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Regeneration processes of a boreal forest in Kamchatka with special reference to the contribution of sprouting to population maintenance

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Abstract

We studied regeneration patterns of three tree species *Picea ajanensis*, *Betula platyphylla* and *Populus tremula* from 1998 to 2000 in the Central Depression of the Kamchatka Peninsula. We paid special attention to the contribution of sprouting to their regeneration. *P. ajanensis* was the only species that regenerated by seedling. In a 40 × 40 m study plot, the density of *P. ajanensis* saplings < 2.0 cm in diameter at basal area (DBH) was 1132, and this was the highest among the three species studied. The number of saplings $\geqslant$ 2 cm in DBH declined sharply with size class. The spatial distribution of *P. ajanensis* saplings (< 2 cm in DBH) showed a significant positive correlation with that of adult trees and a negative correlation with that of gaps. These trends were not changed after re-measurement in 2000, although nearly half of the juveniles had died or been injured during the two years. These results suggest that small *Picea* saplings prefer habitats under the canopy of adult trees rather than in gaps for establishment. Most small individuals of *B. platyphylla* were produced from sprouts. The number of saplings in the smallest size class (< 2 cm in DBH) was much less than that of *P. ajanensis*, although the number of larger individuals did not decrease remarkably. The spatial distribution of *B. platyphylla* saplings showed a positive correlation with that of adult trunks and a negative correlation with that of canopy trees of *P. ajanensis*. These results suggest an effective contribution of sprouts to the regeneration of *B. platyphylla*. *P. tremula* was the only species that could invade big gaps and produce many root suckers efficiently. There were 181 suckers of *P. tremula* in the smallest size class (< 2 cm in DBH) in the study plot, although the number of saplings $\geqslant$ 2 cm in DBH declined abruptly. The spatial distribution of saplings of this species showed a slight positive correlation with that of gaps, and negative correlation with that of adult trees of *B. platyphylla*, *P. ajanensis*, and *P. tremula*. The root suckering strategy of *P. tremula* might be adaptive under severe conditions in high-latitude regions. Our data suggest, however, that it does not necessarily contribute to regeneration in mature forests. The three component species in this forest did not seem to utilize canopy gaps for regeneration; we suggest that gap dynamics do not work in this forest. The sparse canopy, which is a typical character of forests in high-latitude regions, might be a consequence of high mortalities of seedlings and root suckers inside gaps.

Introduction

It is well known that many tree species maintain their populations not only by seeds or seedlings but also by producing sprouts to survive under severe disturbance or stressful conditions (Putz et al. 1983; Koop 1987; Putz and Brokaw 1989; Peterson and Pickett 1991; Sakai et al. 1995). In high-altitude or high-latitude regions, for example, many studies have suggested that sprouting strategies play a very important role on vegetation transition or community dynamics (Peterson and Squiers 1995b; Peterson and Jones 1997; Homma 1997). Thus, the forest dynamics under stressful conditions should be recognized from a viewpoint of combination of seedling regeneration and sprouting. However, only a few studies of forest dynamics have taken this viewpoint (Sonoyama et al. 1997).

The morphological diversity of sprouting strategies has not been fully clarified yet and the classification system is still tentative (see Jeník (1994)). Nevertheless, it is reasonable to classify sprouting into two categories in terms of morphology: 1) trunk suckering, in which plants produce suckers from the trunk or root collar: and 2) root suckering, in which plants produce suckers from roots in the soil (Peterson and Jones 1997). These two strategies may play a similar role in population maintenance in terms of replacement of old or dead trunks by new vigorous ones. Root suckering, however, should be distinguished from trunk suckering, because it has a special potential to utilize canopy gaps and to produce suckers at remote sites from the mother trunk's position (Ogawa et al. 1999; Kitamura et al. 2000).

In this paper, we describe regeneration processes of a *Picea – Betula – Populus* forest in the Central Depression of the Kamchatka Peninsula. Forest dynamics in the Kamchatka Peninsula, which has typical boreal forests of the Asia Pacific region, have not been fully clarified yet. *Picea ajanensis*, *Larix cajanderi*, *Betula platyphylla*, and *Populus tremula* often dominate forests in the Central Depression (Kojima 1994), and the regeneration strategy of each species is remarkably different. The two coniferous species (*P. ajanensis and L. cajanderi*) regenerate by seed and seedlings, whereas the broad-leaved species (*B. platyphylla and P. tremula*) regenerate by a combination of seedling regeneration and sprouting (Takahashi et al. 2001a, 2001b). Moreover, the sprouting strategies of *B. platyphylla* and *P. tremula* differ. The former produces trunk suckers, whereas the latter produces root suckers. Thus, we are able to compare advantages and disadvantages of different regeneration strategies and to discuss the meaning of sprouting strategies in boreal forest communities.

Many studies of sprouting have been made in the context of species biology and plant physiology (Sakai et al. (1995); Cao and Peters (1998); Krasny and Johnson (1992); Shepperd and Smith (1993) etc.). On the other hand, role of sprouting in community dynamics have not been clarified enough, although some studies have been made (Hara 1987; Putz and Brokaw 1989; Peterson and Squiers 1995a, 1995b). In this paper we describe three different regeneration strategies quantitatively, and assess the effects of the three strategies on the spatial structure of the forest. Using our results, we discuss the character of community dynamics of the boreal forest.

Methods

Study site

The study was carried out in a coniferous – broadleaved mixed forest located in the Central Depression of the Kamchatka Peninsula, Russia (56°04′ N, 160°01′ E, 70 m a.s.l.; Figure 1). Annual precipitation recorded at the nearest weather observatory (Kozyrevsk: 56°03′ N, 159°53′ E, 50 m a.s.l.) was approximately 450 mm y^{-1}. (mean 1950–1983). The air temperature (1.5 m above ground level) was measured at the study site from October 1998 to July 1999 with an HOBO XTI weather monitoring station (Onset Computer Co., MA). Monthly mean temperatures in the coldest month (February 1999) and the warmest month (July 1999) were −17.8 °C and 8.1 °C, respectively. The mean daily minimum temperature in February 1999 was −23.3 °C.

A 1-ha plot (100 m × 100 m) was set up in August 1998 in a mature *Picea-Betula* stand on flat ground. Diameters at breast height (DBH) of all trunks $\geqslant$ 2 cm in DBH were measured inside the 1-ha plot. Another former paper by us (Takahashi et al. 2001a, 2001b) reports that only these three species formed the canopy layer. Three shrub species (*Crategus chlorosarca*, *Sorbus kamchatica and Salix bebbiana*) also grew, although they were very rare. The total trunk density was 1071 ha^{-1}, and the total basal area was 25.84 m^2 ha^{-1}. *P. ajanensis* accounted for 51.4% of relative basal area, *B. platyphylla* for 41.9%, and *P. tremula* for 6.6%. *L. cajanderi* was not found near the plot (Takahashi et al. 2001a, 2001b).

Tree measurement

In August 1998, a 40 × 40 m plot was set inside the 1 ha plot for seedling measurements. This plot was divided into sixty-four 5 × 5 m sub-plots. Locations of trunks $\geqslant$ 2 cm in DBH and shapes of canopies were

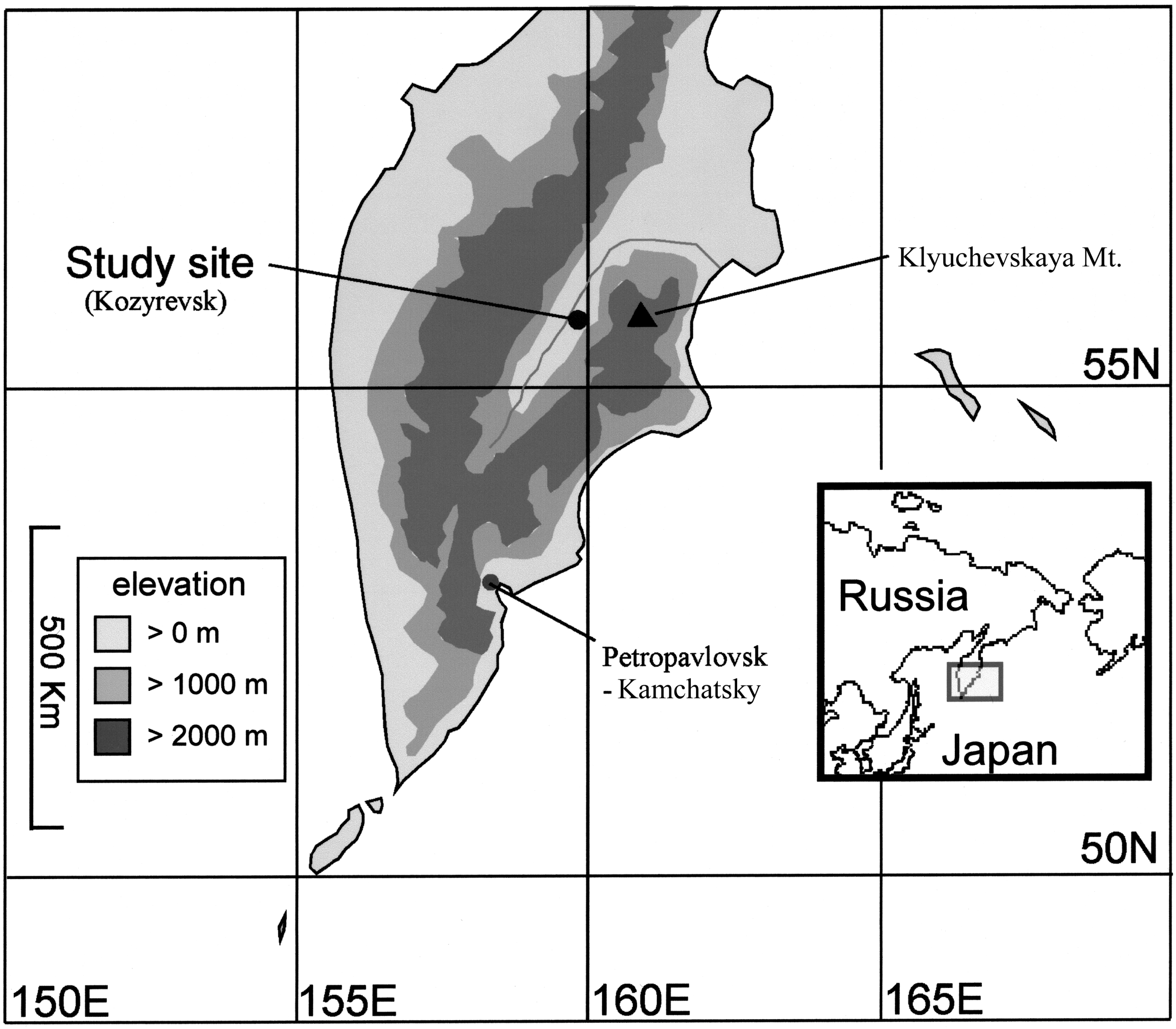

Figure 1. Location of study site.

recorded inside the 40 × 40 m plot, and a crown projection map was made. The numbers of juveniles < 2 cm in DBH were recorded in each sub-plot for analysis of the spatial distribution pattern. Colored plastic tapes numbered all root suckers of *P. tremula*. The mother trunks of all suckers of *B. platyphylla* were recorded. We could not number seedlings of *P. ajanensis* because there were too many.

In August 2000, seedlings inside each sub-plot were measured again to clarify the fate of juveniles. We checked all suckers of *B. platyphylla* and *P. tremula* that we recorded in 1998. Many seedlings of *P. ajanensis* had been injured or had died; we recorded the seedlings as sound, injured, or dead.

Measurements of Populus *root suckers*

All juveniles of *P. tremula* inside the study plot were root suckers. The locations of all suckers inside the plot were recorded, and their ages were estimated by counting the numbers of traces of bud-scales. We dug up specimens of roots and suckers and measured shoot length, shoot diameter at base, shoot growth in 1998 and 1997, shoot age, numbers of traces of dead suckers, root diameter, and abundance of radicles.

Data analysis

To clarify the spatial distribution pattern of juveniles and suckers, we analyzed the correlation between the percentage of canopy cover and the number of juve-

Table 1. Total basal area, relative basal area and DBH class frequency distribution of the three tree species (densities in 40 × 40 m sub-plot). In order to show the size distribution pattern of juveniles in detail, the numbers of trunks smaller than 10 cm DBH are shown at 2-cm intervals. The values of *P. ajanensis* are for seedlings and those of *P.tremula* are for root-suckers. The values of *B. platyphylla* are total numbers of trunks (seedlings + sprouts), and values in parentheses are the numbers of sprouts.

		Picea ajanensis	*Betula platyphylla*	*Populus tremula*
	< 2	1132	57 (55)	181
DBH size class (cm)	< 4	17	14 (9)	2
	< 6	9	6 (3)	0
	< 8	7	8 (3)	0
	< 10	3	4 (1)	0
	< 10	1168	89 (71)	183
DBH size class (cm)	< 20	11	27 (19)	1
	< 30	19	24 (17)	8
	30 ⩽	9	6 (3)	1
	total	1207	146 (110)	193
Basal Area (cm^2 $plot^{-1}$)		19,823.5	21,736.4	4618.9
Relative BA (%)		42.9	47.1	10.0

niles or suckers. Canopy openness and canopy coverage of each species in each sub-plot were estimated from the crown projection map of the 40 × 40 m plot.

In our study, the variables of *Populus* and *Betula* juveniles are not spatially independent because they are clonal species. In this case, we cannot employ usual statistical methods where independence of variables is assumed. Therefore, we employed the following randomization test where the horizontal spatial structures of juveniles and canopy trees were fixed in their own layers (Monte Carlo permutation test; Manly (1990); Palmer and van der Maarel (1995); Pecháčová et al. (1999)). The data sets of the 64 sub-plots were divided into canopy data and forest floor data, and re-sorted randomly. We calculated correlation coefficients for all 512 possible combinations of sub-plots for each layer; i.e. 2 reflections × 4 rotations × 8 x-shifts × 8 y-shifts of the canopy layer, keeping the forest floor layer fixed. If the observed R fell in either 5% tail of the calculated distribution of correlation coefficients, the correlation between the canopy and forest floor layers was assumed to be significantly different from random.

Nomenclature

We referred to the work of Yakubov (1997) for nomenclature.

Results

Species composition and population structure

The population structure and the regeneration pattern differed obviously among the three canopy species. All juveniles of *P. ajanensis* were produced from seeds, while most juveniles of the other species were produced from sprouts. The *P. ajanensis* population had 1132 juveniles in the smallest size class (< 2 cm in DBH; Table 1), but only 17 in the second smallest class (< 4 cm in DBH). The number of larger trunks (⩾ 10 cm in DBH) was approximately the same as that of *B. platyphylla*.

In comparison with *P. ajanensis*, the number of juveniles of *B. platyphylla* in the smallest size class (< 2 cm in DBH) was only 57, and 96% of them were trunk suckers (Table 1). The number of trunks declined moderately as size class increased.

The size class distribution of *P. tremula* showed a bimodal pattern (Table 1). There were 181 juveniles in the smallest size class (< 2 cm in DBH), and all were root suckers. The numbers of trunks in the size classes from 2 cm to 20 cm were approximately zero; thicker trunks appeared mainly in the size classes from 20 cm to 30 cm.

Table 2. Correlations between sapling frequencies in 5 × 5-m sub-plots and percent coverages of canopy layer.

sapling	canopy	1998			2000		
		R	p^1	p^2	R	p^1	p^2
P. ajanensis	*P. ajanensis*	0.382	0.002	0.002	0.411	< 0.001	< 0.001
	B. platyphylla	–0.144	0.225	0.143	–0.113	0.378	0.248
	P. tremula	–0.174	0.169	0.094	–0.129	0.313	0.018
	gap	–0.165	0.194	0.105	–0.248	0.050	0.018
B. platyphylla	*P. ajanensis*	–0.296	0.032	0.010	–0.287	0.021	0.010
	B. platyphylla	0.352	0.004	0.014	0.353	0.004	< 0.001
	P. tremula	0.135	0.287	0.164	–0.075	0.558	0.334
	gap	–0.201	0.110	0.063	–0.201	0.384	0.176
P. tremula	*P. ajanensis*	–0.043	0.737	0.397	–0.253	0.137	0.296
	B. platyphylla	–0.034	0.788	0.440	0.053	0.760	0.365
	P. tremula	–0.173	0.173	0.106	0.053	0.759	0.525
	gap	0.164	0.196	0.082	0.162	0.347	0.175

p^1 = p value of Pearson's correlation; p^2 = p value of randomization sampling test (see text).

Spatial distribution patterns of juveniles in 1998

The spatial distribution patterns of juveniles (< 2 cm in DBH) contrasted between the two dominant species and *P. tremula* (Table 2). The distribution of *P. ajanensis* juveniles was significantly positively correlated with the coverage of the canopy of the same species (R = 0.382, p^1 (1998) = 0.002 by Pearson's correlation, p^2 (1998) = 0.002 in the randomization sampling test). However, the correlation with gap percentage was negative (R = –0.165, p^1 (1998) = 0.194 by Pearson's correlation, p^2 (1998) = 0.105 in the randomization sampling test).

The spatial distribution of *B. platyphylla* juveniles was significantly positively correlated with the canopy coverage of the same species (R = 0.352, p^1 (1998) = 0.004 by Pearson's correlation, p^2 (1998) = 0.014 in the randomization sampling test). However, it had a significant negative correlation with the coverage of *P. ajanensis* (R = –0.296, p^1 (1998) = 0.032 by Pearson's correlation, p^2 (1998) = 0.010 in the randomization sampling test).

P. tremula was the only species whose spatial distribution was slightly positively correlated with the gap percentage (R = 0.164, p^1 (1998) = 0.196 by Pearson's correlation, p^2 (1998) = 0.082 in the randomization sampling test). The location map of *P. tremula* root suckers shows that suckers were distributed mainly inside large gaps or at the edges of canopies, and that thick trunks of this species did not necessarily appear near suckers (Figure 2).

Sprouting strategies of B. platyphylla *and* P. tremula

The trunk suckers of *B. platyphylla* emerged from the base of mother trunks concentrically. The frequencies of suckers emerging from clumps were not very high (Table 3). Ten percent of clumps produced more than 5 trunks, while 40% of clumps produced 2 to 4 trunks. Approximately 51% of genets did not produce any suckers, while ca. 49% of genets provided 75% of trunks by suckering.

The trunk size structure of *B. platyphylla* clumps had a character (Table 4). Most mother trunks accompanied 0.9 to 2.9 trunks of the smallest size class (< 5 cm in DBH), but there were only 0 to 0.57 trunks in middle size classes (maximum size class $\geqslant$ 5 cm). The result suggests that the average clumps should have one mother trunk, a few narrow trunks < 5 cm in DBH and very few middle-sized trunks.

All juveniles of *P. tremula* were root suckers and $\leqslant$ 3 years old (Table 5). We were not able to find any middle-sized suckers in the 40 × 40 m plot. The height growth of suckers was very fast, ranging from ca 12 to ca 40 cm y^{-1} (Table 5). The suckers were derived from thick lateral roots whose diameter was ca. 15 mm on average. At the bottom of suckers, we found from 2 to 13 dead suckers (Figure 3). This shows that suckers were produced repeatedly from the same point on lateral roots and that most of them died within two or three years.

Lateral roots that produced suckers did not produce radicles frequently (Table 5).

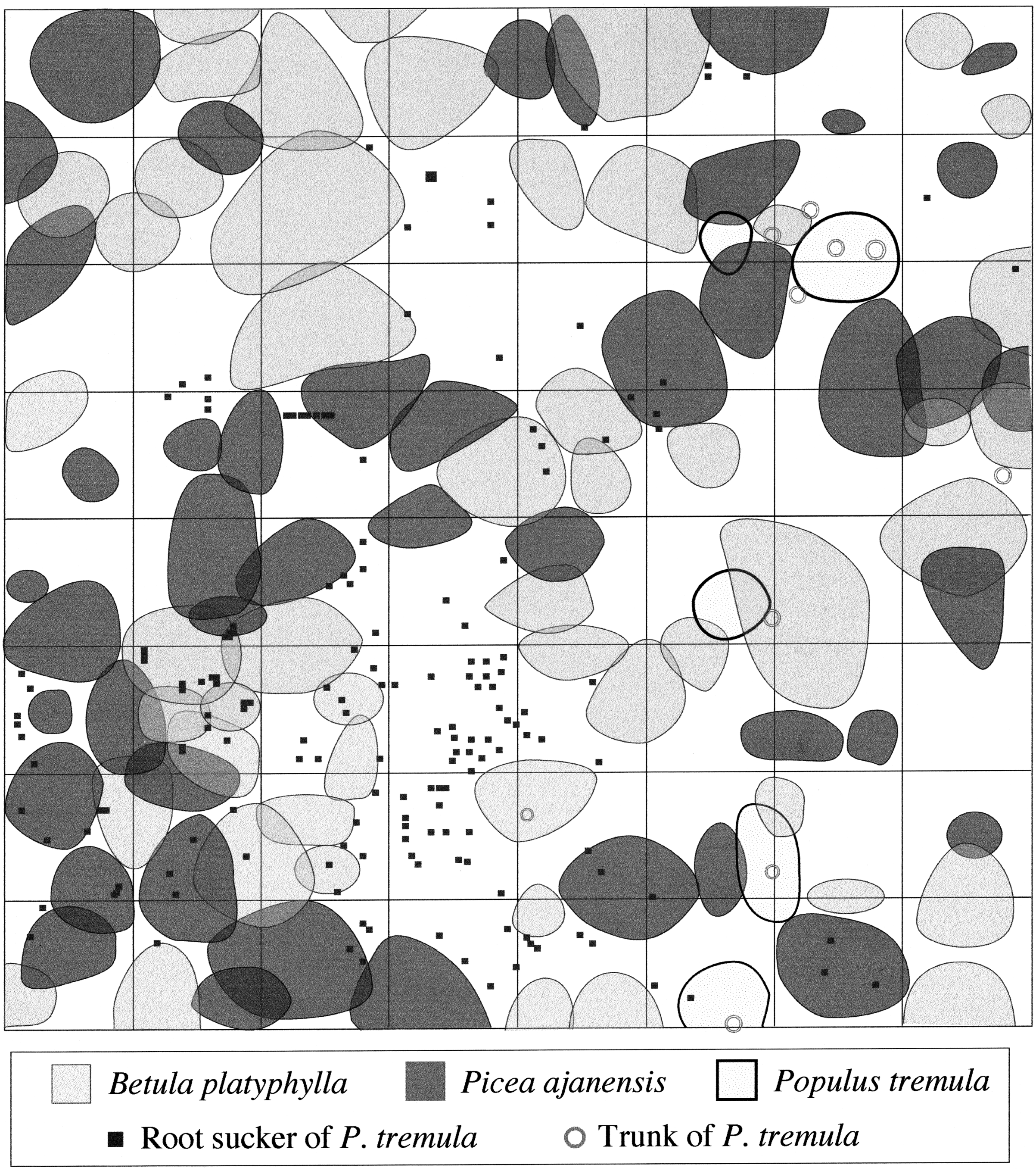

Figure 2. Crown projection map in 40 × 40-m study plot and location of *P. tremula* root sucker. The plot is divided into 64 5 × 5 m sub-plots.

Demographic patterns of juveniles

A lot of juveniles recorded in 1998 were dead by August 2000 (Figure 4). We found many dead or injured *P. ajanensis* seedlings. In 1998, we recorded 1132 *P. ajanensis* juveniles in the 40 × 40-m plot. In 2000, however, at least 238 had died and 256 had been injured, while 460 new individuals had emerged (Figure 4). The injury ratio of *P. ajanensis* juveniles (damaged + dead/total juveniles in sub-plot) was highly

Table 3. Frequency distributions of the number of trunks in a genet and its contribution to the total number of trunks in the 40 × 40-m plot.

no. of trunks in a genet	individual		trunk	
	(no.)	(%)	(no.)	(%)
1	32	50.8	32	24.1
2	16	25.4	32	24.1
3	9	14.3	27	20.3
5	2	3.2	10	7.5
6	1	1.6	6	4.5
7	1	1.6	7	5.3
8	1	1.6	8	6.0
11	1	1.6	11	8.3
total	63	100.0	133	100

negatively correlated with the canopy coverage of the same species (R = −0.324 by Pearson's correlation, P = 0.0078 in the randomization test).

More than 50% of *B. platyphylla* sprouts had died during the two years. Thirty-one of 57 sprouts recorded in 1998 had died and 23 had newly emerged. We could not do a spatial correlation analysis of sprouts mortality with canopy condition because of too many missing data (zero denominators).

About 86% of *P. tremula* root suckers recorded in 1998 had died by August 2000, and only 14% survived (Figure 4). We recorded 304 new root suckers and only 25 old suckers ($\geqslant$ 3 years old). We could not do a spatial correlation analysis of sprouts mortality with canopy condition because of too many missing data (zero denominators).

Spatial distribution patterns of juveniles of all three species in 2000 showed similar trends as those in 1998, although many had died and many new ones had emerged during the two years (Figure 4, Table 2). The distribution of *P. ajanensis* juveniles was significantly positively correlated with the coverage of the canopy of the same species (R = 0.411, p^1 (2000) < 0.001 by Pearson's correlation, p^2 (2000) < 0.001 in the randomization sampling test). However, the correlation with gap percentage was significantly negative (R = −0.248, p^1 (2000) = 0.050 by Pearson's correlation, p^2 (2000) = 0.018 in the randomization sampling test).

The spatial distribution of *B. platyphylla* juveniles showed a significant positive correlation with the canopy coverage of the same species (R = 0.353, p^1 (2000) = 0.004 by Pearson's correlation, p^2 (1998) < 0.001 in the randomization sampling test). However, it had a significant negative correlation with the coverage of *P. ajanensis* (R = −0.287, p^1 (2000) = 0.021 by Pearson's correlation, p^2 (2000) = 0.010 in the randomization sampling test).

P. tremula was the only species whose spatial distribution was slightly positively correlated with gap percentage, although it was not significant (R = 0.162, p^1 (2000) = 0.347 by Pearson's correlation, p^2 (2000) = 0.175 in the randomization sampling test).

Discussion

Population structure and regeneration strategy

The population structure of canopy species was remarkably different among species. *P. ajanensis* regenerated only from seed, and the density of juveniles (< 2 cm in DBH) was very high. The possibility that juveniles could grow larger seemed very low because of the low density of middle-sized trunks. Thus, our results suggest that there is a bottleneck at the juvenile stage in this species.

The population structure of *B. platyphylla* suggests that trunk suckers have a relatively high possibility of growing to the canopy layer, although seedlings cannot establish very well. The contribution of sprouts to the population structure was estimated to be ca. 50% based on the number of genets and ca. 75% based on the number of trunks. These results suggest that the combination of seed regeneration and sprouting maintains the population of this species. We found only a few *B. platyphylla* seedlings on the forest floor in the 40 × 40-m plot. This suggests that there is a bottleneck before the stage of seedling establishment. We could not detect any regeneration inhibitors. Nevertheless, the mature soil or accumulated litter on the forest floor can be a strong inhibitor of *B. platyphylla*'s regeneration, on the basis that artificial scarification, forest fire, and uprooting sometimes strongly accelerate the establishment of *Betula* seedlings (Seiwa and Kikuzawa 1996; Kurahashi et al. 1999). However, the soil surface in the study site was relatively stable and seemed not to be affected by such disturbances. The sprouting habit of this species might be important for keeping mother trees alive until the occurrence of heavy soil disturbance.

The population of *P. tremula* was completely dependent on root suckering, and the mortality of suckers seemed to be very high. Some *Populus* species produce a lot of root suckers just after forest fires and

Table 4. Size structures of trunks of *B platyphylla* suckering clumps in the 100 × 100 m plot. Each value is the mean in the class (total number of trunks in the class / N).

Max. DBH in the clump (cm)	Trunk size class (cm) < 5	< 10	< 15	< 20	< 25	< 30	⩾ 30	total	N (no./ha)
< 5	3.91							3.91	11
< 10	1.86	1.00						2.86	14
< 15	1.30	0.50	1.00					2.80	20
< 20	1.60	0.40	0.50	1.10				3.60	10
< 25	0.90	0.38	0.43	0.14	0.14			3.00	21
< 30	2.75	0.21	0.13	0.04	0.21	1.13		4.46	24
⩾ 30	1.67	0.57	0.14	0.29	0.10	0.00	1.00	3.76	21

Max. = maximum; DBH = diameter at breast height; N = number of genets.

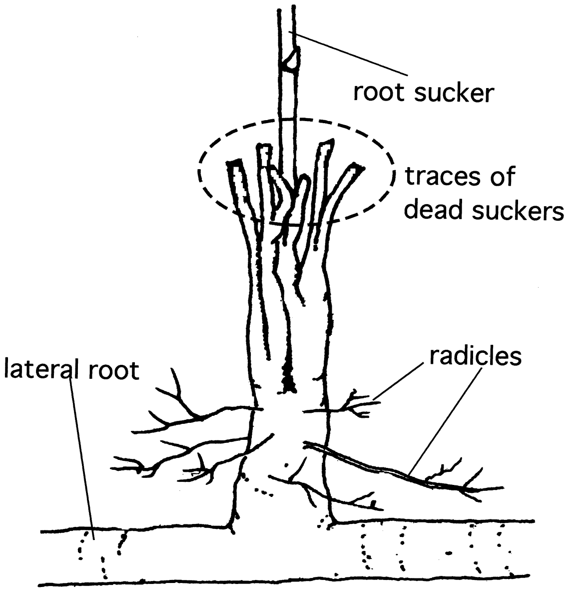

Figure 3. An example of lateral root of *P. tremula.*

regenerate vigorously (Barns 1966; Tuskan and Rensema 1992). In our mature stand, however, *P. tremula* seemed to maintain its population structure only by a small number of suckers that survived on the forest floor with a very low possibility. The low relative dominance of this species would be consistent with the relatively unsuccessful regeneration.

Spatial distribution and regeneration patterns of juveniles

The spatial distribution of juveniles of the three species showed specific patterns. Most juveniles of *P. ajanensis* were significantly concentrated under the canopies of the same species and showed negative correlations with canopy gap percentages. The canopy layer of this stand was relatively sparse (Figure 2), and seed dispersal to gaps would occur frequently. Therefore, we hypothesize that there are some strong inhibitors of seedling establishment inside gaps, and that the high mortality of juveniles inside gaps results in their aggregated distribution under the canopy of mother trees. Strong negative correlation of dead or injured *Picea* juveniles with *Picea* canopy seems to support the hypothesis. Our other paper (Takahashi et al. 2001a, 2001b) on the species composition and architecture of this forest shows that the crown of *P. ajanensis* was very deep, and that middle-sized individuals were distributed near dead or broken canopy trees of the same species. Thus, seedling establishment of *P. ajanensis* occurs under the canopy of the same species and grow vigorously after the dieback of canopy-layer trees. For the reasons mentioned above, we conclude that *P. ajanensis* achieves advanced regeneration under mother trees, but cannot utilize the light conditions inside gaps.

The juveniles of *B. platyphylla* were distributed mainly under mother trees, just like those of *P. ajanensis*. Considering that most juveniles of *B. platyphylla* were trunk suckers, this result seems reasonable. The number of juveniles derived from seed was too small for us to detect whether the species prefers canopy gaps or not. However, it would be reasonable to conclude that most of the population dynamics of this species depends on trunk suckering and the number of juveniles derived from seed is too small to fill canopy gaps in this forest.

P. tremula was the only species whose juveniles were distributed inside gaps by root suckering. Nevertheless, the high mortality of juveniles inside gaps suggests that they cannot utilize this habitat efficiently. We were not able to detect the reason for the

Table 5. Characteristics of lateral roots and shoots of root-sucking *Populus tremula*.

	shoot				lateral root	
	shoot length (cm)	D_0 (mm)	growth in '98 (cm)	growth in '97 (cm)	root diameter (mm)	no. of dead trunk
average	31.3	3.8	26.4	23.6	15.2	7.2
SD	22.4	2.1	14.9	11.4	4.7	5.4
N	24	24	24	5	15	18

shoot		lateral root	
age	frequency (no., %)	absorption root rank	(%)
1	113 (86.3)	–	33.3
2	17 (13.0)	+	44.4
3	1 (0.8)	++	5.6
N	131	+++	16.7
		N	18

D_0 = diameter at the bottom of shoot; SD = standard deviation; N = the number of samples; – = no absorption root; + = a little; ++ = moderate; +++ = frequent

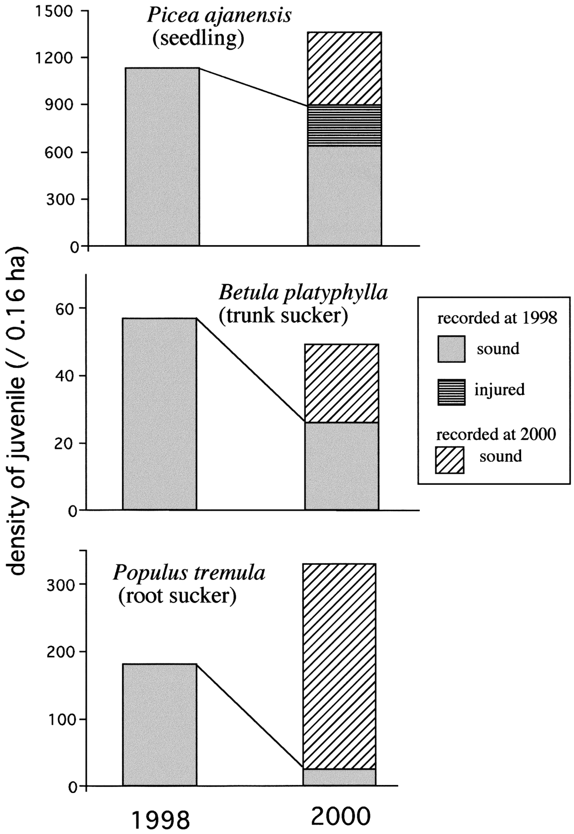

Figure 4. Density change of juveniles from Aug. 1998 to Aug. 2000.

death of young suckers. We observed no heavy disturbances on the forest floor or trace of turion cutting by rodents in the study plot. The density of herbs and grasses was not very high and they seemed not tall enough (< 30 cm in height) to shade *Populus* root suckers. On the other hand, the extreme low temperatures and severe frost in winter could explain the death of suckers. The demography of root suckers of this species has not been investigated yet in detail. Long-term study of the demography of root-suckering species is needed to clarify the role of gaps in the forest.

Sprouting strategies of B. platyphylla *and* P. tremula

B. platyphylla produced suckers concentrically from the bottom of mother trunks. The sprouting clumps have a similar shape to those of *Fagus japonica* and *F. engleriana*, which is called 'root collar sprouting' (Ohkubo et al. 1988; Cao and Peters 1998). Species that use this strategy tend to survive a very long time by replacing old or dead trunks with new vigorous ones (Peterson and Jones 1997). Homma (1997) reported that trunks are formed at least two ways. One is disturbance-induced, in which suckers are produced after trunk deformation or injury by disturbance. The other is non-disturbance-induced, in which disturbance is irrelevant to trunk production. For *B. platyphylla*, the effects of disturbance seemed low, because the frequency of trunk injury was very rare, we consider the species to follow the latter type. A closely related species in Japan, *B. platyphylla* var. *japonica*, seldom produces suckers and regenerates mainly by seed. Comparative study of the two species will clarify the ecology and evolution of the sprouting habit of *Betula*.

Most studies of the clonal growth of *Populus* species (Barns 1966; Kemperman and Barns 1976; Brown and DeByle 1987; Krasny and Johnson 1992) have pointed to quick clonal regeneration after forest fire or artificial cutting. Our paper is the first one showing space acquisition by clonal growth in a mature stand. *P. tremula* produced many root suckers remote from large mother trunks, although the number of canopy trees was small. This species invaded gaps by the root suckering strategy. Nevertheless, because of the high mortality of suckers, the strategy does not seem to contribute to regeneration. Moreover, costs of building and maintaining a lot of thick lateral roots seem very high, and it is doubtful whether the mother trunk can provide all of such costs. Thus, the young root suckers growing in gaps may help lateral roots and may be stocking the photosynthates till heavy disturbance promotes vigorous suckering.

Another interesting point revealed by our study is that lateral roots of *P. tremula* seldom produce absorption roots. Ogawa et al. (1999) reported that lateral roots of the Japanese root suckering cherry (*Prunus ssiori*) neither produce absorption roots and suggested that the wide vascular tissues in the lateral roots transported water and nutrients to suckers with very high conductivity. Considering the characters of *P. tremula*, we can hypothesize that the species has a sophisticated strategy; normal roots, lateral roots, mother trunks and root suckers may be specialized to acquire wide underground space efficiently and to respond quickly after heavy disturbance.

Community dynamics of mature stand in a boreal forest

Our results suggest that gaps in this boreal forest do not benefit but harm seedling establishment. Except in the case of gap formation by big *P. ajanensis* trunks, which accelerates advanced regeneration of this species, it seems impossible for the three species to utilize canopy gaps efficiently. Therefore, it is reasonable to suppose that the community dynamics of this forest would differ from the gap dynamics. Gap formation in temperate or tropical forest facilitates the invasion of light demanding species or accelerates the growth of seedlings, resulting in the alteration of spatial structure (Watt 1947; Hubbell and Foster 1986). The structure of our forest, however, can be supposed to be stable for a long time if heavy disturbance does not occur. Our other papers (Takahashi et al. 2001a, 2001b), which analyze the spatial structure of the canopy and sub-canopy trees in this forest, suggest that the two dominant species are segregated spatially and would not replace each other. Our current study gives strong evidence for this idea from the viewpoint of the spatial distribution pattern of juveniles and emphasizes the importance of suckering in mature boreal forest as a strategy to extend tree life or to prepare quick clonal growth after heavy disturbance.

This is only a case study, and it might be difficult to generalize our results to all boreal forests. However, we proposed a hypothesis to explain the formation of sparse canopy in mature boreal forests. Comparative study with other boreal forests is needed to test our hypothesis.

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