Betula ermanii, a Dominant Subalpine and Subarctic Treeline Tree Species in Japan: Ecological Traits of Deciduous Tree Life in Winter

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Abstract

Betula ermanii (Japanese mountain birch), a dominant tree species of the subalpine and subarctic treeline ecotones in East Asia, was investigated with respect to frost hardiness, bud phenology, and woody-tissue respiration above and below snow at the treeline on Mt. Fuji, Japan. On the Pacific-facing south slope, the minimum air temperature regime at 2450 m altitude is not harmful to the viability of previous year's shoots and emerging leaves. Betula ermanii will approach its upper distribution limit where the risk of spring frost damage in immature tissues interferes with the need for a minimum length of the growing season. In the cold Pacific winter climate of Japan, susceptibility of bursting buds and dehardened shoots to frost down to $-7°C$ late in May is a major determinant for the species' altitudinal distribution limit at 2800 m altitude. It is concluded that two periods of minimum temperature affect the upper distribution of a deciduous broad-leaved tree species in temperate climates: (1) periods of subzero temperature which determine the occurrence of spring frost damage and affect the beginning of the growing season and (2) cool periods during the growing season that affect development and ripening of overwintering plant compartments.

Introduction

Japan is distinguished by an enormous richness of plant species from the evergreen broad-leaved forest communities of Kyushu to the boreal coniferous forests of Hokkaido. The latitudinal spread of these vegetation zones is markedly reduced when compared with the corresponding sequence of European vegetation zones from southern Spain to Scandinavia (Ellenberg, 1980). The diversity of vegetation in Japan is mainly a consequence of the rhythmic shift of the monsoon circulation on the eastern edge of Asia. During summer, the southeast monsoon brings tropical air to the Pacific side of the islands creating a humid climate with more than 2000 mm of annual precipitation.

During winter, Japan's climate is characterized by a strong contrast between the Sea of Japan side and the Pacific side of the islands. The northwest wind of the winter monsoon brings dry, cold air from the Siberian high pressure cell across the Sea of Japan where it is warmed and moistened. The uptake of water vapor is enhanced by both the warm Tsushima current and the duration of sea passage of this air mass. Since the islands lie across the monsoon direction, heavy snowfall occurs on the western part of the archipelago facing the Sea of Japan whereas low snow cover and large daily temperature fluctuations prevail on the Pacific side (Shitara, 1975; Shidei, 1979). The Japanese Alps represent the major barrier for the northwest monsoon and thus enhance this climatic contrast. Therefore, a steep gradient of winter climate conditions exists that represents the driving force for the conspicuous differences in natural vegetation cover between the Sea of Japan side and the Pacific Ocean side (Miyawaki, 1985).

Treelines in Japan broadly continue to reflect the physical effects on, and biological adaptations to, these climatic gradients because the absence of extensive woodland pasturage has prevented subalpine forests from anthropogenic degradation and al-titudinal depression. In those regions of the Japanese Alps where dry but cold winter climate prevails, the forest-alpine transition zone spreads from 2650 m to the upper tree limit. Towards the Sea of Japan, however, the upper distribution limit of the coniferous forests decreases by about 300 m of elevation. Above the coniferous forest belt, Japanese mountain birch (Betula ermanii Cham.) forms open woodlands of 200 to 500 m of vertical spread to the uppermost limit of tree growth at nearly 2900 m altitude in the Japanese Alps. The capability to withstand severe winter climate conditions (Suzuki, 1964, 1973; Kikuchi, 1981) is obviously a prominent feature of the species' ecological constitution to be able to form subalpine and subarctic treelines in the temperate and boreal zones of northeastern Asia (Hämet-Ahti et al., 1974; Sakai and Larcher, 1987).

Therefore, in terms of ecophysiology, the present study aims to investigate the effect of (1) increasing cold on the extent and seasonal variation in frost hardiness of young shoots, (2) the occurrence of spring frost on the course of bud phenology and damage to emerging leaves and (3) snow cover on woody-tissue respiration.

Materials and Methods

STUDY AREAS

On Mt. Fuji (35°21.5′N, 138°43.8′E, 3776 m a.s.l.), experimental study sites were established on the Pacific-facing south slope at 1600, 2000, and 2450 m altitude. At 1600 m a.s.l., B. ermanii is in the range of its lower distribution limit. Between 1600 and 1800 m altitude the montane deciduous broad-leaved forest, dominated by Fagus crenata Blume and Abies homolepis Sieb. & Zucc. is replaced by the subalpine coniferous forest. In the upper subalpine region from about 2000 m upslope, A. veitchii Lindl. and Larix leptolepis Gord. form well-developed stands mixed with A. mariesii Mast. and B. ermanii as the only

deciduous broad-leaved tree species. The upper study site was located in the treeline ecotone near the tree limit at 2500 m a.s.l. On the northwest slope the upper limit for tree life, represented by *B. ermanii* and *L. leptolepis,* is reached at 2800 m altitude while it decreases by 300 m toward the south slope (Ohsawa, 1984; Nakamura, 1992). In the current context a *tree* is defined as an upright woody plant with a dominant above-ground stem higher than the average snow height so that its crown is exposed to the prevailing atmospheric conditions (Ellenberg, 1996; Körner, 1998). A multistem growth habit is a characteristic feature of *B. ermanii* at the treeline and the decrease in its average height from 10 to about 1 m between 2380 and 2500 m a.s.l. is marked.

At each study site five representatives of *B. ermanii* were selected for studies of frost hardiness and woody-tissue respiration. The investigation of bud phenology was based on ten representatives per study site.

FROST HARDINESS

At monthly intervals (from October 1996 to June 1997) cold resistance of shoots formed in the previous growing season (1996) was investigated by an experimental freezing treatment in a cooling bath starting at 0°C down to −47°C at a cooling rate of 5 K h^{-1} (Gansert et al., 1999). Frost hardiness of the shoots was determined using the method of electrolyte leakage from freeze-injured tissues (Hallam and Tibbits, 1988; Silim and Lavender, 1994). According to the method of Flint et al. (1967), an Index of Injury (I_t) was derived from conductivity measurements of the frozen and control (unfrozen) specimens to quantify the degree of cold injury on a percentage basis from 0% (i.e. no freeze damage) to 100% (i.e. tissue completely killed). Frost hardiness was expressed by plotting the I_t-values as a function of freezing temperature.

Cold resistance of emerging leaves at 1600 and 2000 m altitude was determined in mid-May and at the treeline in early June. The fresh samples were exposed to a decreasing temperature regime in a cooling bath starting at +2°C down to −6°C at a cooling rate of 1 K h^{-1}. Frozen specimens were removed at 1°C intervals. Control specimens were stored in a plastic bag in the dark at +6°C. After freezing, the leaf samples were treated in the same way as the shoot samples and the I_t-values were determined.

BUD PHENOLOGY

The course of bud phenology of *B. ermanii* was investigated from late March 1997 to late June 1998. Nine phenological stages were differentiated (Murray et al., 1989; Heide, 1993): buds closed [0], slightly swollen [1], swollen [2], green foliage showing [3], early elongation [4], advanced elongation [5], early frondescence [6], advanced frondescence [7] and frondescence terminated [8]. At each sampling date, 30 vegetative buds were collected randomly from shoots of the upper crown of each of the sample trees and classified according to their phenological stages. All buds per sampling date and study site were treated as a composite sample.

RESPIRATION

Respiration of branches of *B. ermanii* was measured by means of irreversible chemical bonding of CO_2 to soda lime (Edwards, 1982; Raich et al., 1990). A branch segment was enclosed by a cuvette made of high density polystyrene, the outside surface of which was sealed with 0.2 mm aluminum foil. A petri

dish filled with 50 g of dried (130°C, 12 h) soda lime (Wako Chemical Ind., Lot No. LEG 7966) was inserted into the cuvette to ensure the quantitative absorption of CO_2 released from the branch. Preliminary experiments were carried out to prove the absorptive characteristic of this soda lime lot for CO_2 at different concentration levels provided by a CO_2 gas mixing unit, (GMA-2, Walz Company, Germany) and different air humidity at 20°C. A constant ratio of 10% absorbing (i.e. 58 cm^2 petri dish) to generative CO_2 surface (i.e. 580 cm^2 branch segment) was maintained. Two cuvettes per sample tree were mounted at branches of similar girth, one in the upper and one in the lower part. To avoid restriction of CO_2 release from the enclosed branch a constant inner air volume of the cuvettes of 14 dm^3 was maintained. The rate of respiratory CO_2 release was determined by measurements of weight increment of the soda lime samples after exposure for several days in the cuvettes and re-drying. This value was stoichiometrically corrected for water loss during the drying process and reduced by the amount of free air CO_2 accumulated in an empty reference cuvette during the same period at each altitude.

During the cold season from mid-November 1997 to mid-April 1998, a total of 15 experiments were carried out at the treeline. From mid-January to mid-April, branch respiration about 1 m below the snow surface was measured in six experiments derived from three cuvettes. Branch surface temperature was also recorded in 30-min intervals 1 m below and 0.2 m above the snow surface. The Arrhenius-equation was applied for calculating the respiration rate as a function of temperature, using the results of all experiments as the reference basis ($n = 15$).

TEMPERATURE RECORDS ON MT. FUJI

Daily records of air temperature were obtained on Mt. Fuji from four meteorological stations at different altitudes (500, 1280, 1700, and 2350 m a.s.l.) on the west slope from 1970 onward. The highest station is located in the subalpine forest and the others are located in open areas. Air temperature was measured in meteorological shelters 120 cm above ground level at 0900 h. On the southeastern slope (35°21' N, 138°45'E) at about 2400 m altitude, air temperature was recorded continuously under the same conditions from April 1982 to March 1989 (Masuzawa et al., 1989, 1990). On the south slope at 1600, 2000, and at 2450 m a.s.l. air temperature was recorded at 30-min intervals in the upper crown of mature birch trees selected for ecological investigations from July 1996 to May 1998 (Gansert et al., 1999). The Mt. Fuji meteorological observatory which is located near the summit (3772 m a.s.l.) provided daily air temperature records for the past 17 yr and monthly mean and absolute minimum temperatures were available from 1932. Based on these data, the absolute monthly minimum temperature at the treeline was calculated with regard to varying monthly lapse rates of temperature from 0.7°C 100 m^{-1} in August to 1.08°C 100 m^{-1} in February.

STATISTICS

The index of injury (I_t-value) was calculated as the arithmetic mean value of four replicate samples per freezing treatment and sampling date. The range of I_t-values of each set of replicate shoot samples was less than 5% on an average and therefore was omitted from the graphs. For statistical analysis, the Mann-Whitney ranked sum test (*U*-test) was employed. Unless otherwise stated, significant values have $P < 0.01$. The stage of bud phenology was assessed by calculating the mode of each
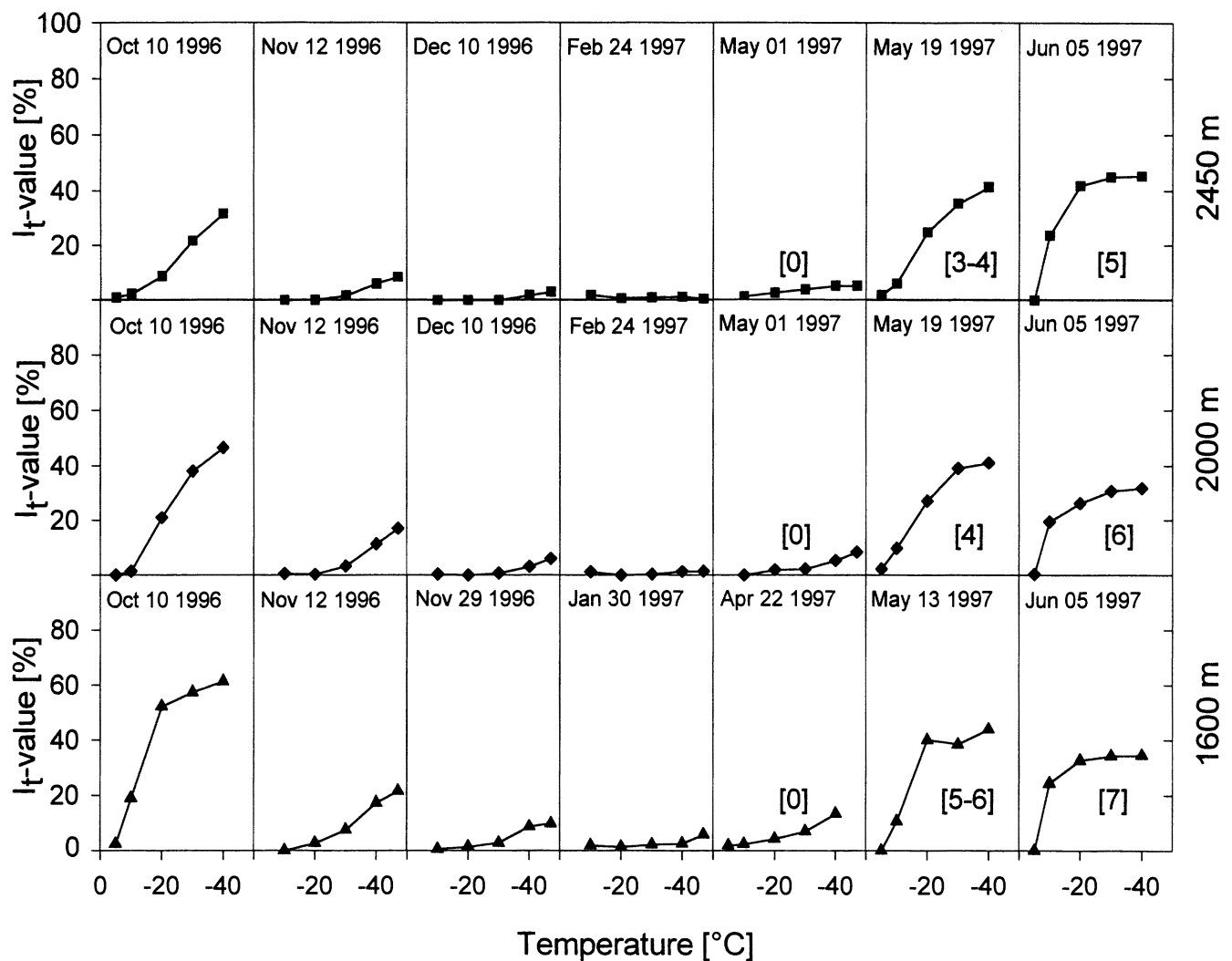
FIGURE 1. Seasonal course of frost injury of previous year's shoots (1996) of Betula ermanii at different altitudes on the Pacific-facing south slope of Mt. Fuji from October 1996 to June 1997. Frost damage is expressed by Flint's Index of Injury (I_t-value). Different stages of bud phenology are indicated by the numbers given in brackets (see text).

composite sample (Sachs, 1992). Temperature dependence of respiration was calculated by means of nonlinear regression analysis.

Results

FROST HARDINESS OF BETULA ERMANII

The altitudinal distribution of B. ermanii was assessed in terms of the species' susceptibility to frost injury in a decreasing temperature climate. Since previous year's shoots carry the buds and mainly consist of parenchymatous tissue, it was hypothesized that these juvenile compartments react significantly to changes of ambient air temperature during the cold season. Differences in both the extent of frost hardiness at a given date and the altitude-related course of cold acclimation and dehardening were determined (Fig. 1).

The decrease of I_t-values from low to high altitude in the period from mid-October to mid-November indicated an enhanced cold acclimation near the treeline. During October, cold resistance of the shoots was strongly increased so that the injurious temperature range was lowered from at least 7 to 22 K below the ambient minimum temperature regime. Therefore, B. ermanii is able to withstand frost down to −15°C which is a

climatic feature of Mt. Fuji in mid-November. By that time, shoots at the upper altitudes were completely frost hardy to −20°C and thus a rapid drop of air temperature from above zero to −10°C, which often occurs during that time, was not harmful. The process of cold acclimation between October and December preceded the temperature decline by at least 2 wk. By early December, freezing to −30°C failed to cause frost injury in shoots from the treeline where such low temperature is not reached naturally. From the many years on record, the minimum air temperature at the treeline has then reached −20°C. At the summit of Mt. Fuji the absolute minimum temperature ever recorded since 1932 was −38°C in late February 1981 (Fig. 2B). At that time of the year, temperature minima of −25°C are usual at the treeline (Fig. 6), and young shoots can then be exposed to even −80°C with little or no injury (Gansert et al., 1999).

In 1997, the onset of dehardening at the treeline could be observed at the beginning of May, which was about 10 d behind the corresponding condition of shoots gathered at 1600 m altitude. Yet cold resistance of the shoots was considerable proven by I_t-values smaller than 5% at −20°C freezing temperature. Dehardening took place before bud swelling was observable along the transect (phenological stage [0]). By mid-May, the delay of dehardening from the low to the high altitude corresponded with
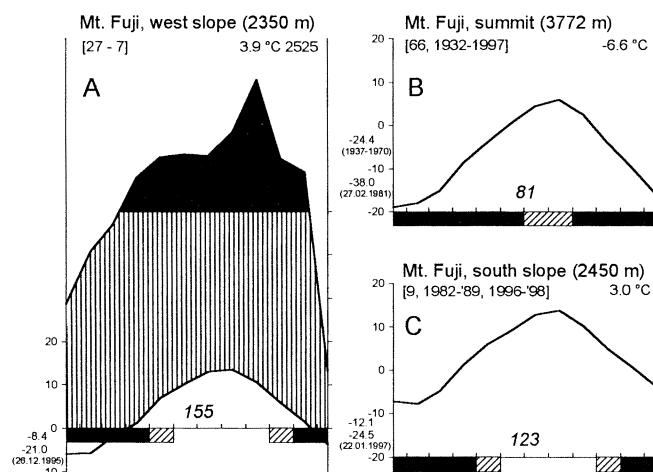
FIGURE 2. Climatic diagrams near the treeline on the west (A) and south slope (C) of Mt. Fuji and at the summit (B). The convention of Walter and Lieth (1967) was used for presenting the data.

Figure 3. Frost injury of emerging leaves of Betula ermanii at different altitudes on the south slope of Mt. Fuji in spring 1997. Young leaves from the treeline were in a similar stage of early frondescence [6] 3 wk later than those from lower altitudes. Vertical bars indicate the range of I_t-values per freezing treatment.

the stages of bud phenology. At 1600 m altitude early frondescence (phenological stage [6]) corresponded with a degree of frost injury down to −20°C which was nearly double that at the treeline where bud elongation had just begun (phenological stage [4]). Until early June, continued dehardening was reflected in a doubling of injury at −10°C at all altitudes ($P < 0.001$). Freezing damage at −20 to −40°C was significantly greater at the treeline, suggesting that dehardening was even more advanced there than at the lower altitudes. The seasonal course of frost hardiness of young shoots of B. ermanii near the treeline at 2450 m altitude reveals that its viability is unlikely to have been affected by the natural low temperature regime either during the sensitive periods of increased frost susceptibility in October and May or by severe frost during midwinter.

Frost damage of emerging leaves in the stage of early frondescence [6] significantly increased at freezing temperatures below −2°C (Fig. 3). Samples gathered at 1600 m altitude showed a significant increase of I_t-value from 17.7 to 44.8% by lowering the freezing temperature from −2 to −3°C. A corresponding increase of frost damage of samples from the treeline was observed between −3 and −4°C, indicating a somewhat higher frost resistance at the higher altitude. Although there was no significant difference in frost susceptibility among the samples down to −2°C, reduced I_t-values of those from the treeline tended in the same direction. Considerable frost damage in all samples could be induced by freezing at −6°C when 70% of the leaf tissue was killed.

BUD PHENOLOGY OF BETULA ERMANII

The course of bud phenology described in terms of the nine different phenological stages given above was observed in spring 1997 and 1998 (Fig. 4). In the 2 yr, the phenological stages were retarded with increasing altitude but the pattern was different. In 1997, buds at 1600 m altitude were in the stage of early frondescence [6] on 19 May, while this stage was reached not before 1 June and 17 June at 2000 and 2450 m altitude, respectively. While the beginning of the growing season, marked by the termination of frondescence (phenological stage [8]), was observed at the lower distribution limit of birch on 17 June 1997, it was delayed for 2 wk at the treeline.

With respect to the daily minimum temperature regime at the treeline buds in the phenological stages [1] and [3] were
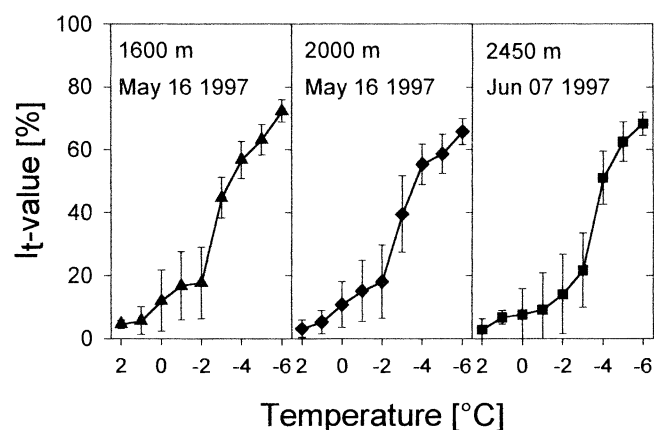
observed 10 d earlier in 1998 than in 1997, when a frost period of 20 d occurred in April (Fig. 5). A third frost period from 19 to 29 May 1997, probably caused a delay of bud phenology so that early frondescence [6] was observed 30 d later than in 1998, when frost had ceased on 9 April. From the many years on
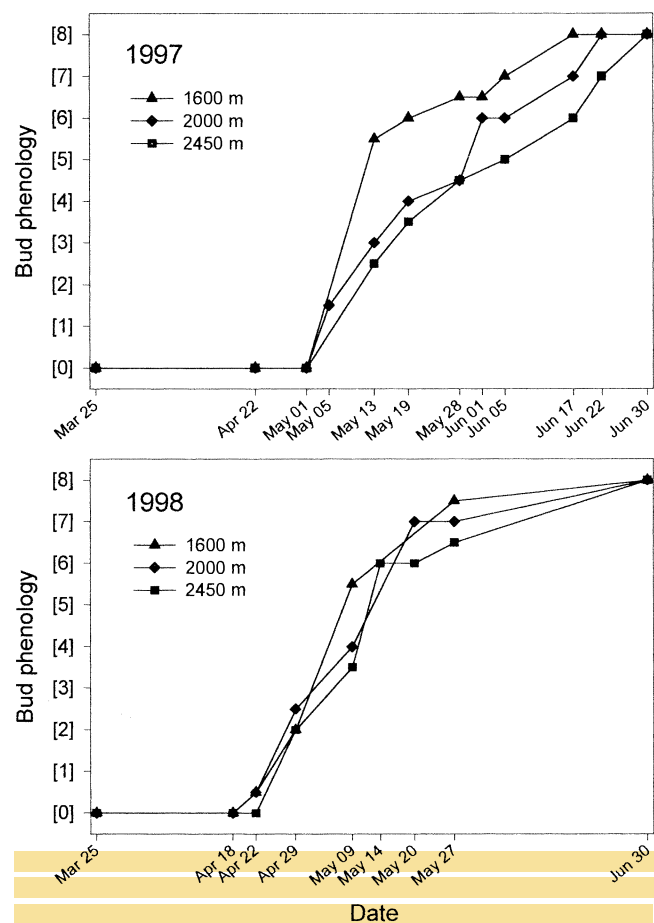

FIGURE 4. The course of bud phenology of Betula ermanii at different altitudes on the south slope of Mt. Fuji in spring 1997 and 1998. Nine phenological stages of vegetative buds from [0] to [8] were differentiated (see text).
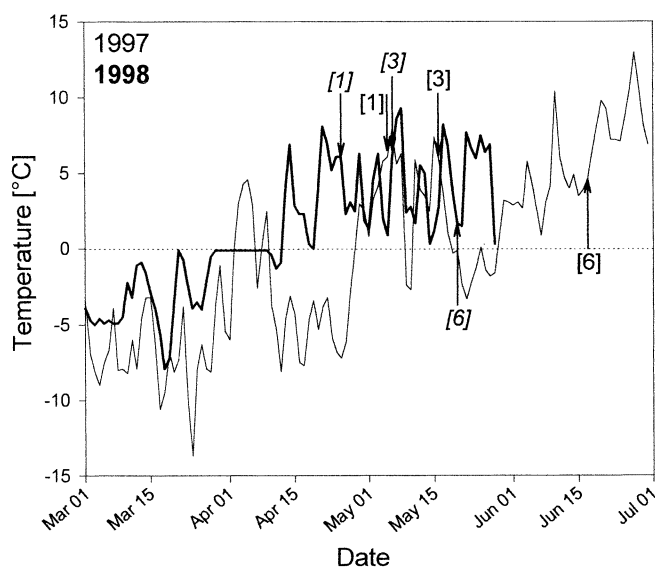
FIGURE 5. *Daily minima of air temperature at the treeline on the south slope of Mt. Fuji during spring 1997 and 1998 (bold line). The numbers given in brackets indicate different stages of bud phenology in both years. Italic numbers indicate phenological stages in 1998.*

record it is concluded that both the monthly mean and absolute minimum temperatures in 1997 were representative for the temperature condition at the treeline (Fig. 2C, Fig. 6) and thus spring was exceptionally warm in 1998.
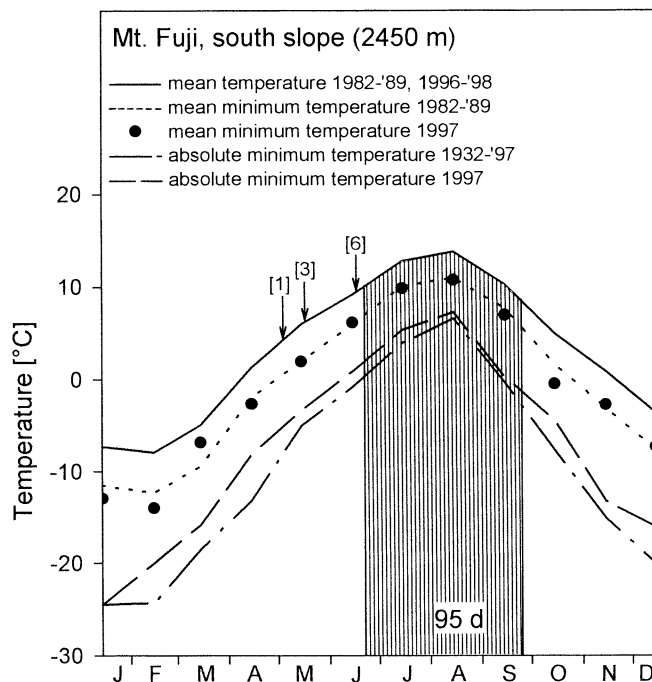

FIGURE 6. *Temperature regime at the treeline on the south slope of Mt. Fuji derived from data records between 1982 and 1989 (Masuzawa et al., 1989, 1990) and from 1996 to 1998 (own data). The absolute minimum temperature curve for the period from 1932 to 1997 was derived from altitude-corrected original records at the summit. The hatched area illustrates the length of the foliate period of B. ermanii at the treeline in 1997. The foliate period was defined as the number of days from the stage of advanced frondescence to advanced leaf yellowing. The numbers in brackets indicate stages of bud phenology in 1997.*
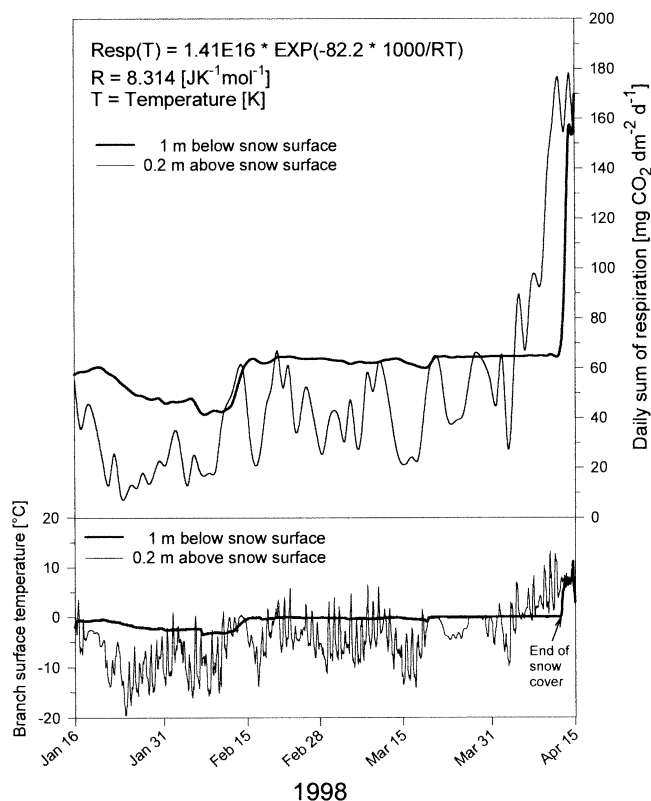

FIGURE 7. *Branch respiration (girth = 26 cm) of Betula ermanii above and below snow at the treeline on Mt. Fuji from mid-January to mid-April 1998. The daily sum of respiration was calculated as a function of temperature using the Arrhenius equation. Branch surface temperature was recorded in 30-min intervals.*

RESPIRATION OF BETULA ERMANII ABOVE AND BELOW SNOW

In winter, oxidative CO_2 release is primarily attributable to maintenance metabolism because metabolic activity for growth is negligible. Therefore, the Arrhenius equation given in Figure 7 quantitatively describes the rates of maintenance respiration (mg CO_2 dm^{-2} d^{-1}) below and above snow with respect to the different temperature regimes. Above snow the daily sum of CO_2 release from the branch surface varied considerably from 10 to 65 mg CO_2 dm^{-2} as a result of temperature fluctuations of more than 10°C d^{-1}, even during periods of permanent frost. About 1 m below the snow surface minimal branch surface temperature was −3.5°C while −9.7°C was recorded above snow. From mid-February until falling snow free in mid-April, the temperature remained nearly constant between 0 and −0.5°C. Thus, the daily sum of respiration also showed little variation around 65 mg CO_2 dm^{-2}.

From mid-January to mid-February, when branches above snow were exposed to severe frost down to −20°C, the calculated amount of total carbon loss below snow (384 mg C dm^{-2} of branch surface and 30 d) was twice as much as above. Considering the entire cold period until frost above snow had ceased on 4 April, this difference of carbon loss added up to 0.44 g C dm^{-2} of branch surface. Assuming a photosynthetic carbon gain of 4.3 to 8.6 mg C dm^{-2} of leaf area h^{-1} under saturating light conditions at the treeline (600 μmol quanta m^{-2} s^{-1}, own measurements), it takes about 7 to 15 d at ambient light conditions to compensate for the estimated enhanced carbon loss below snow.

Discussion

As shown here, carbon loss of branches or stems will increase under snow and this loss will affect the pool of stored carbohydrate reserves. Given that there is a 9 mo leafless period for *B. ermanii* at the treeline, the importance of pool size for nonstructural storage compounds in relation to metabolic consumption and its shift with tree age is brought into focus. How much do cold resistance and maintenance above and below snow contribute to the depletion of storage compounds? Under snow, carbohydrate metabolism of deciduous versus coniferous tree species has yet to be investigated in terms of pools and fluxes. Since photosynthetic active radiation (PAR) does not penetrate into snow deeper than about 30 cm (Körner, 1999) photosynthesis of green needles will stop if snow accumulates further. High and prolonged snow cover will thus increase the overall carbon loss of conifers because at temperatures around 0°C needles represent a substantial respiring plant compartment. A negative carbon balance during wintertime was found for *Pinus sylvestris, Picea excelsa,* and *Pinus cembra* (Tranquillini, 1964; Ungerson and Scherdin, 1965). Schulze et al. (1967) stated that the treeline of *Pinus aristata* in the White Mountains of California might be determined in part by negative carbon balances throughout three or four consecutive years. On the other hand, a conspicuous decline of the respiration rate in wintertime, as it was observed for *Pinus cembra* at the treeline, minimizes carbon loss to the maintenance rate (Wieser, 1997).

Several meters of snow produce considerable physical gradients such as increasing pressure or decreasing porosity which causes restriction of gaseous diffusion from the surface to the ground (Sakai and Larcher, 1987; Körner, 1999). Branches or stems packed in snow therefore experience extremely high variations of CO_2-concentrations of even more than 2000 ppm (Mariko et al., 1994), depending on the distance below the snow surface and above the ground level. Simultaneously, oxygen supply in compact snow at temperatures around the freezing point is likely to be insufficient (Sakai and Larcher, 1987). The effect of these gaseous gradients on respiration of needles and woody-tissues has yet to be clarified to provide a quantitative assessment of aboveground carbon loss under snow.

Shibata and Ando (1993) have shown that annual radial growth of *Betula ermanii* increased considerably from 2000 to 2500 m altitude while annual wood production was nearly unaffected. They related radial growth increment to bark photosynthesis which is more favoured in the open treeline ecotone than in the coniferous forests with low light intensity and cooler conditions beneath the canopy. During winter, the rate of CO_2 release from shoots and branches with intact chlorenchyma can be reduced by bark photosynthesis depending on ambient light and temperature conditions. Own measurements of gas exchange (infrared CO_2 analysis) of shoot internodes (d $\leq$ 5 mm) of potted *B. ermanii* saplings revealed that even at 0°C bark photosynthesis counterbalanced respiratory CO_2 release (0.04 μmol CO_2 m^{-2} s^{-1}) at a photosynthetic photon flux density of 850 μmol m^{-2} s^{-1}. However, a net uptake of CO_2 was not observed. Similar results were obtained from other deciduous tree species, e.g., *Larix decidua, Populus tremula, Fraxinus americana* (Keller, 1973), or *P. tremuloides* (Foote and Schaedle, 1976) during the winter months. Under snow however, photosynthetic CO_2 refixation soon becomes ineffective due to insufficient light intensities.

Though bark photosynthesis supports the annual carbon gain of a tree this is above all a function of the length of the growing season. In 1997, the foliate period was restricted to 95

d (22 June to 25 September), but in 1998 it started 3 wk earlier. This time shift was obviously related to the above-average warm period from mid-April 1998 onward, when daily minima did not drop below 0°C (Fig. 5). The lack of a frost period appears to be the reason for the early beginning of the growing season. Hence, the course of daily minimum temperature in early spring is obviously a major determinant for the beginning and thus the length of the growing season. Studies of budburst in *B. pubescens* and *B. pendula* prove that warm periods in early spring considerably reduce the thermal time requirement (accumulated day degrees >0°C) for budburst and thus advance budburst (Heide, 1993). Regarding *B. pendula,* the timing of budburst can be most accurately described by a model that takes into account both the length of the photoperiod, indicated by calendar date as operational variable and the temperature after the calendar date that has been iteratively fixed to 21 March (Häkkinen et al., 1998). Supposed that the start of bud ontogenesis of *B. ermanii* was around the vernal equinox, the sum of daily minima of air temperature above 0°C until phenology stage [3] was nearly the same in both years (1997: 92.5°C, 1998: 92°C). However, the thermal time requirement until early frondescence (phenology stage [6]) was higher in 1997 (176.2°C) than in 1998 (152.1°C) which reflects the pronounced delay of emerging leaves due to frost during an advanced stage of bud phenology.

Betula ermanii ceases shoot growth by late July (Koike, 1995) and requires about 75 d to complete shoot development (Koike, 1990), which was about three quarters of the length of the growing season in 1997. Thus, it becomes evident that the species will approach its upper distribution limit where the need for a minimal season length interferes with the occurrence of spring frost damage in young shoots, burst buds and emerging leaves. With a lapse rate of minimum temperature of 1.05°C 100 m^{-1} in May, calculated from the temperature records, frost down to -7°C is likely to occur at 2800 m altitude until late in this month. As shown here, such frost events can cause considerable damage to emerging leaves and will also be harmful to young shoots. Koike (1995) also found that leaves of *B. ermanii* were injured by exposure to -3°C for 2 h. Though birch is able to permanently produce new leaves, a retarding effect of late spring frost on the coming growth period of several weeks is inevitable. It is therefore concluded that the minimum temperature regime during the early stage of the growth period is one of the primary climatic variables that affects the upper distribution of deciduous treeline-forming tree species.

In Japan, Kira (1948, 1949) related forest zones with temperature by introducing a Warmth Index which is calculated as $WI = \Sigma(t - 5)$ where t is the monthly mean temperature above 5°C. In those regions where snow has little impact on tree growth it is postulated that the boundary between subalpine coniferous forests and the alpine zone will form at altitudes with a warmth index of 15 month-degrees, assuming an adiabatic lapse rate of 0.55 K 100 m^{-1} (Kira, 1949; Ohsawa, 1990). Taking the warmth index of 15 on the species level (Kira, 1949) this boundary is represented by *B. ermanii, Larix leptolepis, Abies sachalinensis, Picea jezoensis, P. jezoensis* var. *hondoensis* Rehd., *A. mariesii,* and *A. veitchii.* Using the temperature records on the south slope of Mt. Fuji, we calculated an average warmth index of 16.8 month-degrees for 2800 m altitude over the past 25 yr, which indicates sufficient summer warmth for growth of these species. Though *A. mariesii* and *A. veitchii* are wide-spread in the subalpine belt of Mt. Fuji, their absence in the treeline ecotone points to other limiting factors for survival than warmth, e.g., snow break or ice blast in winter. Windblown scoria causes considerable abrasion of needles which can be observed on the

windward semicircles of branches of *L. leptolepis*. From late October to early December 1997, we measured a considerable increase in transport rates of windblown scoria from 3.5 to 31.5 g m^{-2} d^{-1} at 50 cm above the ground from 2450 to 2700 m altitude, respectively. For that purpose dust-traps equipped with a vane were used that could change with the wind.

Alternatively, the proposal that in temperate climates tree-lines occur at altitudes where 10°C is the minimum mean temperature of the warmest month (Brockmann-Jerosch, 1919; Daubenmire, 1954; Grace, 1989) is highly coincident with Kira's postulation. We calculated a mean temperature of 10.4°C in July for the same altitude and period mentioned above. In the sub-arctic region of northern Sweden, the upper limit of the birch forest at about 680 m altitude coincides with a mean air temperature of the warmest month of 10.5°C (Körner, 1998). In a survey of forest limits in humid East and South Asia, Ohsawa (1990) demonstrated that the correlation between altitudes corresponding to both temperature indices of forest limits was extremly high ($r = 0.95$, $n = 226$, calculated as linear regression line). This can be explained by the fact that both indices reflect minimum heat requirements during the growing season which affects species-specific growth, reproduction and completion of the annual life cycle (Tranquillini, 1979; Tuhkanen, 1980; Körner, 1998). It is therefore concluded that two periods of minimum temperature are of significance for the upper distribution limits of deciduous broad-leaved tree species in temperate climates (1) periods of subzero temperature which determine the occurrence of spring frost damage and affect the beginning of the growing season and (2) cool periods during the growing season which affect development and ripening of overwintering plant compartments. Regarding *B. ermanii*, both limits coincide at about 2800 m altitude on the Pacific Ocean side of central Honshu. The formation of forest limits by coincidence of minimum temperature requirements during summer and winter has also been described for the northern limit of the tropical evergreen broad-leaved forests in Japan (Ohsawa, 1991). Since most of the expansion growth of trees in temperate and boreal climate regions takes place in the early growing season, the temperature regime during this period appears to have a greater effect than means exceeding 10°C. Malyshev (1993) concludes that temperatures exceeding 0 or 5°C are more influential for the arctic forest boundary in Eastern Europe and Siberia than temperatures above 10°C. Moreover, the duration of the growing season probably has a greater effect than the sum of the temperatures during the growing season. The significance of either minimum temperature regime on tree survival in high-mountain environments can only be evaluated by coupling long-term measurements of bioclimate with investigations that aim to detect periods and mechanisms of thermal sensitivity of plant compartments during the annual life cycle of juvenile and mature tree individuals.

Acknowledgments

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