Research Square

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The leaf litterfall patterns of Alnus alnobetula subsp. maximowiczii Chery at the timberline of Mt. Fuji, central Japan

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Research Article

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Abstract

Alnus alnobetula subsp. *maximowiczii* Chery is a dwarf shrub found at the timberline of Mt. Fuji. This species has been suggested to promote soil eutrophication in two ways: it can fix aerial nitrogen through symbiosis with nitrogen-fixing bacteria in its root system, and its fallen leaves are rich in nitrogen. In this study, we investigated the defoliation and leaf dispersal pattern of *A. alnobetula* subsp. *maximowiczii* at the timberline of Mt. Fuji. The petioles of all leaves of *A. alnobetula* in the research plots were marked with vinyl tape. The marked leaves were collected in November, when all leaves had fallen, and their locations were recorded. We found that leaf litter of this species was scattered above the dwarf shrub community, with the distribution of fallen leaves likely influenced by prevailing winds. The fallen leaves trapped in herbaceous patches above the timberline may contribute to soil eutrophication and accelerate the upward elevational movement of the timberline.

Introduction

The genus *Alnus* constitutes approximately 30 species distributed in temperate and subarctic regions of the Northern Hemisphere and the Andean Mountains of South America (Dincă and Peticilă 2019). Alder species are deciduous, broad-leaved, woody plants, ranging from tall trees to shrubs, that are distributed over a wide range of environments, from low-elevation wetland forests (Fujita and Fujimura 2008; Hurd and Raynal 2004; Prieditis 1997) to alpine zones (Dakskobler et al. 2013; David 2010; Masuzawa 1985). Members of the genus form symbiotic relationships with the nitrogen-fixing bacterium *Frankia* sp. (Ghelue et al. 1997; Roy et al. 2007). The nitrogen content of alder leaves is high, and the rate of nitrogen loss from leaves during the defoliation period is low (Dawson and Funk 1981; Sakio and Masuzawa 1992). Because the nitrogen content of fallen leaves is accordingly high (Masuzawa and Kimura 1987), *Alnus* species are used as fertilizer trees and shrubs (Baig 1992; Yanai 2002).

Ten species of alder are distributed in Japan, including the tall alder (*A. japonica* Steud.) found in lowland wetlands (Fujita and Fujimura 2008), the tall alder (*A. hirsuta* Turcz. var. *hirsuta*) present in frequently disturbed riparian areas (Kikuchi 1968), and the dwarf shrub alder (*A. alnobetula* subsp. *maximowiczii* Chery (Chery 2015), henceforth referred to as *A. alnobetula*) that forms communities in alpine zones around forest limits (Masuzawa 1985). On Mt. Fuji, *A. alnobetula* is distributed together with *Salix reinii* Franch. et Sav. ex Seemen as a mantle community near the timberline (Masuzawa 1985). In the timberline ecosystem of Mt. Fuji, soil nitrogen content is low in the bare soil above the tree line and is markedly higher in the alder community below (Masuzawa 1985).

In recent years, the timberline of Mt. Fuji has advanced rapidly upwards, and the degree of vegetation cover above the timberline has dramatically increased (Sakio and Masuzawa 2012; 2020). The role of *A. alnobetula* as a driving force in this process has attracted attention. The nitrogen content of leaves of this alder is higher, and its leaf nitrogen loss rate during the defoliation period is lower, than that of *Salix reinii* and other deciduous trees distributed at the forest limit (Sakio and Masuzawa 1992). Although this

defoliation promotes eutrophication of the soil around the timberline, little is known about the dynamics of *A. alnobetula* leaf loss.

To examine how *A. alnobetula* affects soil eutrophication in the timberline ecosystem of Mt. Fuji, we investigated the following issues: 1) seasonal changes in *A. alnobetula* defoliation, 2) leaf dispersal distance, and 3) distribution pattern of fallen leaves.

Materials and methods

Materials

Alnus alnobetula subsp. *maximowiczii* Chery is a deciduous, broad-leaved shrub that grows to several meters in height (Fig. 1a). In Japan, the species is distributed in subalpine to alpine zones from central Honshu to Hokkaido. At the forest limit of alpine zones, *A. alnobetula* forms dwarf shrub forests 1–2 m in height. On Mt. Fuji, the species forms 1–2 m tall mantle communities at the timberline (Masuzawa 1985). The leaves of this alder have a higher nitrogen content than those of deciduous, broad-leaved trees such as *S. reinii* and *Betula ermanii* Cham., which are also distributed at the same elevation. In addition, the rate of nitrogen loss from leaves during the defoliation period is lower than that of other timberline species (Sakio and Masuzawa 1992). Nodules are formed on the roots of this tree (Fig. 1b) that are symbiotic with the nitrogen-fixing bacterium *Frankia* (Ghelue et al. 1997; Roy et al. 2007). At the forest limit of Mt. Fuji, *A. alnobetula* exhibits high photosynthetic rates, and community production is as high as that of beech forests in the upper cool-temperate zone (Sakio and Masuzawa 1987).

Study Site

The research site (35°21’N, 138°45’E) is located at the timberline (ca. 2,400 m) on the southeastern slope of Mt. Fuji, where the vegetation is recovering from damage caused by the 1707 volcanic eruption of Hoei-Zan, a parasitic crater (Fig. 2a; Masuzawa 1985; Sakio and Masuzawa 2012; 2020). The vegetation at the timberline of Mt. Fuji changes dramatically as one proceeds down the slope, with variations in herbs, deciduous shrubs, deciduous conifers, and evergreen conifers. The timberline vegetation comprises deciduous dwarf trees: *A. alnobetula*, *S. reinii*, *Lalix kaempferi* Carrière, and *B. ermanii* (Fig. 2b). Downslope of the dwarf vegetation, the forest composition changes from *L. kaempferi* forest to coniferous evergreen forest, of which *Abies veitchii* Lindl. and *Picea jezoensis* Carrière var. *hondoensis* Rehdervar. are dominant.

Methods

On August 6, 1979, plot A (1 × 8 m) and plot B (1 × 5 m) were established in a population of 1–2-m high dwarf shrubs of *A. alnobetula* at the forest limit (Fig. 3). Each plot was set up with a 2-m pole placed at each corner and interconnected by rope. The petioles of all leaves of *A. alnobetula* in the plots were marked with 3-mm wide vinyl tape (Fig. 1a). A total of 5,991 and 7,147 leaves were marked with different-

colored tape in plots A and B, respectively. The marked leaves were then scattered around the forest limit as the defoliation period approached. The marked leaves were collected on November 12, when all the leaves had fallen, and their locations were recorded. Locations were determined by dividing the study area into 2.5-m grids and counting the number of fallen leaves in each grid. We collected 4,166 leaves scattered from plot A and 5,776 leaves scattered from plot B. The recovery rates of leaves from plots A and B were 69.5% and 80.8%, respectively.

On May 25, 1980, four litter traps were set up in plot C in the *A. alnobetula* community. The litter traps were constructed of cheesecloth (approximately 1.0-mm mesh) mounted in a square wooden frame with a 0.5-m^2 (71 cm on one side) opening. The contents of the litter traps were collected and transported to the laboratory approximately every 2 weeks between June and November at 1980 and 1981. We counted the number of *A. alnobetula* leaves in the four litter traps. The average (± SD) of the four traps was calculated.

On June 16, 1981, plot C (1 × 3 m) was established in a dwarf shrub community of 2.4-m high *A. alnobetula* at the forest limit (Fig. 3). The plot was set up with a 2-m pole placed at each corner and interconnected with rope. The plot was divided into 40-cm layers starting from the ground surface, and the number of leaves distributed in each layer was counted. Leaf counts were taken approximately every 2 weeks until early November when all the leaves had fallen.

Results

Seasonal defoliation pattern

Leaf development of *A. alnobetula* began in early June and continued until early July in plot C. The number of attached leaves peaked in mid-July and then gradually declined until early October, and most fell off by mid-October. The number of attached leaves tended to be higher in the upper layers of the canopy, except for the uppermost layer. Throughout the growing season, more than 90% of attached leaves were present 80 cm above the ground (Fig. 4). Leaves were rarely seen below 40 cm above the ground. Defoliation of *A. alnobetula* began in September and peaked in October (Fig. 5). In 1980, defoliation occurred nearly half a month earlier than in 1981, but the defoliation pattern was almost the same. A single defoliation peak was observed, in contrast to the bimodal leaf fall reported for other alder species.

Fallen leaf dispersal distances and distribution patterns

Most fallen leaves from *A. alnobetula* in plots A and B were found within the plots. Leaf dispersal was mainly upwards and towards the right side of the slope, i.e., to the east. Some fallen leaves from plot B were distributed downslope (Fig. 6). All leaves scattered above the forest limit were not distributed on bare ground and instead were trapped in patches of *S. reinii* or *Fallopia japonica* Ronse Decr. var. *japonica*.

The number of fallen leaves decreased rapidly with increasing dispersal distance. More than 90% of fallen leaves were dispersed within 5 m. The maximum fallen leaf dispersal distance was 43 m. Dispersal distance patterns of leaves from plots A and B were similar (Fig. 7).

Discussion

The timberline vegetation varies dramatically on Mt. Fuji. Moving downward from bare ground where no vegetation has invaded, the landscape changes to grassland, then to the forest edge, and finally to subalpine coniferous forest, all over a distance of approximately 200 m (Masuzawa 1985). Soil moisture content in the A layer gradually increases with decreasing elevation, and soil nitrogen and carbon content increase rapidly near the dwarf shrub community constituting the forest boundary (Masuzawa 1985). This pattern suggests that fallen leaves from dwarf shrubs contribute to the eutrophication of soils at the tree limit. The dwarf shrub community comprises the following woody plant species: *A. alnobetula*, *S. reinii*, *B. ermanii*, and *L. kaempferi*. Given its symbiosis with *Frankia*, which forms root nodules, the major contributor to soil eutrophication among these species may be *A. alnobetula*. The nitrogen content of *A. alnobetula* leaves is higher than that of *S. reinii* and *B. ermanii* (Sakio and Masuzawa 1992), and little nitrogen is lost, even during the leaf fall season (Masuzawa and Kimura 1987).

In this study, we clarified the seasonal pattern of defoliation of *A. alnobetula* at the tree limit. We determined that the leaf growth period is only 4 months, from mid-June to mid-October, and that defoliation occurs rapidly during early to mid-October (Figs. 4 and 5). In regard to different alder species, the first peak of defoliation of *A. japonica*, *A. hirsuta* var. *hirsuta*, *A. inokumae* Murai et Kusaka, and *A. glutinosa* Gaertn. occurs in early summer (Kikuzawa 1980). In contrast, no defoliation of *A. alnobetula* takes place in early summer, and the number of leaves that have fallen by September is less than 10% of the total number of fallen leaves. In addition, no particular leaf position is selectively prone to leaf fall in *A. alnobetula*. In this study, bimodal defoliation of *A. alnobetula* was rarely observed, unlike *A. japonica* and *A. hirsuta* var. *hirsuta* (Fig. 5). To produce leaf material during the very short growth period, *A. alnobetula* thus relies on its high photosynthetic ability (Sakio and Masuzawa 1987).

Most fallen leaves of *A. alnobetula* were scattered around individual plants (Figs. 6 and 7). In a fallen-leaf movement experiment using *S. schwerinii* E.L.Wolf *subsp. yezoensis* Vorosch. and *S. udensis* Trautv. et C.A.Mey., the number of fallen leaves also rapidly decreased according to their distance from individuals (Abe et al. 2014). The deposition of deciduous leaves of *A. alnobetula* to the east above the slope may have been caused by seasonal winds from the west, with this distribution pattern possibly influenced by prevailing winds blowing from the west in autumn and winter (Oka 1980) around the southeastern slopes of Mt. Fuji. In experiments with *S. schwerinii* subsp. *yezoensis* and *S. udensis*, Abe et al. (2014) obtained similar results in regard to wind direction and leaf dispersal direction.

Alnus alnobetula defoliation would be expected to increase soil nitrogen content around the tree limit. *Alnus alnobetula* litterfall was found over 30 m above this line (Fig. 6). The nitrogen fixation in saplings of this species were measured under natural conditions in the subalpine zone of Mt. Fuji. The amount of

annual nitrogen fixation is almost the same as that of nitrogen used for annual growth (Tsutsumi et al. 1993).

The fallen leaves, which were trapped by herbaceous plants such as *F. japonica* var. *japonica* and by dwarf shrubs, should increase soil eutrophication in these patches. Such patches contribute to soil eutrophication and serve as nurse plants that protect tree seedlings from severe environments, such as drought and strong winds (Endo et al. 2008; Minami and Watanabe 2007; Nabeta et al. 2015). When a patch of *F. japonica* var. *japonica* expands, a doughnut phenomenon, in which the center of the patch becomes hollow, is observed (Masuzawa 1995). Evergreen conifers, namely, *A. veitchii* and *P. jezoensis* var. *hondoensis*, have been observed invading these central regions harboring eutrophic soils surrounded by nurse plants (Sakio and Masuzawa 2020). The higher nitrogen content of soil at the center of the patch may be due not only to the decomposition of fallen *F. japonica* var. *japonica* leaves, but also to *A. alnobetula* leaves originating from the timberline. In the present study, all fallen leaves observed above the forest limit were trapped in herbaceous plant and shrub patches. More fallen leaves were likely scattered above the timberline but may have been blown away by strong winds. Tobita et al. (2013) showed that *Alnus hirsuta* Turcz. var. *sibirica* C.K.Schneid. supplies leaf litter that has a high nitrogen content and rapid decomposition rate, and contributes to rapid nitrogen accumulation through N_2 fixation in the soil. Urli et al. (2020) suggested that *A. alnobetula* obtained a substantial proportion of its nitrogen through biological fixation.

On the basis of these results, we hypothesize that deciduous leaves of *A. alnobetula* shrubs growing in the timberline have a significant impact on soil eutrophication above the forest on Mt. Fuji.

Declarations

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Conflict of interest

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Author contributions

TM conceived the study. TM and HS designed the research. TM and SH performed the research. SH analyzed data. SH wrote the paper. All the authors approved the final version of the manuscript.

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Figures

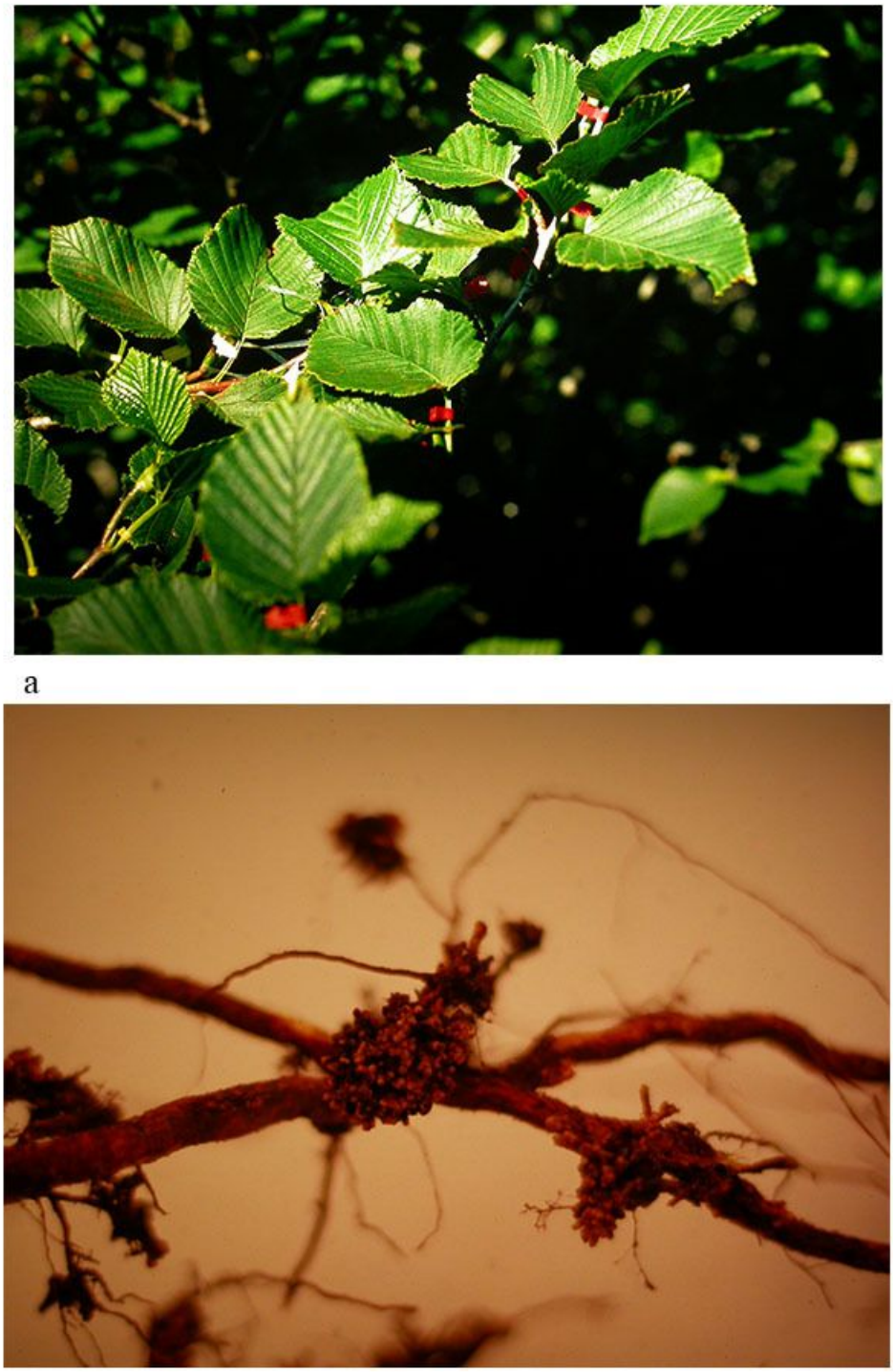


Figure 1

Leaves and root nodules of *Alnus alnobetula* subsp. *maximowiczii*. (a) Leaves of *A. alnobetula*. Petioles of all leaves of *A. alnobetula* in each plot were marked with vinyl tape. (b) Root nodules on *A. alnobetula*.



a



b

Figure 2

Research site at the timberline of Mt. Fuji. *Alnus alnobetula* subsp. *maximowiczii* dwarf shrubs are located at the tree limit. (a) Timberline of Mt. Fuji. (b) *A. alnobetula* dwarf shrub.

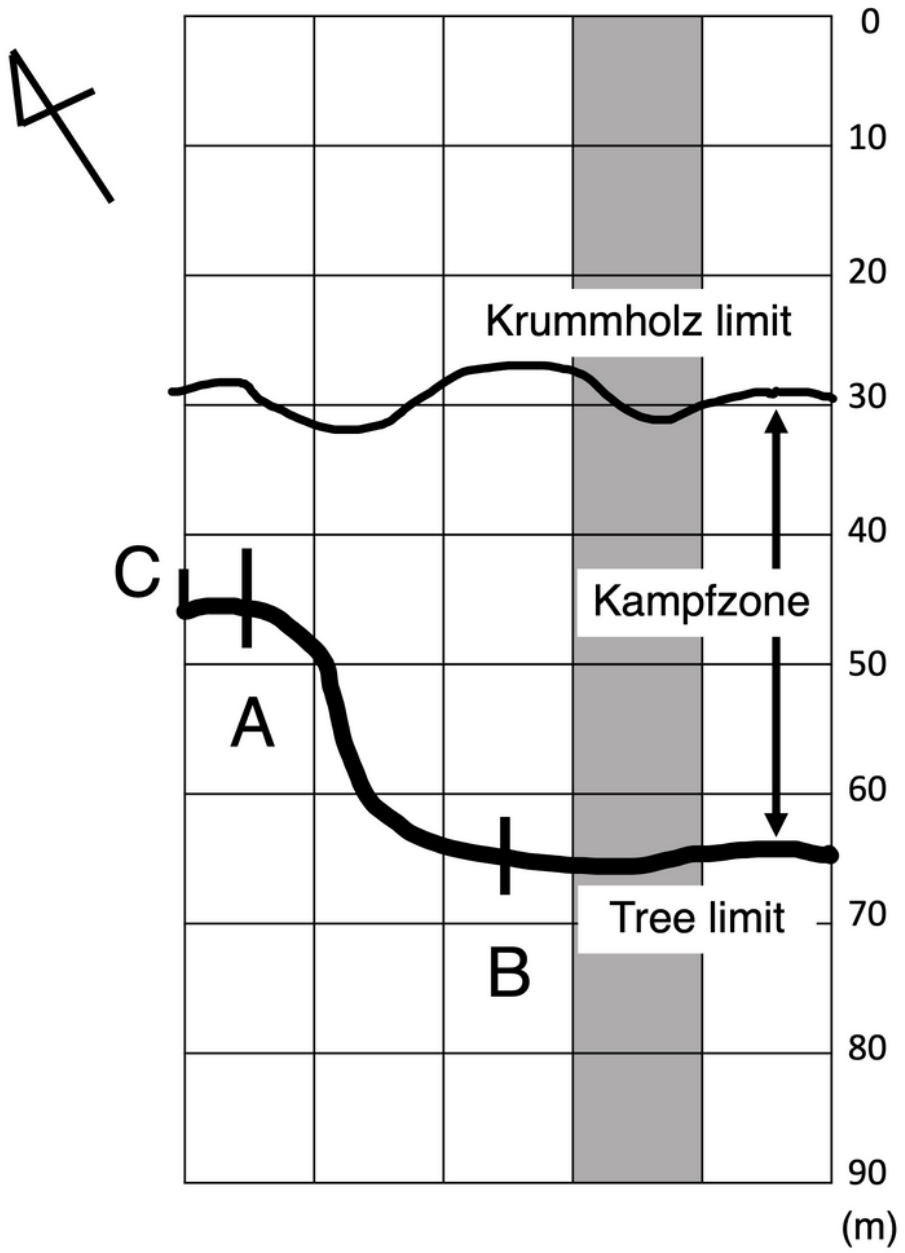


Figure 3

Research site of *Alnus alnobetula*subsp. *maximowiczii* dwarf shrub vegetation at the timberline of Mt. Fuji. The three black vertical lines (A, B, and C) indicate the survey plots. The gray area is a permanent plot where trees are being surveyed (Masuzawa1985; Sakio and Masuzawa 2012; 2020).

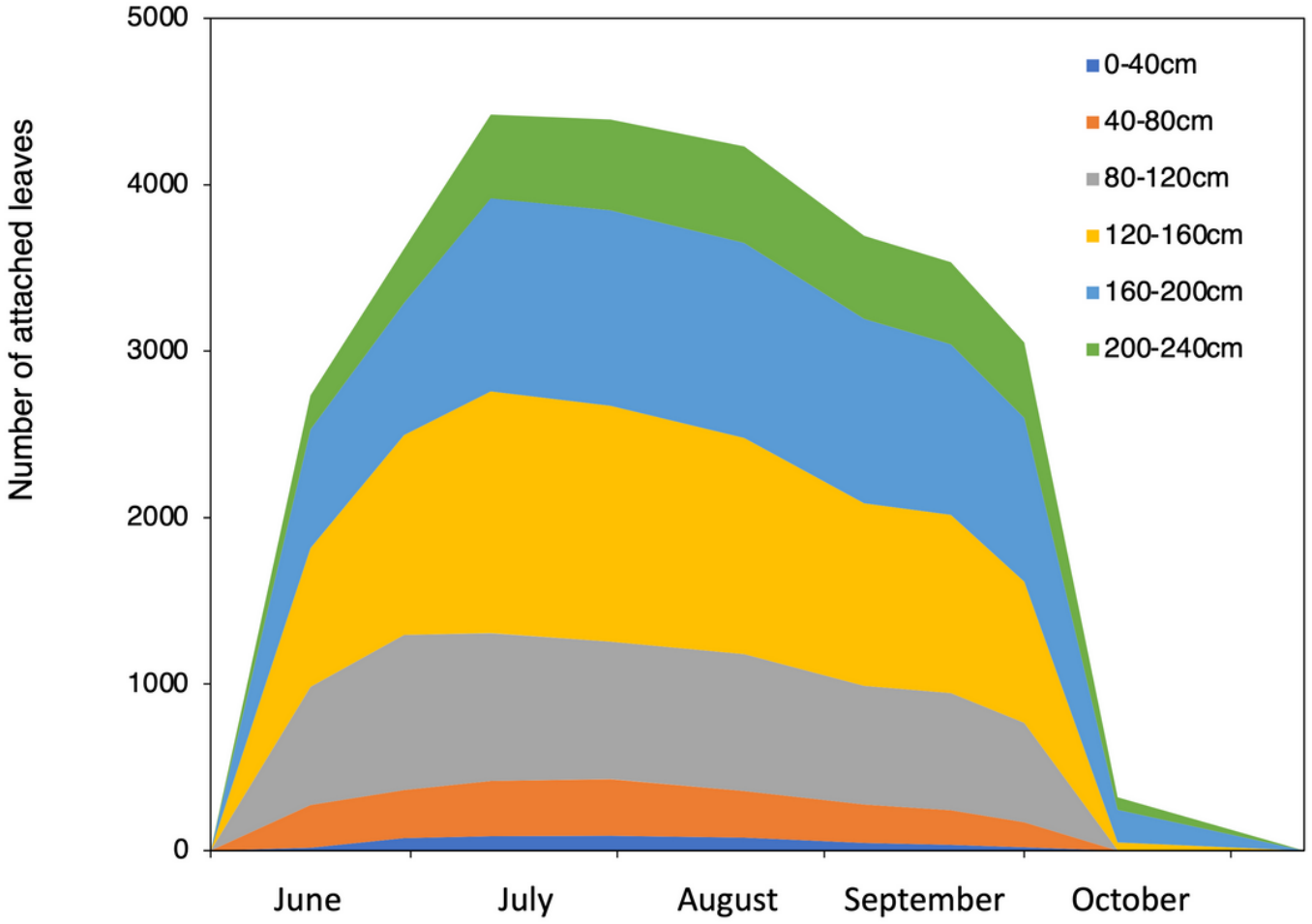


Figure 4

Pattern of leaf dynamics across seasons in 1981. The number of attached leaves per 3 m2 is shown.

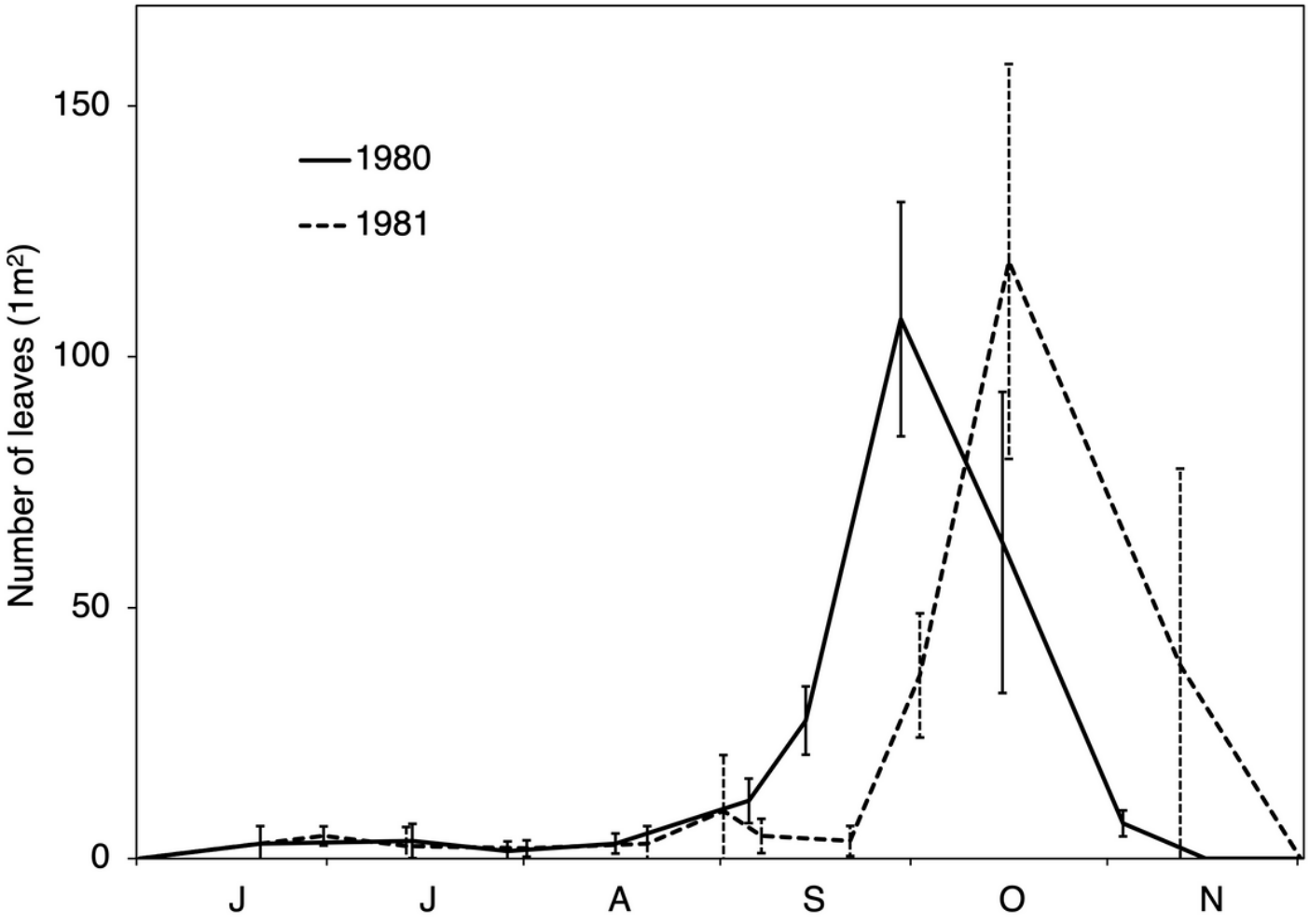


Figure 5

Seasonal defoliation pattern. The number of fallen leaves in 1980 and 1981 is shown. Values shown are means ± SD (n = 4 in 1980 and 1981).

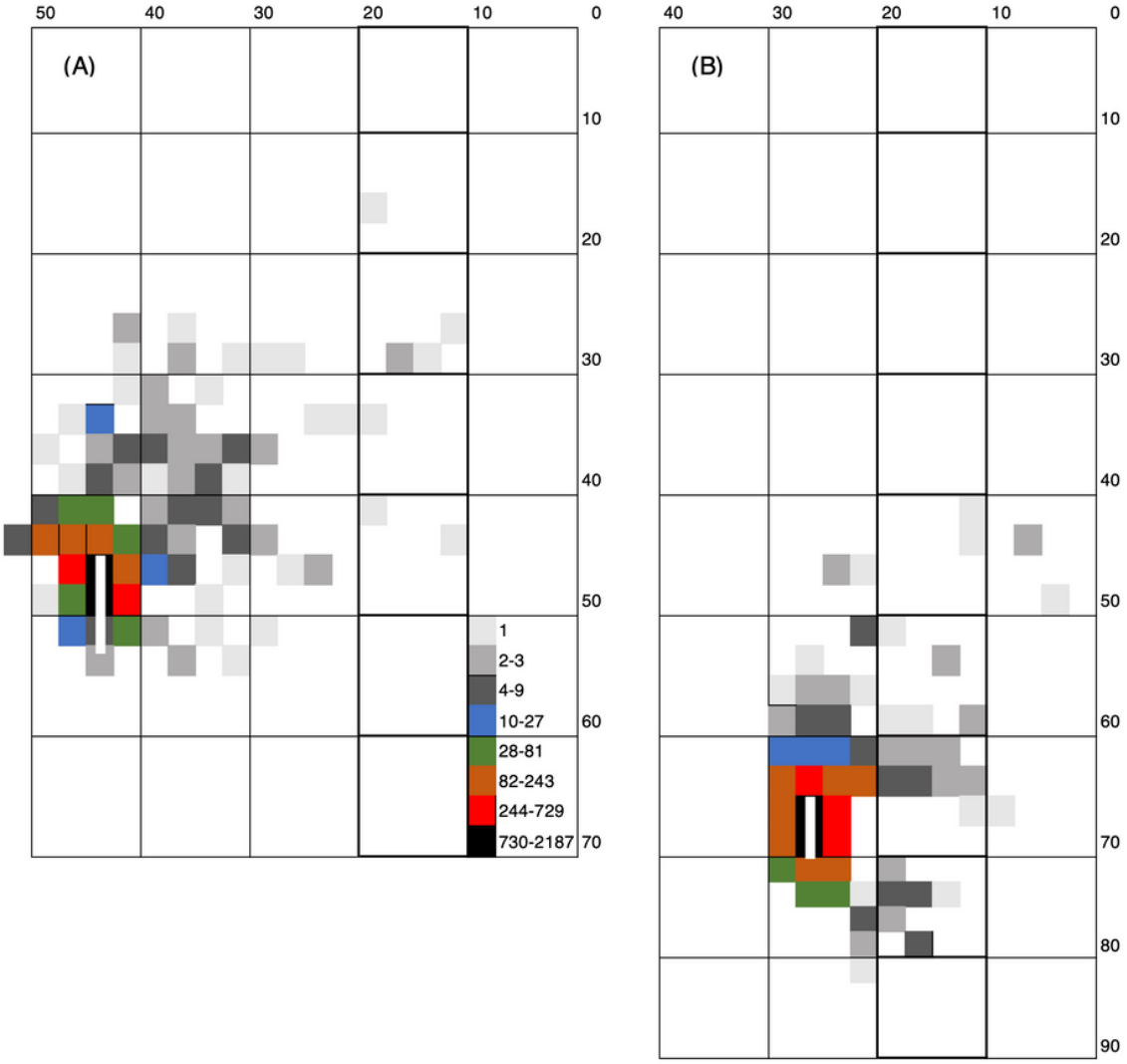


Figure 6

Fallen leaf dispersal pattern. The top of the figure corresponds to the upper slope. Plots A and B were respectively located 45–53 m and 65–70 m downslope.

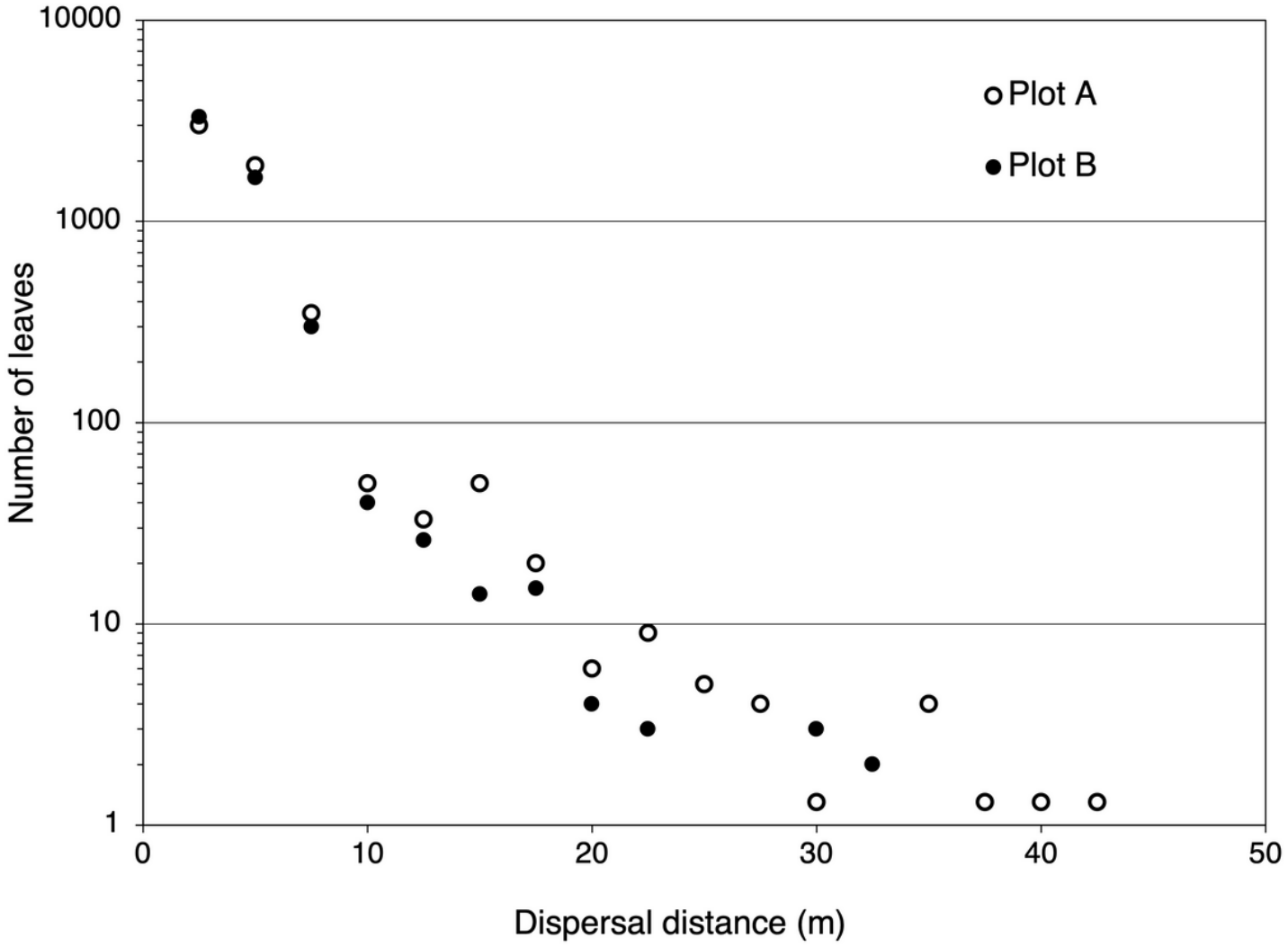


Figure 7

Dispersal distances of fallen leaves.