microsite area of quadrats/total area of quadrats). To determine whether the numbers of current or old seedlings on two microsites are significantly different, we used a χ^2 -test for two microsites. To check the difference of survival rate of current seedlings on soil and fallen logs, we also used a χ^2 -test.

3. Results

3.1. Microsites and *Sasa*

Six types of microsites, such as soil, fallen logs, stumps, buttresses, root mounds, and rocks were observed; rocks did not exist in the *Sasa* stand (Table 2). The proportion of each microsite area on the forest floor was similar between two stands, and no significant difference was detected (χ^2 -test, $P > 0.05$). Soil comprised almost two-thirds of the forest floor in both stands, and fallen logs occupied 13–16% of the forest floor. Only about 12–19% were occupied by other microsites.

In the *Sasa* stand, all values of the *Sasa* characteristics (number, coverage, and culm height) were

Table 2

Percentage area (%) occupied by various microsites (soil, fallen logs, stumps, buttresses, root mounds, and rocks) on the forest floor in stands without (non-*Sasa* stand) and with (*Sasa* stand) *Sasa* understorey in a subalpine old-growth forest, central Japan

Microsite	Non- <i>Sasa</i> stand	<i>Sasa</i> stand
Soil	65.4	74.8
Fallen logs	15.5	13.2
Stumps	6.3	2.0
Buttresses	6.3	9.1
Root mounds	0.6	0.9
Rocks	5.8	0
Total	100.0	100.0

obviously higher in Ss-quadrats than in Sn-quadrats (Table 3; *t*-test and Mann–Whitney *U*-test, $P < 0.01$).

3.2. Old seedlings on different microsites

A total of 1486 old seedlings occurred in three types of quadrat (Table 4). Number of old seedlings varied largely among species, degree of *Sasa* coverage, and microsites. *A. mariesii* or *A. veitchii* was the most, and *P. jezoensis* var. *hondoensis* was the least abundant species in all quadrats. Most old seedlings occurred on soil and fallen logs, and those on other microsites were about 10% of total number of old seedlings. Of *Abies*, occurrence of old seedlings was mainly on soil, but some seedlings on other microsites, such as fallen logs, stumps, buttresses, and rocks. Of *P. jezoensis* var. *hondoensis* and *T. diversifolia*, occurrence of old seedlings was mainly on fallen logs.

Table 3

Number (mean \pm S.D., culms m^{-1}), coverage (mean \pm S.D., %), and culm height (mean \pm S.D., cm) of *Sasa* in the *Sasa* stand. Sn-quadrat: quadrats with *Sasa* cover $< 40\%$; Ss-quadrat: quadrats with *Sasa* cover $\geq 40\%$ ^a

	Quadrat	
	Sn-quadrat	Ss-quadrat
Number	11.8 \pm 16.2 (0–51)	30.3 \pm 19.2 (0–85)**
Coverage	13.5 \pm 16.0 (0–35)	66.4 \pm 24.6 (40–100)**
Culm height	44.9 \pm 24.0 (10–95)	67.1 \pm 19.4 (25–105)**

^a Range of values is given in parentheses. Symbols mean significant differences between Sn- and Ss-quadrats (*t*-test and Mann–Whitney *U*-test.

** $P < 0.01$.

Table 4

Absolute number of old seedlings (age ≥ 1 year old and height ≤ 15 cm) occurred on different microsites and area of each microsite (m^2) in a subalpine old-growth forest, central Japan^a

Quadrat	Total	Microsite					
		Soil	Fallen logs	Stumps	Buttresses	Root mounds	Rocks
N-quadrat species							
<i>A. mariesii</i>	342	274	29	10	20	0	9
<i>A. veitchii</i>	100	69	15	1	13	0	2
<i>Abies</i> ^b	103	61	34	3	1	0	4
<i>P. jezoensis</i> var. <i>hondoensis</i>	47	1	44	0	1	0	1
<i>T. diversifolia</i>	115	34	73	3	3	0	2
Area of microsite	124.0	81.1	19.3	7.9	7.9	0.8	7.2
Sn-quadrat species							
<i>A. mariesii</i>	145	133	6	3	3	0	0
<i>A. veitchii</i>	252	223	10	10	9	0	0
<i>Abies</i> ^b	157	117	24	10	6	0	0
<i>P. jezoensis</i> var. <i>hondoensis</i>	2	0	2	0	0	0	0
<i>T. diversifolia</i>	54	15	30	1	6	2	0
Area of microsite	56.0	39.2	6.2	1.6	8.4	0.8	0
Ss-quadrat species							
<i>A. mariesii</i>	38	17	15	0	6	0	0
<i>A. veitchii</i>	67	37	20	0	9	1	0
<i>Abies</i> ^b	33	12	15	0	6	0	0
<i>P. jezoensis</i> var. <i>hondoensis</i>	5	0	4	0	1	0	0
<i>T. diversifolia</i>	26	0	15	0	11	0	0
Area of microsite	76.0	59.6	11.3	1.1	3.6	0.4	0

^a N-quadrat: quadrats in the non-*Sasa* stand; Sn-quadrat: quadrats with *Sasa* cover $< 40\%$ in the *Sasa* stand; Ss-quadrat: quadrats with *Sasa* cover $\geq 40\%$ in the *Sasa* stand.

^b Could not be identified to species.

Table 5

Number of old seedlings (age ≥ 1 year old and height ≤ 15 cm) on soil and fallen logs in N-quadrat, Sn-, and Ss-quadrats^a

Species	N-quadrat		Sn-quadrat		Ss-quadrat	
	Soil	Fallen logs	Soil	Fallen logs	Soil	Fallen logs
<i>Abies</i> ^b	404 (389)	78 (93) n.s.*	473 (443)	40 (70)**	66 (98)	50 (18)**
<i>A. mariesii</i>	274 (245)	29 (58)**	133 (120)	6 (19)**	17 (27)	15 (5)**
<i>A. veitchii</i>	69 (68)	15 (16) n.s.*	223 (201)	10 (32)**	37 (48)	20 (9)**
<i>Abies</i> ^c	61 (77)	34 (18)**	117 (122)	24 (19) n.s.*	12 (23)	15 (4)**
<i>P. jezoensis</i> var. <i>hondoensis</i>	1 (36)	44 (9)**	0 (2)	2 (0)	0 (3)	4 (1)
<i>T. diversifolia</i>	34 (86)	73 (21)**	15 (39)	30 (6)**	0 (13)	15 (2)

^a N-quadrat: quadrats in the non-*Sasa* stand; Sn-quadrat: quadrats with *Sasa* cover $< 40\%$ in the *Sasa* stand; Ss-quadrat: quadrats with *Sasa* cover $\geq 40\%$ in the *Sasa* stand.

^b *Abies mariesii* + *A. veitchii* + unidentified *Abies*. Number of seedlings on each microsite was compared with a χ^2 -test. The expected values of seedlings on each microsite are given in parentheses. The expected value of seedlings on each microsite = (total number of seedlings) \times (each microsite area of quadrats/total area of quadrats). d.f. = 1.

* $P > 0.05$ (n.s.).

** $P < 0.01$.

^c Could not be identified to species.

In N-quadrats, old seedlings of *A. mariesii* occurred more frequently on soil than on fallen logs (Table 5; χ^2 -test, $P < 0.01$), while occurrence of those of *A. veitchii* was not different between two microsites (χ^2 -test, $P > 0.05$). In Sn-quadrats, both old seedlings occurred significantly more frequently on soil than on fallen logs (χ^2 -test, $P < 0.01$). On the other hand, in Ss-quadrats, they occurred significantly more frequently on fallen logs than on soil (χ^2 -test, $P < 0.01$). Of *P. jezoensis* var. *hondoensis* and *T. diversifolia*, old seedlings occurred much more frequently on fallen logs than on soil (Table 5; χ^2 -test, $P < 0.01$). On soil, only one old seedling of *P. jezoensis* var. *hondoensis* occurred in N-quadrats, and old seedlings of *P. jezoensis* var. *hondoensis* in Sn- and Ss-quadrats and those of *T. diversifolia* in the Ss-quadrats did not occur.

3.3. Occurrence and survivorship of current seedlings on different microsites

A total of 1834 current seedlings occurred on soil and fallen logs in three types of quadrats; total number of current seedlings for *Abies*, *P. jezoensis* var. *hondoensis* and *T. diversifolia* was 400, 167, and 1267, respectively. Many current seedlings of *Abies* emerged mainly from June to July, while those of *P. jezoensis* var. *hondoensis* and *T. diversifolia* emerged mostly in July (Fig. 2). Many current seedlings died as soon as emerged, and the 42.8–50.1% of current seedlings died by the end of September 1998. Although, the survival rates were different, these trends did not vary among species, quadrats, and microsites.

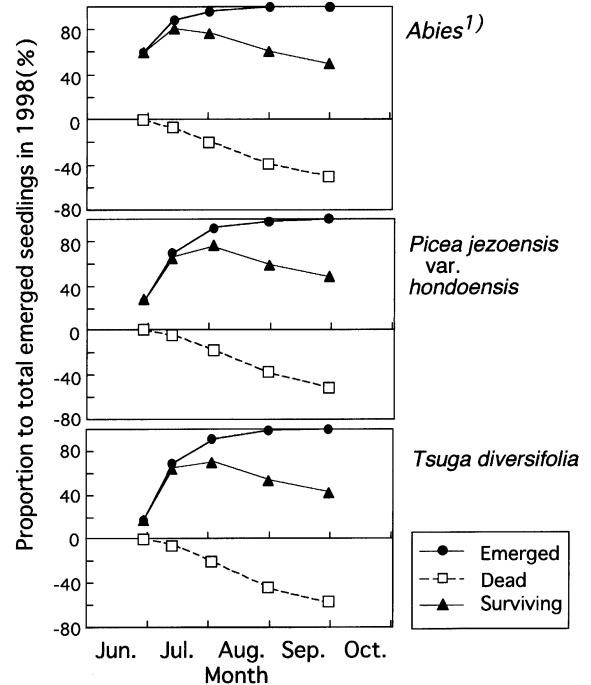


Fig. 2. Proportion of emerged, dead, and surviving current seedlings to total emerged seedlings from June to October 1998. *Abies*: could not be identified to species.

The difference in abundance of current seedlings emerged in 1998 between on soil and on fallen logs was small compared with that of old seedlings. The occurrence of *Abies* current seedlings was not significantly different between two microsites in the N- and Sn-quadrats (Table 6; χ^2 -test, $P > 0.05$), but

Table 6
Number of current seedlings emerged in 1998 on soil and fallen logs in N-, Sn-, and Ss-quadrats^a

Species	N-quadrat		Sn-quadrat		Ss-quadrat	
	Soil	Fallen logs	Soil	Fallen logs	Soil	Fallen logs
<i>Abies</i> ^b	127 (123)	25 (29) n.s.*	124 (119)	14 (19) n.s.*	80 (92)	30 (18)**
<i>P. jezoensis</i> var. <i>hondoensis</i>	88 (100)	36 (24)**	10 (10)	2 (2) n.s.*	22 (26)	9 (5)**
<i>T. diversifolia</i>	185 (226)	95 (54)**	443 (444)	71 (70) n.s.*	310 (398)	163 (75)**

^a N-quadrat: quadrats in the non-*Sasa* stand; Sn-quadrat: quadrats with *Sasa* cover < 40% in the *Sasa* stand; Ss-quadrat: quadrats with *Sasa* cover \geq 40% in the *Sasa* stand

^b could not be identified to species. Number of current seedlings on each microsite was compared with a χ^2 -test. The expected values of seedlings on each microsite are given in parentheses. The expected value of seedlings on each microsite = (total number of seedlings) \times (each microsite area of quadrats/total area of quadrats). d.f. = 1.

* $P > 0.05$ (n.s.).

** $P < 0.01$.

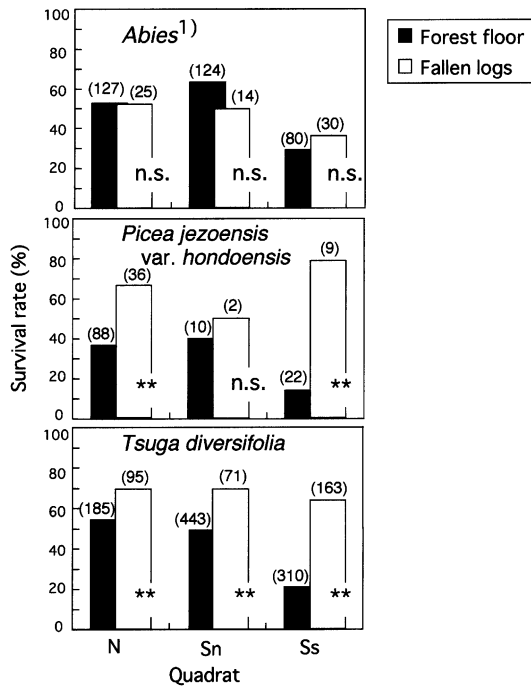


Fig. 3. Survival rates (%) of current seedlings emerged in 1998 on soil and fallen logs in different quadrats at last census. N-quadrat: quadrats in the non-*Sasa* stand; Sn-quadrat: quadrats with *Sasa* cover < 40% in the *Sasa* stand; Ss-quadrat: quadrats with *Sasa* cover \geq 40% in the *Sasa* stand. Number of current seedlings on each microsite is given in parentheses. Symbols: (n.s.) $P > 0.05$; (*) $P < 0.05$; (**) $P < 0.01$ (χ^2 -test, d.f. = 1). *Abies*: could not be identified to species.

was greater in number on fallen logs than on the soil in Ss-quadrats (χ^2 -test, $P < 0.01$). *P. jezoensis* var. *hondoensis* and *T. diversifolia*, were not significantly different between two microsites in Sn-quadrats (χ^2 -test, $P > 0.05$), but significantly greater in number on fallen logs than on the soil in other quadrats (χ^2 -test, $P < 0.01$).

Survival rate of current *Abies* seedlings at final census time was not significantly different between on soil and on fallen logs, although that on soil was slightly higher in Sn-quadrats, and slightly higher on fallen logs in Ss-quadrats (Fig. 3; χ^2 -test, $P > 0.05$). Of *P. jezoensis* var. *hondoensis*, survival rate of current seedlings was not significantly different in Sn-quadrats (χ^2 -test, $P > 0.05$), but significantly higher on fallen logs than on soil in N- and Ss-quadrats (χ^2 -test, $P < 0.01$). The survival rate of current *T. diversifolia* seedlings was consistently higher on fallen logs than

on soil, regardless of the degree of *Sasa* coverage (χ^2 -test, $P < 0.01$).

4. Discussion

4.1. Safe site for seedlings of four conifer species

The suitable microsite for seedling recruitment varies with genus or species. Harper (1977) named this site as a 'safe site'. In this study, occurrence of old seedlings of *P. jezoensis* var. *hondoensis* and *T. diversifolia* was significantly greater in number on fallen logs than on soil. For these species, fallen logs would appear to be safe sites for their seedling recruitment. Similar results have been obtained for *P. engelmannii* by Knapp and Smith (1982), for *T. diversifolia* by Nakamura (1992), and for *P. sitchensis* and *T. heterophylla* by Harmon and Franklin (1989).

Some studies reported that *Abies* seedlings can occur on soil (Knapp and Smith, 1982; Taylor and Qin, 1988), but others indicate that *Abies* seedlings recruited on fallen logs for *A. alba* (Szewczyk and Szwagrzyk, 1996) and *A. sachalinensis* (Takahashi, 1997). In this study, *Abies* seedlings could occur on soil as well as fallen logs, as there was no significant difference for the occurrence of its old seedlings on both microsites in the non-*Sasa* stand (Table 5). The plausible explanation of these phenomena is the difference of seed size (Grubb, 1977; Gray and Spies, 1997). Larger seeds produce larger seedlings with rapidly growth of long root compared with smaller seeds (Schaal, 1980; Knapp and Smith, 1982). Rapid root growth and penetration into soil may be important for avoiding drought or temperature extremes (Baker, 1972). In this study, *P. jezoensis* var. *hondoensis* ($(178-199) \times 10^3$ seeds m^{-3}) and *T. diversifolia* ($(71-142) \times 10^3$ seeds m^{-3}) seeds are smaller ones, while *A. mariesii* (18×10^3 seeds m^{-3}) and *A. veitchii* (24×10^3 seeds m^{-3}) seeds are larger one (Asakawa et al., 1981). For *Picea* and *Tsuga* seedlings, a thick litter layer on the forest floor may prevent their roots reaching the mineral soil (Knapp and Smith, 1982; Gray and Spies, 1997). *Abies* seedlings, which germinated from large seeds, have long root and can penetrate into deep soil (Zobel and Antos, 1991). Seed characteristics and early growth of seedlings

would decide the variation of safe site for seedling recruitment.

Suitable microsites for the recruitment of conifer seedlings were formed at various stages after seedling emergence on the forest floor. Although, main cause to characterize various safe sites is thought to be seed size, other hypothesis have been proposed, such as burial by litter (Christy and Mack, 1984), pathogen (McKee et al., 1982), and competition with understory vegetation (Harmon and Franklin, 1989). If the timing to characterize the safe site varies, seedlings might be affected by various causes at different growth stages. The results suggest that the factors before and after seedling emergence interact to determine the recruitment of seedlings on different microsites.

4.2. Effects of *Sasa* on the seedling recruitment

Occurrence of old seedlings on soil and fallen logs was strongly affected by *Sasa*. Density and decaying degree of fallen logs were similar irrespective of presence or absence of *Sasa* (Narukawa and Yamamoto, unpublished data). Density of old *Abies* seedlings on fallen logs decreased a little with increased coverage of *Sasa*, 39 and $38 \times 10^3 \text{ ha}^{-1}$ in Sn- and Ss-quadrats, respectively. While that on soil decreased largely; 121 and $11 \times 10^3 \text{ ha}^{-1}$ in Sn- and Ss-quadrats, respectively. Thus, the occurrence of old *Abies* seedlings was relatively greater in number on fallen logs under *Sasa* cover. Many studies revealed that presence of *Sasa* understory inhibits the seedling recruitment of many tree species (Nakashizuka and Numata, 1982a,b; Nakashizuka, 1987, 1988; Hiura et al., 1996; Takahashi, 1997). Vigorous growth and high density of *Sasa* culms reduce space for seedling growth and dense cover decreases understory light on the forest floor. Its litter is difficult to decompose and the thick litter layer on the soil prevents seedling recruitment on the forest floor. Fallen logs, which are 'elevated sites', can probably have more light and avoid invading *Sasa* (Yamamoto, 1993). Our results show that relative importance of fallen logs for seedling recruitment site of *Abies* increased under the presence of *Sasa* understory. For *Picea* and *Tsuga*, elevated surfaces were primarily important as a recruitment site irrespective of the presence or absence of *Sasa*. Under dense *Sasa* cover in the subalpine coniferous forest, elevated sites, such as fallen logs therefore become more important as

the recruitment site not only for *P. jezoensis* var. *hondoensis* and *T. diversifolia* seedlings but also for *Abies* seedlings.

4.3. Fallen logs as a recruitment site

This study also indicates characteristics of two microsites, such as soil and fallen logs on the forest floor. The surface area of fallen logs covered on the forest floor was small (13.3–15.5%), which is similar or a little larger compared with other values reported (Graham and Cromack, 1982; Szewczyk and Szwagrzyk, 1996). On the other hand, soil covered large area of the forest floor. Therefore, tree recruitment on soil seems to be more abundant than on fallen logs. However, seedlings on soil are more affected by the suppression by understory vegetation, such as *Sasa*, compared with those on fallen logs. Veblen (1986) showed that dominant *Abies lasiocarpa* had a greater recruitment rate and survival rate for its canopy population, but minor *Picea engelmannii* could maintain its present abundance because its lower recruitment rate was compensated by a lower mortality rate and a longer longevity in the North American spruce-fir forest. In this study, *Abies* seedlings have variation for the recruitment site, they can usually recruit on soil and change their major recruitment site into fallen logs under dense *Sasa* cover. For *P. jezoensis* var. *hondoensis* and *T. diversifolia*, recruitment sites are restricted to fallen logs, which are small but unaffected microsite. It is suggested that the various characteristics of species life history and the presence of various microsites, and their interactions with *Sasa* may be one of possible factors to maintain the coexistence of conifers in subalpine coniferous forest in Japan.

Acknowledgements

We thank the Usuda District Forest Office for permitting this survey, and K. Kato and the member of Forest Ecology and Physiology Laboratory at Nagoya University for supporting the field survey. We also thank to S. Abe, M.E. Harmon, S. Iida, H. Tanouchi, and N. Tomaru for their helpful advices for this study, and to two anonymous reviewers for their kind comments on this paper.

References

- Asakawa, S., Katsuta, M., Yokoyama, T., 1981. Seeds of woody plants in Japan: Gymnospermae, Japan Forest Tree Breeding Association, Tokyo, Japan (in Japanese).
- Baker, H.G., 1972. Seed weight in relation to environmental conditions in California. *Ecology* 53, 997–1010.
- Beatty, S.W., Stone, E.L., 1986. The variety of microsites created by tree falls. *Can. J. For. Res.* 16, 539–548.
- Campbell, J.J.N., 1985. Bamboo flowering patterns: a global view with special reference to east Asia. *J. Am. Bamboo Soc.* 6, 17–35.
- Christy, E.J., Mack, R.N., 1984. Variation in demography of juvenile *T. heterophylla* across the substratum mosaic. *J. Ecol.* 72, 75–91.
- Duncan, R.P., 1993. Flood disturbance and the coexistence of species in a lowland podocarp forest, South Westland, New Zealand. *J. Ecol.* 81, 403–416.
- Franklin, J.F., Dyrness, C.T., 1973. Natural vegetation of Oregon and Washington. United States Forest Service General Technical Report PNW-8, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.
- Franklin, J.F., Maeda, T., Ohsumi, Y., Matsui, M., Yagi, H., Hawk, G.M., 1979. Subalpine coniferous forests of central Honshu, Japan. *Ecol. Monogr.* 49, 311–334.
- Graham, R.L., Cromack Jr., K., 1982. Mass, nutrient content and decay rate of dead boles in rain forests of Olympic National Park. *Can. J. For. Res.* 12, 511–521.
- Gray, A.N., Spies, T.A., 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. *Ecology* 78, 2458–2473.
- Grubb, P.J., 1977. The maintenance of species-richness in plant communities: The importance of regeneration niche. *Biol. Rev. Cambridge Philosophical Soc.* 52, 107–145.
- Harmon, M.E., Franklin, J.F., 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology* 70, 48–59.
- Harper, J.L., 1977. *The Population Biology of Plants*. Academic Press, New York.
- Hiura, T., Sano, J., Konno, Y., 1996. Age structure and response to fine-scale disturbances of *Abies sachalinensis*, *P. jezoensis*, *Picea glehnii*, and *Betula ermanii* growing under the influence of a dwarf bamboo understory in northern Japan. *Can. J. For. Res.* 26, 289–297.
- Kimura, M., 1963. Dynamics of vegetation in relation to soil development in northern Yatsugatake Mountains. *Jpn. J. Bot.* 18, 255–287.
- Knapp, A.K., Smith, W.K., 1982. Factors influencing understory seedling establishment of engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. *Can. J. Bot.* 60, 2753–2761.
- Kohyama, T., 1984. Regeneration and coexistence of two *Abies* species dominating subalpine forests in central Japan. *Oecologia* 62, 156–161.
- Kubota, Y., Konno, Y., Hiura, T., 1994. Stand structure and growth patterns of understory trees in a coniferous forest, Taisetsuzan National Park, northern Japan. *Ecol. Res.* 9, 333–341.
- Lusk, C.H., 1995. Seed size, establishment sites and species coexistence in a Chilean rain forest. *J. Veg. Sci.* 6, 249–256.
- Makita, A., 1992. Survivorship of a monocarpic bamboo grass, *Sasa kurilensis*, during the early regeneration process after mass flowering. *Ecol. Res.* 7, 245–254.
- Makita, A., Konno, Y., Fujita, N., Takada, K., Hamabata, E., 1993. Recovery of a *Sasa tsuboiana* population after mass flowering and death. *Ecol. Res.* 8, 215–224.
- McKee, A., Laroi, G., Franklin, J.F., 1982. Structure, composition and reproductive behavior of terrace forests, South Fork Hoh River, Olympic National Park. In: Starkey, E.E., Franklin, J.F., Matthews, J.W. (Eds.), *Ecological Research in National Parks of the Pacific Northwest*. OR State University, Forest Research Laboratory, Corvallis, Oregon, pp. 22–29.
- Nakamura, T., 1992. Effect of bryophytes on survival of conifer seedlings in subalpine forests of central Japan. *Ecol. Res.* 7, 155–162.
- Nakashizuka, T., 1987. Regeneration dynamics of beech forests in Japan. *Vegetatio* 69, 169–175.
- Nakashizuka, T., 1988. Regeneration of beech (*Fagus crenata*) after the simultaneous death of undergrowing dwarf bamboo (*Sasa kurilensis*). *Ecol. Res.* 3, 21–35.
- Nakashizuka, T., 1989. Role of uprooting in composition and dynamics of an old-growth forest in Japan. *Ecology* 70, 1273–1278.
- Nakashizuka, T., Numata, M., 1982a. Regeneration process of climax beech forests. I: Structure of a beech forest with the undergrowth of *Sasa*. *Jpn. J. Ecol.* 32, 57–67.
- Nakashizuka, T., Numata, M., 1982b. Regeneration process of climax beech forests II: Structure of a forest under the influences of grazing. *Jpn. J. Ecol.* 32, 473–482.
- Ohwi, J., Kitagawa, M., 1983. *New Flora of Japan*. Shibun, Tokyo.
- Orians, G.H., 1982. The influence of tree-falls in tropical forests on tree species richness. *Tropical Ecol.* 23, 255–279.
- Oshima, Y., Kimura, M., Iwaki, H., Kuroiwa, S., 1958. Ecological and physiological studies on the vegetation of Mt. Shimagare I: Preliminary survey of the vegetation of Mt. Shimagare. *Bot. Mag., Tokyo* 71, 289–300.
- Peterson, C.J., Pickett, S.T.A., 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. *J. Veg. Sci.* 1, 657–662.
- Peterson, C.J., Carson, W.P., McCarthy, B.C., Pickett, S.T.A., 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. *Oikos* 58, 39–46.
- Putz, F.E., 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* 64, 1069–1074.
- Schaal, B.A., 1980. Reproductive capacity and seed size in *Lupinus texensis*. *Am. J. Bot.* 67, 703–709.
- Shidei, T., 1974. Forest vegetation zones. In: Numata, M. (Ed.), *The Flora and Vegetation of Japan*. Kodansha, Tokyo and Elsevier, Amsterdam, pp. 87–124.
- Suzuki, E., Ota, K., Fuziwara, K., 1987. Regeneration process of coniferous forests in northern Hokkaido I: *Abies sachalinensis* forest and *Picea glehnii* forest. *Ecol. Res.* 2, 61–75.
- Szewczyk, J., Szwagrzyk, J., 1996. Tree regeneration on rotten wood and on soil in old-growth stand. *Vegetation* 122, 37–46.

- Takahashi, K., 1994. Effect of size structure, forest floor type and disturbance regime on tree species composition in a coniferous forest in Japan. *J. Ecol.* 82, 769–773.
- Takahashi, K., 1997. Regeneration and coexistence of two subalpine conifer species in relation to dwarf bamboo in the understorey. *J. Veg. Sci.* 8, 529–536.
- Taylor, A.H., Qin, Z., 1988. Regeneration patterns in old-growth *Abies-Betula* forests in the Wolong natural reserve, Sichuan, China. *J. Ecol.* 76, 1204–1218.
- Tsuchida, K. (Ed.), 1991. *Nature in Mt. Yatsugatake*. Shinano–Mainichi Press, Nagano, Japan (in Japanese).
- Veblen, T.T., 1982. Growth patterns of *Chusquea* bamboos in the understory of Chilean *Nothofagus* forests and their influences in forest dynamics. *Bull. Torrey Bot. Club* 109, 474–487.
- Veblen, T.T., 1986. Treefalls and the coexistence of conifers in subalpine forests of the central Rockies. *Ecology* 67, 644–649.
- Yamamoto, S., 1993. Gap characteristics and gap regeneration in a subalpine coniferous forest on Mt. Ontake, central Honshu, Japan. *Ecol. Res.* 8, 277–285.
- Yamamoto, S., 1995. Gap characteristics and gap regeneration in subalpine old-growth coniferous forests, central Japan. *Ecol. Res.* 10, 31–39.
- Zobel, D.B., Antos, J.A., 1991. Growth and development of natural seedlings of *Abies* and *Tsuga* in old-growth forest. *J. Ecol.* 79, 985–998.