Short communication

Season and substrate effects on the first-year establishment of current-year seedlings of major conifer species in an old-growth subalpine forest in central Japan

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Received 8 July 2004; received in revised form 18 October 2004; accepted 13 February 2005

Abstract

Seasonal and substrate effects on first-year seedling establishment of major conifer species (Abies mariesii, Abies veitchii, Picea jezoensis var. hondoensis, and Tsuga diversifolia) were assessed in an old-growth subalpine forest in central Japan. Older seedlings (≥1 year) were more abundant on woody debris (WD), such as fallen logs, than on soil. It is known that this preferential seedling establishment on WD is determined by the first-year seedling establishment. The present results indicate that first-summer seedling survivorship clearly contributes to the creation of such seedling–substrate associations, because mortality during the first-summer was greater on soil than WD but that during the first-autumn/winter was not different. Although the standardized mortality rate of current-year seedlings on WD was not so different among the three seasons, that on soil significantly decreased in the winter; indicating that soil is not an unsuitable substrate for seedling survivorship during snow-covered winter. Thus, it can be concluded that biotic and abiotic factors enhancing seedling mortality on soil are most active during summer, and seedling–substrate associations seem to be determined mainly during the first-summer soon after seedling emergence. Furthermore, the first-year survivorship of P. jezoensis var. hondoensis, which has smaller-sized seeds/seedlings that are disadvantageous for early survival, decreased with progressing WD decay toward soil. This suggests that the properties of WD also affect current-year seedling survivorship, especially for species sensitive to substrate properties. In conclusion, initial survivorship affects seedling bank dynamics, and such early dynamics are greatly regulated by the highly heterogeneous substrate availability on forest floors.

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Keywords: Fallen logs; Seedling bank; Seedling mortality; Seedling survivorship; Woody debris

1. Introduction

In the Northern hemisphere, mature boreal and subalpine forests consisting of evergreen conifer species such as fir (Abies), spruce (Picea), and
hemlock (Tsuga) have conifer seedling banks in their understorey (Morin and Laprise, 1997; Greene et al., 1999; Duchesneau and Morin, 1999; Parent et al., 2003; Mori et al., 2004). Significant seedling–substrate associations are clearly recognized in these forests (Simard et al., 1998, 2003; Parent et al., 2003). Substrate availability on forest floors is highly spatially heterogeneous, and woody debris (WD), which is mainly composed of fallen logs, is an especially preferable substrate for conifer seedlings (Franklin et al., 1979; Harmon and Franklin, 1989; Takahashi et al., 2000; Mori et al., 2004).

Initial seedling survivorship can modify the entire demography of a species (Gray and Spies, 1997); therefore several studies have focused on the early dynamics of conifer seedling banks (Duchesneau and Morin, 1999; Simard et al., 2003; Mori et al., 2004). A previous study by the authors in an old-growth subalpine forest characterized by Abies mariesii Masters, Abies veitchii Lindley, Picea jezoensis var. hondoensis (Sieb. Et Zucc.) Carrière, and Tsuga diversifolia (Maxim.) Masters demonstrated that early seedling establishment, especially first-year establishment, is the main factor in the creation of seedling–substrate associations (Mori et al., 2004). In this previous study, although current-year seedlings of the major conifer species were shown to germinate irrespective of substrate type, older seedlings (>1 year old) were distributed preferentially on WD rather than soil (Mori et al., 2004), indicating that WD functions as a safe site for first-year seedling survivorship. Factors that impede seedling survivorship on soil include intense drought (Arnott, 1973; Greene et al., 1999), pathogenic fungi (Cheng and Igarashi, 1987), competition with understorey vegetation (Harmon and Franklin, 1989; DeLong et al., 1997; Cornett et al., 1998; Duchesneau and Morin, 1999), and smothering by broadleaf litter accumulation (Chrsity and Mack, 1984; DeLong et al., 1997; Duchesneau and Morin, 1999). Such agents of mortality against seedlings are expected to have different effects depending on the season. For instance, drought is most apparent in summer, and leaf litter smothers seedlings after leaf-fall in autumn. However, it is unknown when current-seedling mortality most intensively occurs during the first-year, and whether seedling mortality during each season is affected by substrate types. Detecting the effects of season and substrate on current-year seedling mortality would contribute to further clarification of the seedling bank dynamics of conifer species.

Although WD on the forest floor is quite important for conifer survivorship and establishment, all WDs are not necessarily excellent substrates for conifer seedlings. It is known that WD properties greatly differ among decay classes (Harmon et al., 1986; Takahashi et al., 2000). Our earlier study suggested that, because WD properties become closer to those of soil with progressing decay the survivorship of conifer seedlings on WD might be affected by the WD decay class on which each seedling emerges (Mori et al., 2004). Therefore, when considering seedling–substrate associations, it would be advantageous to confirm the effects of various WDs belonging to different decay classes on seedling mortality/survivorship.

The first-year establishment of conifer seedlings is an important aspect of the dynamics of coniferous forests. By specifically focusing on the mortality and survivorship of seedlings growing on various heterogeneous substrates including each type of decayed WD and soil during each season in the first-year, this study aims to clarify the mechanisms involved in the first-year seedling establishment of major conifer species in an old-growth subalpine forest.

### 2. Methods

#### 2.1. Study site

The study site is located within a subalpine forest (altitude 2050 m, 35°56′N, 137°28′E) on Mt. Ontake (peak 3067 m) in central Japan. Average annual precipitation is approximately 2500 mm and the average annual temperature is about 3–4 °C. The forest floor is snow-covered from mid November or early December to late May or early June. From 1995 through 1999, maximum snow depths in the study plot ranged from 175 to 230 cm. Sasa, the dwarf bamboo that dominates the understorey of many Japanese forests was not present in the study plot, and the ground layer consisted of herbs and mosses. The vegetative features of the subalpine forests of Mt. Ontake have been described previously (Franklin...
et al., 1979). The study forest is characterized by four major conifer species, *A. mariesii*, *A. veitchii*, *P. jezoensis* var. *hondoensis* and *T. diversifolia*, and one hardwood species, *Betula ermanii* Cham. The compositional characteristics of the study forest are given in Mori and Takeda (2004).

### 2.2. Field methods

In the previous study by the authors (Mori et al., 2004), ten $5\text{ m} \times 5\text{ m}$ subplots were randomly designated within a $100\text{ m} \times 100\text{ m}$ study plot in the forest stand. Within each subplot, substrate was defined as woody debris (WD; downed logs and rotten stumps), mound, rock or soil. Moreover, WD was classified into five subcategories according to decay class applying the criteria of Sollins (1982), which range from recent dead trees (decay class I) to visibly decaying logs/stumps that are close to soil (decay class V). In total, the 10 subplots were divided into 125 substrates. The location and projected area covered by all substrates in each subplot were described. The relative areas of each substrate are given in Mori et al. (2004).

In July 2003, the numbers of seedlings newly germinated on each substrate (current-year seedlings) were counted within each subplot, and the rooting substrate and species of all the germinated seedlings were recorded. In addition, each germinated seedling was marked with a tiny numbered flag. Any additional germination or mortality of the current-year seedlings were surveyed in censuses at approximately one-month intervals until 30 October 2003 (throughout the growing season), and in 26 May 2004 (after snow-melt). Since species of *A. mariesii* and *A. veitchii* are hard to identify separately, their seedlings were grouped together as *Abies* spp.

### 2.3. Data analyses

To compare the seasonal differences in mortality rate of seedlings on each substrate type, the standardized mortality rate ($m$; month$^{-1}$) was calculated as:

$$w = \frac{\ln N_0 - \ln N_t}{t}$$

where $N_0$ and $N_t$ are the number of seedlings on each substrate at the beginning of each season and surviving to the end of each season, respectively, and $t$ is the time interval (month) (Condit et al., 1995). $N_0$ of summer $m$ was defined as the total number of germinated seedlings during the 2003 growing season, since all current-year seedlings had appeared by late September (Mori et al., 2004). Each $m$ in the summer, autumn, and winter were based on the measurements at 30 September 2003 (prior to broadleaf-falls), 30 September to 30 October 2003 (prior to snow-fall), 30 October to 27 May 2004 (assuming a snow-covered period), respectively. To assess the statistical significance of $m$ on each substrate for each season, 95% confidence intervals were calculated using the normal approximation to the binomial variance. In calculating each seasonal $m$ on WD substrates, for *Abies* spp. and *T. diversifolia*, seedlings on all WD decay classes were pooled as seedlings on WDs to satisfy the sample number required for statistical analysis. For *P. jezoensis* var. *hondoensis* seedlings on WD substrates, each seasonal $m$ was calculated for each WD decay class.

To analyze the substrate effects on the seedling mortality during each season, the ratio of seedlings that died during each season to the total number of seedlings alive at the end of the previous season was calculated. Again, the ratio in the summer was calculated using the total number of seedlings germinated in 2003. For *Abies* spp. and *T. diversifolia*, differences in the ratio of seedlings that died during each season were tested only between the WDs and soil substrates using Fisher’s exact test to satisfy the sample number required for analysis. For *P. jezoensis* var. *hondoensis*, differences in the ratio of seedlings that died during each season were analyzed among substrate types (each WD decay class and soil) using the $\chi^2$-test.

### 3. Results

The survivorship of current-year seedlings on each substrate is shown in Fig. 1. No conifer seedlings germinated on WD I, and only one current-year seedling of *T. diversifolia* was found growing on WD II (survived during the growing season but died during winter). In more decayed WD substrates and soil, current-year seedlings appeared, and the death of seedlings occurred soon after emergence. Further, on the soil substrate, the seedlings alive at the time of
next-year’s spring (survived until May 2004) were more abundant in the order of Abies spp, T. diversifolia, and P. jezoensis var. hondoensis.

Throughout the first-year, many seedlings died. Fig. 2 shows the seasonal differences in the standardized mortality rate ($m$) of seedlings on each substrate type. In the WD substrates, $m$ of seedlings was not significantly different among three seasons. In contrast, on the soil substrate, $m$ of Abies spp. and P. jezonensis var. hondoensis seedlings was significantly ($P < 0.05$) lower in the first-winter than in the first-summer or -autumn. For T. diversifolia seedlings on soil, $m$ showed a tendency to decrease in the first-winter, although this was not statistically significant.

The proportion of seedlings that died during each season is shown in Fig. 3. For all species, the proportion of seedlings that died during the first-summer was significantly greater on the soil substrate compared to the WD substrate. However, during the first-autumn and -winter, the proportion of seedling deaths was not different between the substrate types.

As a result of season and substrate effects on the current-year seeding mortality, the first-year survivorship of P. jezonensis var. hondoensis seedlings was different among the substrate types; this significantly decreased with progressing decay in the order of WD III, IV, V, and soil (Fig. 4).

4. Discussion

The significance of substrate types for seedling establishment and survival is well known for boreal and subalpine conifer species. Specifically, woody debris (WD) (or coarse woody debris (CWD)), such as fallen logs, is an important substrate for the seedlings of many conifer species (Knapp and Smith, 1982; Harmon and Franklin, 1989; Takahashi, 1994; DeLong et al., 1997; Duchesneau and Morin, 1999).

In the authors’ previous study, seedlings ($\geq$1 year old) of the major conifer species in the study forest were found to be significantly more abundant on non-
soil substrates, especially WD, because of the preferential first-year establishment of current-year seedlings (Mori et al., 2004). In the present study, the proportion of current-year seedlings that died during the summer was significantly greater on soil than on WDs, but deaths during the autumn and winter were not different between substrate types (Fig. 3), indicating that first-summer survivorship plays a major role in creating preferential seedling establishment on the WDs. Differences in the first-summer survivorship between substrate types are probably related to substrate conditions such as moisture availability for germinants (Mori et al., 2004). Several studies have demonstrated differences in the autumn–winter survivorship of germinants between substrate types (DeLong et al., 1997; Simard et al., 2003), because of broadleaf litter accumulation in these periods, which smothers seedlings growing on non-elevated microsites such as soil. However, the present results suggest that the seedling burial by deeper leaf-litter on soil during autumn–winter seems to have relatively less impact on determining soil as an unfavorable substrate for first-year survivorship of conifer seedlings in this forest. In fact, in contrast to the seedlings on the WDs, the standardized seedling mortality rate during the winter clearly decreased only on soil (Fig. 2); further indicating that soil cannot be regarded as an unsuitable substrate for seedling survivorship during a snow-covered winter. Therefore, it seems that the biotic and abiotic factors enhancing the mortality of seedlings growing on soil (Mori et al., 2004) are most active during summer and diminish in later seasons. Accordingly, the seedling–substrate associations of these conifer species are determined mainly during the first-summer soon after emergence.

Evidence of seedling–substrate associations can be observed not only between WDs and soil, but also among different WD decay classes (Chrsity and Mack, 1984; Takahashi et al., 2000; Mori et al., 2004). Previous results suggested that the inhibitive effects on current-year seedling survivorship might be more intense with progressing WD decay classes from III, IV, V, to on soil (Mori et al., 2004), because the properties of WD become closer to those of soil (Chrsity and Mack, 1984). This should be especially conspicuous in species that are sensitive to substrate properties. Compared to Abies spp., seedlings of P. jezoensis var. hondoensis and T. diversifolia establish on a narrower range of substrates as a result of their smaller-sized seeds/seedlings (Mori et al., 2004), and the first-year survival percentage of seedlings that germinated on soil decreases from a high for Abies spp. (seed size is the largest), then T. diversifolia, and finally P. jezoensis var. hondoensis (seed size is the smallest) (Fig. 1). The first-year survivorship of P. jezoensis var. hondoensis seedlings actually significantly decreased with progressing WD decay toward a soil-like quality (Fig. 4), although unfortunately this could not be tested for T. diversifolia seedlings. This result clearly demonstrates the significant association between WD decay status and the probability of seedling survivorship/establishment, especially for the more substrate-restricted species such as Picea and Tsuga.

Consistent with reported arguments (Duchesneau and Morin, 1999; Simard et al., 2003), initial seedling
survivorship has a significant effect on the seedling bank dynamics in this subalpine forest. This study demonstrates that such early dynamics, which are especially drastic during the first-summer, are greatly regulated by the highly heterogeneous substrate availability on the forest floor. For further clarification of the seedling bank dynamics in coniferous forests, it will be of essential to quantify the detailed properties of each substrate, including those of the various WD decay levels.

Acknowledgements

We thank Dr. H. Takeda, Dr. T. Osono, Mr. H. Ishikawa, Mr. T. Hishi, Mr. Y. Doi, Ms. Y. Mizumachi, Ms. M. Hirano, Ms. C. Kobayashi, Mr. S. Katsumata, and Ms. M. Mizumachi for their support in the field research. We also thank the editors and the anonymous reviewers for their reading and improving the manuscript. This study was supported by a JSPS Research Fellowship for Young Scientists awarded to AM.

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