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The role of decaying log microsites in the regeneration dynamics of a subalpine forest on Mt. Fuji

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The relationship between tree occurrence and decaying log microsites was examined in a forest site and a windfall site on Mt. Fuji. In the forest site, the population density of trees, mostly softwoods, on decaying logs was higher than that on the ground irrespective of tree size. The population size (i.e. actual number of individuals) of trees on decaying logs was diminished more greatly than that on the ground as their size increased. In the windfall site, the density of softwoods on decaying logs was higher than that on the ground, while every hardwood took the reverse pattern. The population size of trees, especially hardwoods which appeared only in this site, was negligible on the decaying logs. The decaying logs contributed to the survival of specific trees in a specific site, but less frequently led them to canopy replacement of the forest. The state of decaying logs changed due to bryophyte dynamics in the windfall site. The authors focused on this change and discussed the reason why decaying logs contributed less to forest canopy replacement and to occurrence of hardwoods.

Keywords
bryophyte dynamics, canopy disturbance, canopy replacement, decaying log, regeneration site, subalpine forest

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1 Introduction

The forest floor is a mosaic of microsites. The occurrence, growth, and survival of tree seedlings vary depending on microsites. Decaying logs[1-4], tree buttresses[1,5], rocks[5], and soil mounds and pits formed by tree uprooting[6-8] are representative and important microsites for successful recruitment of tree seedlings in boreal and temperate forests of the Northern Hemisphere.

Numerous investigations have reported the significance of decaying logs as a safe site (*sensu* Harper[9]) for major softwoods, such as *Tsuga*[2-4,10], *Picea*[3,4,11], *Thuja*[11] and *Abies*[1,10]. Various assumptions have been made about advantageous characteristics of the decaying log for the colonizer. These characteristics include high capacity of moisture retention[12], freedom from pathogenic fungi[13] and competitors inhabiting on the forest floor[3,4], presence of rich nutrients through microbial nitrogen fixation[14], ability to support high populations of active ectomycorrhizal associations[12], and less build-up of leaf litter obstructing colonizer resource acquisition[2]. It is natural to consider that the characteristics of decaying logs should be helpful for the recruitment of any trees in a forest. Nevertheless, the availability of decaying logs has been scarcely examined except for the softwoods with a certain shade tolerance.

Recruitment of less shade-tolerant trees, chiefly hardwoods, is dependent on exposure of mineral soil through disturbing events such as windfalls[15,16] and forest fire[17,18]. The occurrence of disturbing events contributes to the removal of litter and bottom layer vegetation and to the

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availability of suitable light conditions. Soil mounds and pits formed by tree uprooting were representative microsites rich in mineral soil and light resources but poor in litter and competitive vegetation[16,19-21]. It is a well-known fact that microsites associated with recent disturbing events promoted the recruitment of fewer shade-tolerant trees. However, it does not mean the absence of availability of decaying logs for their successful recruitment. *Betula alleghaniensis* Britton would ideally be recruited in mineral soil at the canopy openings of the eastern North American forests[19,20], but they were predominantly recruited on decaying logs when there was no such site[19,22,23]. This alternative strategy was likely to be present in the trees with similar preference in recruitment conditions.

Regeneration is difficult for any trees in the understory of an intact forest due to scarcity of light resources or mineral soil. Therefore, canopy openings created by disturbing events attract tree successors and encourage the local regeneration process[24]. Individual trees filling the canopy openings often have their origin in the understory of the former intact forest and are parts of advanced regeneration[25,26]. In terms of forest regeneration, sporadic recruitment and survival of individual trees in the intact forest understory may be as important as recruitment of those in the canopy openings.

In this study, the relationship between tree occurrence and decaying logs was examined in a subalpine forest on Mt. Fuji, central Japan. In particular, the focus was on the availability of decaying logs for the long-term survival and regeneration of trees including less shade-tolerant species in the forest understory. Our purpose was to define the role of decaying logs (rather than recruitment dynamics of seedlings) in the regeneration dynamics of the forest through examining the contribution of the microsite to the occurrence of trees in different size class.

2 Study site and methods

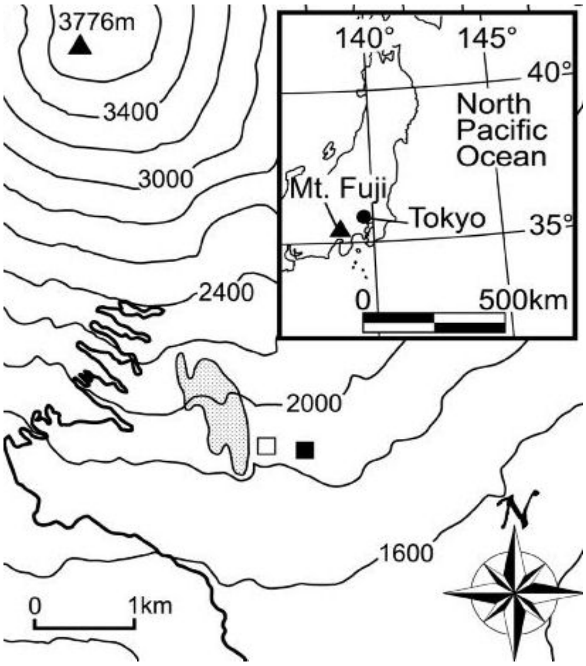

Fig.1 Location of study sites.

The study sites were located on a southeast slope of Mt. Fuji (35°21' N, 138°43' E, 3776 m a.s.l.). Inclination is up to 20 degrees, with no marked undulation on the study sites. The contour line interval is 200 m. Legend: Solid square, forest site; open square, windfall site; dotted area, area slashed by typhoon disturbance; and heavy line, roadway.

2・1 Site description

Study sites were set up in a subalpine zone on a southern slope of Mt. Fuji (35° 21′ N, 138° 43′ E; altitude: 3776 m), Honshu, Japan (Fig.1). Subalpine forests occur in an altitudinal range of 1800–2400 m on the slope, and the forest canopy consists primarily of evergreen conifers[27]. The centre of our study site was located at an altitude of 1850 m. The mean annual temperature was 5.1 °C according to the temperature lapse rate of Mt. Fuji[28] and observation data in the past 20 years at Gotemba, the nearest meteorological station[29]. The mean annual precipitation was 2852 mm at the metrological station. The heaviest precipitation occurred from May to September, while the winter (December to February) was relatively dry (−280 mm). The parent material is composed of basaltic scoria and lavas[30].

The organic soil layer was generally shallow (ca. 20 –30 cm deep) in the study sites.

Two sites were selected for this study: a forest site and a windfall site. The forest site was mature and included diverse tree species in the canopy. The forest site was sparsely dotted with conifers of >20 m in height and >50 cm in diameter at the breast height. The majority of the forest canopy consisted of trees of 15 m in height and 30 cm in diameter. The dominant species was *Abies veitchii* Lindl. Other members in the canopy layer were *Tsuga diversifolia* (Maxim.) Masters, *Picea jezoensis* var. *hondoensis* (Mayr) Rehder, *Larix kaempferi* (Lamb.) Carriere, and *Betula ermanii* Cham. There was no evidence of the occurrence of recent disturbing events and the forest canopy was almost closed. The sub-canopy layer included *Sorbus commixta* Hedl. and *Tilia japonica* (Miq.) Simonkai in addition to those species in the canopy layer. The forest understory was depauperate. A perennial plant, *Cacalia adenostyloides* (Franch. et Savat.) Matsum., covered less than 10% of the forest floor. A patchy community of the mosses *Hylocomium splendens* Hedw.,*Pleurozium schreberi* (Brid.) Mitt., and *Pogonatum contortum* (Brid.) Lesq. was the major vegetation on the forest floor (approximately 40%). Other part of the ground were covered with thin needle litter and woody debris. Rocks and exposed mineral soil were infrequently seen.

The windfall site was an elliptical area (ca. 30 m × 60 m) with no forest canopy as a result of a typhoon disturbance in 1996. There was no forest canopy and very few trees of >4 m in height survived. The ground was occupied by a considerable herbaceous vegetation. Several sun plants–including *Eupatorium chinense* L. var. *sachalinense* (Fr. Schm.) Kitam. and *Aster ageratoides* Turcz. subsp. *leiophyllus* (Fr. et Savat.) Kitam.–dominated the vegetation (up to 70% ground coverage in the summer). Moss communities were infrequently seen. Patches of feather mosses (e.g., *H. splendens* and *P. schreberi*) appeared restrictedly in the place that had not suffered soil disturbance. Patches of *Pogonatum* spp. and *Polytrichum* spp. appeared in various places including exposed substrates. The moss community covered less than 20% of the ground. Other parts of the ground were covered with thin needle litter and woody debris. Rocks and exposed mineral soil were frequently seen as a result of canopy tree uprooting and soil erosion.

Fig.2 An example of a canopy tree (*P. jezoensis* var. *hondoensis*) which regenerated on a fallen log.
The height of a canteen put on the base of the tree is approximately 25 cm. The age of the tree is 100 years at least estimated from the DBH and the preceding studies, Yatoh[31,32]. A fallen log which functioned as regeneration site is lying under the base of the tree. The photograph was taken at a forest edge on Sep. 15, 2004.

2・2 Methods

Three 20 m × 50 m quadrats were prepared in the forest site and six 10 m × 10 m quadrats were prepared in the windfall site in June 2005. The total sampling area was 3000 m^2 and 600 m^2 in the forest site and windfall site, respectively. Each quadrat was divided into 5 m × 5 m sub-quadrats. Every tree in each sub-quadrat was counted and their height, diameter, and rooting microsites were recorded. Because our concern was in long-term survival, data were collected from individuals with a height larger than 20 cm. The exact age of sampled trees was unknown; however, observation indicated that softwoods had survived for at least 5 or more years and hardwoods for 3 or more years. The diameter was measured at the base of the main stem with trees <200 cm tall and at the breast height (130 cm) with trees >200 cm tall. Rooting microsites were classified into two categories, decaying logs and the ground, based on the presence of a nurse log or stilt roots. Fig.2 shows an example of a canopy tree (*P. jezoensis* var. *hondoensis*) which regenerated on a decaying log. The age of the tree was 100 years at least which was estimated from the DBH and the studies of Yatoh[31,32]. The decaying log which functioned as a regeneration site was well preserving its shape over a long period of time. In addition, the development of organic soil layer was poor and shallow in our study area. Therefore, we could observe the presence of considerable aged nurse log and stilt roots and judge the rooting microsites of trees sufficiently. Individuals having stilt roots but lacking woody materials under the roots (as successors from a soil mound) were classified as "the ground." Sample trees were classified as follows according to their tree height and diameter at breast height (DBH): 1) sapling class, <200 cm tall; 2) sub-canopy class, >200 cm tall, <15 cm DBH; and 3) canopy class, >200 cm tall, >15 cm DBH.

The state and abundance of the decaying logs (>30 cm in diameter) were recorded in both sites. The decaying logs were classified into four decay types according to their surface condition: (I) no vegetation, hard sapwood; (II) covered with thin moss mat (<2 cm), elastic sapwood; (III) covered with thick moss mat (>2 cm), soft sapwood; and (IV) no vegetation, soft sapwood. The moss mat of Type II consisted primarily of *Scapania bolanderi* Austin and *Heterophyllium affine* (Hook.) M. Fleisch. The moss mat of Type III consisted primarily of *H. splendens* and *P. schreberi.* Based on the successional sequence of bryophytes on fallen logs[33], the resident time of each log at the forest floor is long in order from Type-I to Type-III, but unknown for Type-IV. Most decaying logs classified into Type-I have its origin in the typhoon disturbance in 1996 in all likelihood. The available space of a decaying log for tree recruitment is considered to be trapezoidal. Thus, the silhouette area of a decaying log was computed from the minimum and maximum diameters and length of the decaying log. The cumulative area of the decaying log was considered to be the areal abundance of decaying logs in each site.

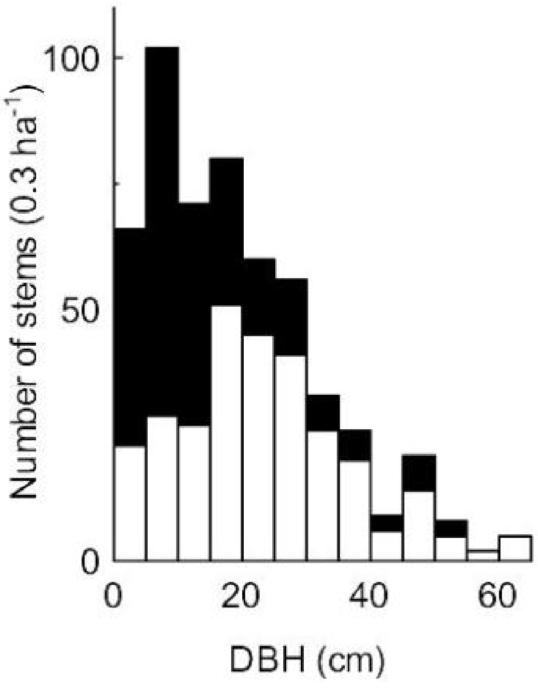

Fig.3 Diameter at breast height (DBH) distribution of sub-canopy and canopy trees (>200 cm tall) in the forest site.
The white portion of the bars represents the number of stems of the dominant conifer *A. veitchii*.

Table1 Decay types[*1] and areal abundance of decaying logs[*2] ($m^2 \cdot 600\ m^{-2}$) in the forest site and the windfall site. Figures in parenthesis show the percentage of logs in each decay type to the total within respective site. The decaying logs occupied 8.5% and 20.9% of the forest floor of the forest site and the windfall site, respectively.

Site	Decay type I	II	III	IV	Total
Forest site	0.4 (0.8)	27.0 (53.1)	13.0 (25.6)	10.5 (20.7)	50.8 (100)
Windfall site	80.7 (64.3)	3.5 (2.8)	8.4 (6.7)	33.0 (26.3)	125.6 (100)

[*1]Classified based on the surface conditions of a log. Type-Ⅰ: hard sapwood with no vegetation, Type-Ⅱ: elastic sapwood with thin moss cover, Type−Ⅲ: soft sapwood with thick moss cover, Type−Ⅳ: soft sapwood with no vegetation. See text.
[*2]Computed from the silhouette area of decaying logs within the sampled area of 3000 ㎡ in the forest site and 600 ㎡ in the windfall site.

3 Results

Seven tree species were observed in the forest site. The total basal area of trees (>200 cm tall) was 73.9 $m^2\ ha^{-1}$. The occurrence of each tree species (by percentage) was: *A. veitchii*, 70%; *T. diversifolia*, 9%; *P. jezoensis* var. *hondoensis*, 9%; *B. ermanii*, 7%; *S. commixta*, 4%; *L. kaempferi*, 1%; and *T. japonica*, 1%. For convenience, these trees are referred to by their genus names hereafter.

Fig.3 shows the combined DBH distribution of canopy and sub-canopy trees (i.e., >200 cm tall) in three quadrats of the forest site (3000 m^2). The DBH distribution took a reversed J shape overall, whereas *Abies*, which was the dominant species of the forest, had a mode of DBH between 15 cm to 30 cm.

The state and areal abundance of decaying logs substantially differed between the two sites (Table 1). The Type-I log was infrequently seen in the forest site, accounting for only 0.8% of the total amount of decaying logs. Type-II logs accounted for about 50% of the total amount. Type-III and Type-IV logs each accounted for about 20% of the total. The areal abundance of decaying logs was 50.8 $m^2 \cdot 600\ m^{-2}$; they occupied 8.5% of the ground in the forest site. In contrast, the presence of Type-I logs was conspicuous in the windfall site, accounting for 64.3% of the recorded decaying logs. Type-II and Type-III logs were scarce, each accounting for <10% of the total. Type-IV logs accounted for 26.3% of the total. The areal abundance of decaying logs was 125.6 $m^2 \cdot 600\ m^{-2}$; they occupied 20.9% of the ground in the windfall site. The areal abundance of decaying logs in the windfall site was twice as high as that in the forest site. However, the abundance of Type-II and Type-III logs was one-eighth and one-third, respectively, of that in the forest site.

Table 2 shows the relationship between the population density of trees ($n \cdot 100\ m^{-2}$) and microsites. The population density was computed assuming that the decaying logs and the ground had the same areal abundance in a site (i.e., 100 m^2). In the forest site, the density of *Picea*, *Abies, Tsuga* and *Sorbus* on decaying logs was higher than that on the ground in all the size class. The difference in the density between microsites was more conspicuous in younger size classes as for these species. In the sapling class (<200 cm tall), the density of *Picea*, *Abies* and *Tsuga* on decaying logs was 17.3, 7.6 and 6.7 times as high as that on the ground, respectively. The greatest difference in the density between microsites was observed in *Sorbus*. The density of *Sorbus* on decaying logs was 18.6 times as high as that on the ground. The density of these four species on decaying logs decreased as their size class increased. The difference in the density between microsites was minimal in the canopy class; nevertheless the density of trees on decaying logs was 2 to 4 times as high as that on the ground in the class. The density of *Betula* was higher on the decaying logs than on the ground only in the sub-canopy class. The density of other hardwoods and Larix was higher on the ground than on the decaying logs, or entirely lacked in the forest site. In the windfall site, the height of treesdid not exceed 200 cm and all individuals were classified into the sapling class. The density of saplings of *Picea*, *Abies* and *Tsuga* on decaying logs was higher than that on the ground. Among these species, the largest difference in the density between microsites was

Table 2 Relationship in the density of trees (n・100 m^{-2}) and microsites in the forest site and the windfall site. Figures are the number of individuals which set the area of each microsite at 100 m^2.

Species Microsite	Forest site Sapling[*1]	 Sub-canopy	 Canopy	 All individuals	Windfall site Sapling
Picea jezoensis var. *hondoensis*					
Decaying logs	20.8	1.2	1.2	23.2	9.5
Ground	1.2	0.1	0.5	1.9	8.0
Abies veitchii					
Decaying logs	19.7	9.4	10.6	39.7	34.9
Ground	2.6	2.0	6.7	11.3	9.6
Tsuga diversifolia					
Decaying logs	19.3	14.2	2.8	36.2	9.5
Ground	2.9	2.2	0.7	5.8	4.2
Larix kaempferi					
Decaying logs	−	−	0.0	0.0	0.0
Ground	−	−	0.1	0.1	1.3
Sorbus commixta					
Decaying logs	13.0	3.5	1.2	17.7	4.8
Ground	0.7	1.7	0.3	2.8	11.0
Betula ermanii					
Decaying logs	0.0	0.8	0.0	0.8	7.9
Ground	0.2	0.2	0.9	1.3	12.7
Tilia japonica					
Decaying logs	−	0.0	−	0.0	−
Ground	−	0.1	−	0.1	−
Prunus incisa					
Decaying logs	−	−	−	−	1.6
Ground	−	−	−	−	3.8
Acer spp.					
Decaying logs	−	−	−	−	1.6
Ground	−	−	−	−	10.1

[*1] Size class: Sapling, <200 cm tall; Sub-canopy, >200 cm tall and <15 cm DBH; Canopy, >200 cm tall and >15 cm DBH.

Table 3 Relationship between the occurrence of softwoods and microsites in the forest site and the windfall site.

	Forest site (n・3000 m^{-2})				Windfall site (n・600 m^{-2})
Species Microsite	Sapling[*1]	Sub-canopy	Canopy	All individuals	Sapling
Picea jezoensis var. *hondoensis*					
Decaying logs	53	3	3	59	12
Ground	34	3	15	52	38
Frequency	60.9	50.0	16.7	53.1	23.3
Abies veitchii					
Decaying logs	50	24	27	101	44
Ground	71	54	185	310	228
Frequency	41.3	30.8	12.7	24.6	16.2
Tsuga diversifolia					
Decaying logs	49	36	7	89	12
Ground	80	60	18	158	20
Frequency	38.0	37.5	28.0	36.0	37.5
Larix kaempferi					
Decaying logs	−	−	0	0	0
Ground	−	−	3	3	6
Frequency	−	−	0.0	0.0	0.0

[*1] Size class: Sapling, <200 cm tall; Sub−canopy, >200 cm tall and <15 cm DBH; Canopy, >200 cm tall and >15cm DBH.
Decaying logs, Ground: Number of individuals; Frequency: Percentage frequency of tree occurrence on the decaying logs.

observed in *Abies*. The density of *Abies* on decaying logs was 3.6 times as high as that on the ground. The density of all other species, including *Sorbus*, was higher on the ground than on the decaying logs. Compared with the forest site, the difference in the density between microsites was small in every species in the windfall site.

Table 3 shows the relationship between the population size of softwoods and microsites. The population size is the actual number of individuals observed in the sample area of 3000 m^2 and 600 m^2 in the forest site and the windfall site, respectively. In the forest site, the population size of *Picea* on decaying logs was larger than that on the ground in the sapling class (<200 cm tall). More than half of *Picea* saplings (60.9%) occurred on the decaying logs. The population size of *Abies* and *Tsuga* was also large on the decaying logs in the sapling class, but their frequency was not exceeding 50% on the decaying logs. The occurrence of *Larix* was limited to the ground irrespective of size class. The population size of softwoods on decaying logs tended to be small in older size class, whereas such logs was decreased as size class increased. The change in the frequency of occurrence of *Tsuga* change in the frequency of occurrence of *Tsuga* differed from *Picea* and *Abies* in respect of the transition and extent. The frequency of *Tsuga* on decaying logs was hardly changed between the sapling and sub-canopy class and minimally decreased 10.0% through size class increase. On the other hand, the frequency of *Picea* and *Abies* on decaying logs decreased constantly as size class increased. They decreased the frequency on decaying logs by 44.2% (*Picea*) and 28.6% (*Abies*) through size class increase. The occurrence of softwoods was more associated with the decaying logs in the order of *Tsuga*, *Picea, Abies* and *Larix* in the largest size class. In the windfall site, the population size of softwoods on decaying log was

Table 4 Relationship between the occurrence of hardwoods and microsite in the forest site and the windfall site.

Species Microsite	Forest site (n・3000 m^{-2}) Sapling[*1]	Sub−canopy	Canopy	All individuals	Windfall site (n・600 m^{-2}) Sapling
Sorbus commixta					
Decaying logs	33	9	3	45	6
Ground	20	47	9	76	52
Frequency	62.3	16.1	25.0	37.2	10.3
Betula ermanii					
Decaying logs	0	2	0	2	10
Ground	5	6	25	36	60
Frequency	0.0	20.0	0.0	5.3	14.3
Tilia japonica					
Decaying logs	−	0	−	0	−
Ground	−	2	−	2	−
Frequency	−	0.0	−	0.0	−
Prunus incisa					
Decaying logs	−	−	−	−	2
Ground	−	−	−	−	18
Frequency	−	−	−	−	10.0
Acer spp.					
Decaying logs	−	−	−	−	2
Ground	−	−	−	−	48
Frequency	−	−	−	−	4.0

[*1] Size class: Sapling, <200cm tall; Sub-canopy, >200cm tall and <15cm DBH; Canopy, >200cm tall and >15cm DBH.
Decaying logs, Ground: Number of individuals; Frequency: Percentage frequency of tree occurrence on the decaying logs.

smaller than that on the ground. The saplings of tendency was lacked or weak on the ground. Therefore, the frequency of occurrence on decaying *Larix* was entirely absent on the decaying logs. The frequency of occurrence on decaying logs was the highest for *Tsuga* (37.5%). The second highest frequency was showed by *Picea* (23.3%), followed by *Abies* (16.0%). These frequencies were lower than those in the forest site without exception. Compared with the forest site, the population size of softwoods was large on the ground, while it was small on the decaying logs except for *Tsuga*.

Table 4 shows the relationship between the population size of hardwoods and microsites. In the forest site, *Sorbus* and *Betula* were observed in all size classes, and *Tilia* was observed only in *the* sub-canopy class. The population size of *Sorbus* on decaying logs was larger than that on the ground in the sapling class. Their frequency of occurrence on decaying logs was 62.3% in the class and was higher than that of any other species in the forest site. The population size of *Sorbus* was not different between the sapling class and the sub-canopy class, but the frequency of occurrence on decaying logs decreased largely (46.2% reduction). They had 25.0% in the frequency of occurrence on decaying logs in the canopy class. This frequency matched that of *Picea* which showed the highest frequency in the canopy class.

The population size of *Betula* on the ground was larger than that on the decaying logs constantly. They occurred on the decaying logs in he sub-canopy class only and the frequency was

20.0%. The pattern in the occurrence of *Betula* was unique; it was rarely observed in the younger size classes but dominant in the canopy class of hardwoods. The occurrence of *Tilia* was entirely absent on the decaying logs. There was no trend common to hardwoods in the transition of the frequency in conjunction with the size classes. In the windfall site, *Prunus incisa* Thunb. ex Murray and *Acer* spp. were observed along with the species from the forest site. The population size of hardwoods on decaying logs was smaller than that on the ground. Although *Betula* was the most prevalent species on the decaying logs, their population was composed by ten individuals (14.3% in the frequency). The population size of other hardwoods on decaying logs was also small (less than six individuals) and the frequency of *Sorbus* and *P. incise* was about 10% and of *Acer* spp. was only 4% on that place. Compared with the forest site, the population size of hardwoods was large in the windfall site. This enlargement practically originated from an increase in the population size on the ground.

4 Discussion

A plant that promptly established after a disturbance can enjoy greater availability of resources[24]. Consequently, the recruitment and accumulation of young trees prior to the disturbance should be helpful for successful regeneration of any tree species. It is well known that the decaying logs are important to the successful seedling recruitment of many softwoods[1-4,10,11] and a few hardwoods[19,22,23]. However, the requirements of trees for regeneration may not be the same as that for recruitment[11,34]. The importance of decaying logs for successful regeneration can be evaluated from two perspectives. One is the influence on individual regeneration, and the other is the influence on community regeneration.

The influence of decaying logs on individual regeneration can be seen in the population density of trees (Table 2). The authors found dramatically high density of *Picea*, *Abies*, *Tsuga* and also *Sorbus* on the decaying logs in the forest site. This result partly met our expectation that the advantageous characteristics of decaying logs contribute to the regeneration of any tree. On the other hand, the density of *Larix* and other hardwoods on the decaying logs was quite low or absent in this site. The suitable sites for regeneration differ by species chiefly because of differences in shade-tolerance[35].

The relative light intensity in the forest site was only 3.5%[36]. Such light environment cannot have allowed the light-demanding species to survive. Although the availability of decaying logs for successful regeneration of individuals seems to be significant, there is some doubt in its reliability. The authors found that the difference in the density between microsites was diminished as the size class of trees increased. Resembling the canopy class in the forest site, the difference in the sapling density between microsites was little in the windfall site. Moreover, the density of every hardwood on decaying logs was smaller than that on the ground in the windfall site. These facts implied that the decaying logs contributed less to trees to reach the forest canopy and contributed less to the regeneration possibility of trees in the windfall site, specifically for hardwoods. The mechanism of change in the availability of decaying logs and the influence of change on the community regeneration were discussed below.

The influence of decaying logs on community regeneration can be seen in the population size (Table 3, Table 4). Maintenance of the relationship between a plant and a microsite over different developmental stages indicates the crucial nature of microsites to the survivorship of the plant[11]. Thus, the transition in frequency of occurrence in conjunction with the size classes becomes a measure of the contribution of decaying logs to the long-term survival of each tree. The authors found that softwoods decreased in the frequency of occurrence on decaying logs as the size class changed in the forest site (Table 3). This transition indicates that individuals colonizing on decaying logs could not participate in canopy replacement, contrary to the expectation from the abundant sapling occurrence. Harmon[37] pointed out the probability that bark sloughing and bole fragmentation will prevent successful tree regeneration on decaying logs. Initial establishment of *Tsuga*, *Picea,* and *Abies* was fostered on the decaying logs in the subalpine forests of central Japan[4,38]. Their early survival improved on decaying logs (seen in this study) but their regeneration seemed to be difficult on the decaying logs. *Tsuga* persisted well on decaying logs in all three size classes compared with the other species. It seems to be a result of the shallowly spread root system of *Tsuga*[39] which might be preventing fragmentation of the decaying logs. The transition in the frequency of *Sorbus* showed a similar pattern to that of the softwoods (Table 4). Saplings of *Sorbus* occurred on decaying logs at the highest frequency among all examined species (62.3%). Their frequency of occurrence was equal to or higher than those of softwoods in the sub-canopy and canopy classes. On the other hand, the occurrence of *Sorbus* saplings on the ground clearly heightened in the windfall site. These results suggest that the decaying logs offered the substitutive site for colonization of *Sorbus* and supported their survival in the forest understory. The silhouette area of the decaying logs accounted for only 8.5% of the ground in the forest site. Considering this quantitative sparseness, the contribution of the decaying log to long-term survival of *Picea*, *Abies*, *Sorbus*, and especially *Tsuga* in the forest understory could be significant.

The occurrence of young individuals of *Betula* was rare in the forest site regardless of established position; nevertheless, they participated in the formation of the forest canopy. A similar but more extreme pattern was shown by *Larix*. A *Betula* seed was able to germinate under low light conditions in the forest interior, but it was unable to sustain subsequent growth and survival[40]. *Betula* is a typical species that regenerates depending on a intense disturbance in the subalpine forests of central Japan[35,41]. *Larix* is a pioneer tree species of Mt. Fuji[42] and they often colonized at bright places such as the tree-limit[27]. Whether they were seeded on decaying logs or not, the shade tolerance of these trees would have been insufficient for surviving under intact forest canopies. The DBH distribution of the dominant tree *Abies* had a mode between 15 cm and 30 cm in diameter (Fig. 2). This type of population structure has been reported for *Abies lasiocarpa* (Hook.) Nutt. in a subalpine forest in the Rocky Mountains of North America that regenerated after a large-scale blowdown[43]. Individuals of *Betula* and *Larix* in the canopy class seem to be successors at the time of such an event. Numerous saplings of *Betula* and a few saplings of *Larix* were observed in the windfall site but occurred primarily on the ground like other deciduous trees (*Sorbus*, *P. incise* and *Acer* spp.). The contribution of decaying logs to the long-term survival of less shade-tolerant trees was somewhat evident (e.g., *Sorbus*) but mostly negligible in both sites.

In the forest site, the canopy trees had regenerated from the ground surface. One possible cause of this regeneration manner is the deterioration of the state of decaying logs through regeneration dynamics of the forest. The areal abundance of Type-II and Type-III decaying logs was considerably low in the windfall site compared with that in the forest site. These decaying logs were characterized by the presence of moss mats on the surface. The moss mats increased the surface roughness of the log and promoted soil formation by accumulating litter[44]. The decaying logs supporting conifer seedlings often possessed a surface moss mat[2,11,38]. More than 80% of *Abies* and *Picea* seedlings were actually on decaying logs with moss mats in this region (N. Katsumata, unpublished paper). The windfall site was abundant in decaying logs of Type-I and Type-IV instead of a smaller amount of moss-covered logs. The origin of the Type-I log was damaged trees after typhoon disturbance in 1996, and the origin of the Type-IV log was a consequences of the decline of moss communities on decaying logs. Type-IV logs appear similar to Type-II and Type-III logs except for the moss mat. The difference in the cumulative areal abundance of Type-II, Type-III, and Type-IV logs between sites was only 5.5 m^2 ・ 600 m^{-2}. The state of decaying logs was changed from Type-II and Type-III to Type-IV through decline of the bryophyte community after the disturbance. This change must have caused the mortality of trees with an immature root system by depriving them of a rooting medium and mechanically pulling down the plant body. In a similar manner to the canopy trees in the forest site, the trees regenerating in this site show less evidence of the decaying log contribution to their successful regeneration.

The authors found a low occurrence of less shade-tolerant trees on decaying logs in the windfall site. Recruitment of less shade-tolerant trees must have been attempted under brighter conditions after the disturbance. However, the decaying logs available for their recruitment (i.e., moss-covered logs) no longer remain. The decaying logs occupied 20.9% of the ground in the windfall site, creating an obstacle to regeneration of less shade-tolerant trees that lagged behind in colonization. Sollins[45] reported that a fallen log required twenty years to permit tree colonization in an old-growth coniferous forest in the Cascade Range of North America. As a consequence, less shade-tolerant trees were forced to recruit and regenerate in limited areas on the ground.

A mixture of hardwoods in a coniferous forest improved the resistance to windthrow[46] and changed the forest dynamics from a cyclical regeneration system of conifers to an occasional regeneration system of mixed forest (i.e., gap regeneration)[47,48]. The decaying logs contributed to the occurrence of advanced regeneration of *Sorbus* in the forest understory. They live for more than 100-years[1], but hardly participate in the canopy formation because of lack of sufficient height, even after fully developed. Thus, the presence of advanced regeneration of *Sorbus* seems to be less important to the forest dynamics.

The principal role of decaying logs in the forest dynamics is to build and maintain the population of softwoods in the forest understory. This contribution will not fully lead to individual regeneration but has a role in making a time lag of ingress between softwoods and hardwoods (including light demanding conifer, *Larix*) in the disturbed area. The decaying logs support cyclical regeneration of conifer-dominant forests rather than mixed forests in this region.

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富士山亜高山帯林の更新動態における腐朽倒木の役割

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富士山亜高山帯の針葉樹優占林（樹林地）ならびに風害により林冠が破壊された立地（風倒地）において，地表面に分布する倒木の量的･質的構成を定量化するとともに，倒木と樹木分布の関連性を明らかにした．樹林地では，材が腐朽し，表面が蘚苔類群落で覆われた倒木が多く記録された．風倒地には，材が腐朽していても，表面が蘚苔類群落で覆われていない倒木が多く記録された．樹林地に出現した 7 種の樹木のうち，カラマツを除く針葉樹 3 種とナナカマドの分布密度は，個体サイズに関わらず倒木上で地表面より高かった．これら樹木の個体数は個体サイズが大きいほど倒木上で少なく，地表面に分布する個体の比率が高かった．倒木は樹木生存の場として有効ではあるが，それほど林冠更新には結びついていなかった．風倒地には樹高 200cm 以下の樹木のみが出現した．カラマツを除く針葉樹 3 種の分布密度は倒木上で地表面より高かった．ただし，立地間の分布密度の差は樹林地に比べ小さかった．落葉樹の分布密度は地表面で倒木上より高かった．樹木個体数は針葉樹でも落葉樹でも倒木上より地表面で多かった．風倒地だけで記録された落葉樹 2 種は倒木上にほとんど出現しなかった．風倒地において倒木の樹木生存の場としての有効性は低下していた．倒木の量的･質的構成を立地間で比較検討した結果，風倒地で倒木上の蘚苔類群落が衰退したことが明らかとなった．このことに着目して，倒木が林冠更新に大きく寄与しない理由を検討した．そして，林冠破壊後に生じる蘚苔類群落の衰退により，倒木上に生育する個体が排除されるためと推察した．さらに，倒木上で更新した落葉樹が概して少ない理由を検討した．そして，蘚苔類群落の衰退により質的に変化した倒木が，林冠破壊後に侵入を開始する落葉樹の定着を妨げるためと推察した．当地域において，倒木は定着した樹木の林冠到達を保証する立地ではないが，樹林内において樹木稚樹の個体群を拡大･維持する働き，さらに林冠破壊後に陽樹性の強い樹木の侵入を妨げる働きをもつと考えられた．これらは耐陰性をもった針葉樹が優占林分を形成することに寄与すると結論した．

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