

WATER RELATIONS OF *PINUS PUMILA* IN THE SNOW MELTING SEASON AT THE ALPINE REGION OF MT. TATEYAMA

Emiko MARUTA¹, Takashi NAKANO², Atsushi ISHIDA³,
Hajime IIDA⁴ and Takehiro MASUZAWA⁵

¹Faculty of Science, Toho University, 2-1, Miyama 2-chome, Funabashi 274

²Faculty of Science, Tokyo Metropolitan University, 1-1, Minami-Ohsawa, Hachioji-shi, Tokyo 192-03

³Forestry and Forest Products Research Institute, Tsukuba Norin Danchi, P.O. Box 16, Tsukuba 305

⁴Yoshida Scientific Museum, 574-1, Yoshida, Kurobe 938

⁵Faculty of Science, Shizuoka University, 836, Ohya, Shizuoka 422

Abstract: During the snow melting season of 1994, some exposed needles of *Pinus pumila* turned yellow in the alpine zone (2450 m) on Mt. Tateyama. However, relative water content (RWC) of the needles was far over the lethal RWC. Temperatures of soil and stems below snowpack remained near 0°C during midday on 7 May, whereas those of needles and shoots over snowpack increased to 15°C under high solar radiation. This result shows that transpired water from needles may be sufficiently replenished with water stored in sapwood of stems in the spring. It is concluded that desiccation is an unlikely cause of needle die-back. The most likely alternative explanation appears to be freezing damage, because freezing tolerance of most plants rapidly decreases in spring when minimum air temperature is often below zero in night at high altitude.

1. Introduction

Pinus pumila, a creeping evergreen conifer, is a dominant species in the alpine zone of Central Japan. The tree height is different corresponding to its micro-habitat. On a ridge where snow depth is less during winter, the tree height is very low (50 cm >) and dead stems are conspicuous. Sometimes, ridges are free of *P. pumila*. There are also no or few *P. pumila* in snow-bed sites where snow melting is retarded. *P. pumila* appears to grow best in a habitat with favorable snow depth during winter.

Timberline conifers sometimes suffer from winter desiccation due to an unfavorable water balance (TRANQUILLINI, 1979; HADLEY and SMITH, 1983, 1986). At such a site, soil and stem water freeze, thus becoming unavailable to trees in winter. Cuticular water loss may exceed impeded absorption during the winter, possibly owing to inadequate cuticle development in a short and cool growing season (WARDLE, 1968; BAIG and TRANQUILLINI, 1976; TRANQUILLINI, 1979) and/or cuticle abrasion by wind-blown ice particles (HADLEY and SMITH, 1983, 1986).

The creeping form of *P. pumila*, growing above the timberline, may cause its shoots to avoid winter desiccation. However, needles in the surface layer emerging from snowpack often suffer from injury in the spring snow melting period. Some needles turn yellow all over the surface layer of the canopy. In particular, this yellowing is conspicuously observed at convex sites and west-facing slopes of ridges around Murodo

Daira on Mt. Tateyama.

The hypotheses for the cause of spring die back are as follows: (1) Roots and stems may be frozen or near 0°C during the snow-melting season. On the other hand, leaf temperature and transpiration rate of needles may increase during bright, sunny days. Water movement through stems may be too small to replenish this water loss. Such water unbalance may cause desiccation and subsequent injury; (2) Freezing resistance of conifers rapidly decreases in spring (SAKAI, 1982). When the tissues are no longer winter-hardy, low temperatures may be the main cause responsible. The purposes of this study are to measure water relations of *P. pumila* in the spring snow-melting season, to evaluate hypothesis (1) as a possible cause of die back, and to relate spring water relations of *P. pumila* to its micro-habitats.

2. Study Site

Mt. Tateyama (137°37'N, 36°35'E), located at the north end of the Hida mountain range, is characterized by heavy snow and strong wind during winter, due to the northwest seasonal wind across the Japan Sea. Measurements from 1976 to 1989 at Murodo (2450 m a.s.l.) at the base of Mt. Tateyama show that the annual maximum snowpack depth varies from 4 to 9 m and snowpack depth varies greatly according to topography (HIGUCHI *et al.*, 1991).

The study was carried out at Murodo Daira which is a plateau at about 2500 m a.s.l. (Fig. 1) and bounded by peaks (*ca.* 3000 m a.s.l.) on the east side. Timberline is located at about 1500 m on the western slope. At Murodo Daira, *P. pumila* communities, deciduous broad-leaved shrubs (*Alnus maximowiczii* and *Betula ermanii*) and mesic herbaceous communities are distributed according to topography. Namely, *P. pumila*,

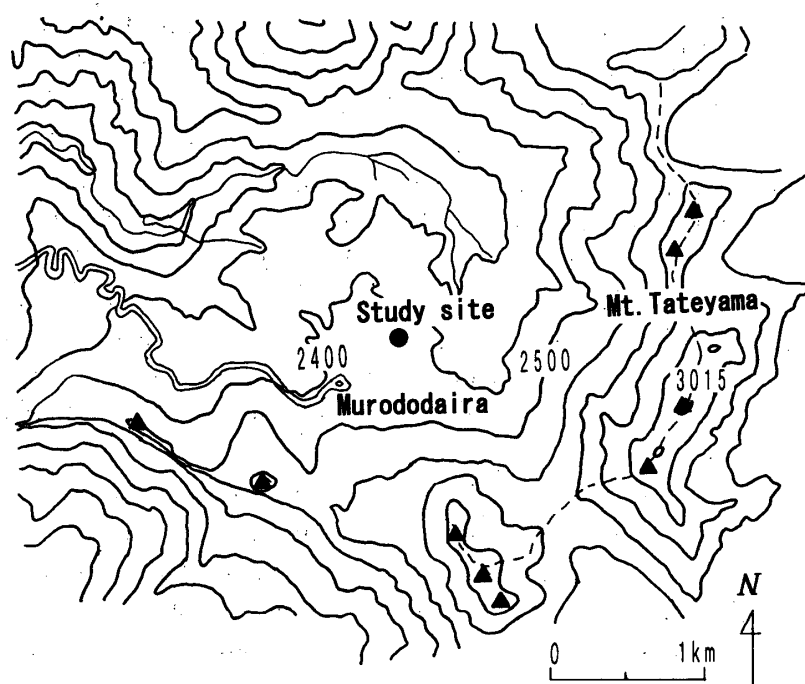


Fig. 1. Location of the study site.

deciduous broad-leaved shrubs and herbaceous communities occur usually on the upper part, the middle part and the bottom of a slope, respectively. The *P. pumila* community studied was located at a convex site (Fig. 1). The canopy height was 50 to 70 cm and the canopy diameter was about 10 m. *Gaultheria pyroloides*, a dwarf evergreen tree (15 cm high) occurred from the peripheral zone to the inside of the canopy, on the east side. During winter, the site would be exposed to strong wind and have less snowpack due to the convex topography. Westerly winds prevail throughout the year.

3. Methods

3.1. Microclimate

From November 1993 to July 1994, air and soil surface temperature within the canopy were measured with a platinum resistance thermometer probe (Pt 100 ohm, Model KDC-S3, Kona System Co. Ltd., Sapporo, Japan) and the data were stored in data-loggers (Kadec US, Kona System Co. Ltd., Sapporo, Japan).

In November 1993, copper-constantan thermocouples were prepared for measurements of stems, needles and soil temperatures in the next spring. Thermocouples (0.1 mm diameter) were inserted into the stems at heights of 9 cm and 20 cm. They were also inserted into the stems of 5 yr and 1 yr shoots at heights of 40 cm and 50 cm, respectively. These were also attached to the needle surfaces of the upper canopy. For measurements of soil temperatures under the canopy, at the peripheral part of the canopy and on bare ground, thermocouples (0.3 mm) were buried at depths of 1 cm, 10 cm and 30 cm. A quantum sensor (IKS-25, Koito-Kogyo Co. Ltd., Tokyo, Japan) was located over the canopy for measurement of the photosynthetically active photon flux density (PPFD).

On 7 and 8 May 1994, temperature measurements were made by recording every 5 min with a data-logger (Thermodac-E, Eto-Denki Co. Ltd. Tokyo, Japan). At this time, surface layers of *P. pumila* at the study site were already exposed, whereas snowpack depth was still over 3 m at snow-accumulated sites. Some parts of exposed needles were turned yellow.

3.2. Relative water content (RWC) and viability of needles

On 8 May 1994, 1 yr shoots (emerged in 1993) were collected for measurements of RWC and viability. At this time, snowpack depth was about 20 cm within the canopy and declined at the periphery. Eleven samples each were randomly collected from the upper (exposed needles) and lower (shaded needles) layers of the canopy above the snowpack, and below the snowpack. In all samples from the upper layer, some needles were turned yellow. Leaves of *G. pyroloides* in the peripheral zone were already exposed, whereas those within the canopy were still buried under snowpack. Eleven samples each of *G. pyroloides* were also collected from both parts.

Samples were immediately placed in plastic bags, sealed and stored at 5°C or below in a styrofoam container and transported to the laboratory. Relative water content (RWC), the percentage of the actual water content to that at complete saturation, is well indicative of water status of a leaf (LARCHER, 1980). Relative water content (RWC) of needles was measured in accordance with the well-established method for

conifer needles (HADLEY and SMITH, 1983). Namely, needles except yellow ones were separated from a shoot and fresh weight (FW) of needles was weighed as soon as possible. Then, needles were soaked for 4 days in distilled water at 20°C. After 4 days of soaking, the turgid needle weight (TW) was weighed. Dry weight (DW) was weighed after drying for 2 days at 80°C. Relative water content (RWC) of needles was determined by the following equation

$$\text{RWC (\%)} = \frac{\text{FW} - \text{DW}}{\text{TW} - \text{DW}} \times 100.$$

For samples from the upper layer of the *P. pumila* canopy, RWC of only green needles was measured. Needle viability was determined by calculating the percentage of needles remaining green.

4. Results

Air and soil temperatures within the canopy were near 0°C in November 1993 and decreased to -8°C in February 1994 (Fig. 2). They increased gradually from March. The upper needles may have been exposed above the snowpack by mid-April, because air temperature was above 0°C and its daily changes became greater in mid-April. On the

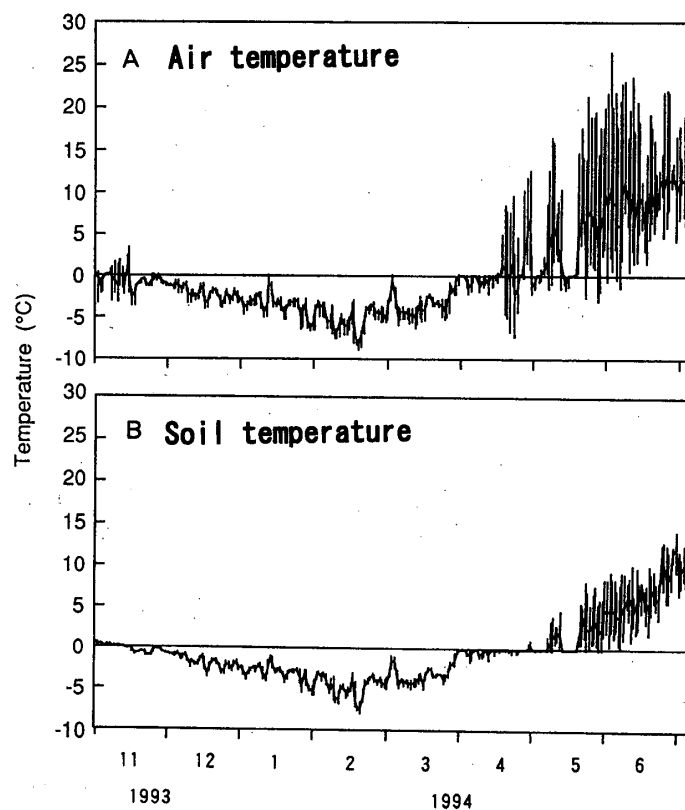


Fig. 2. Air and soil surface temperatures within the canopy of *Pinus pumila* in the winter of 1993–1994, at Murodo (2450 m a.s.l.) on Mt. Tateyama.

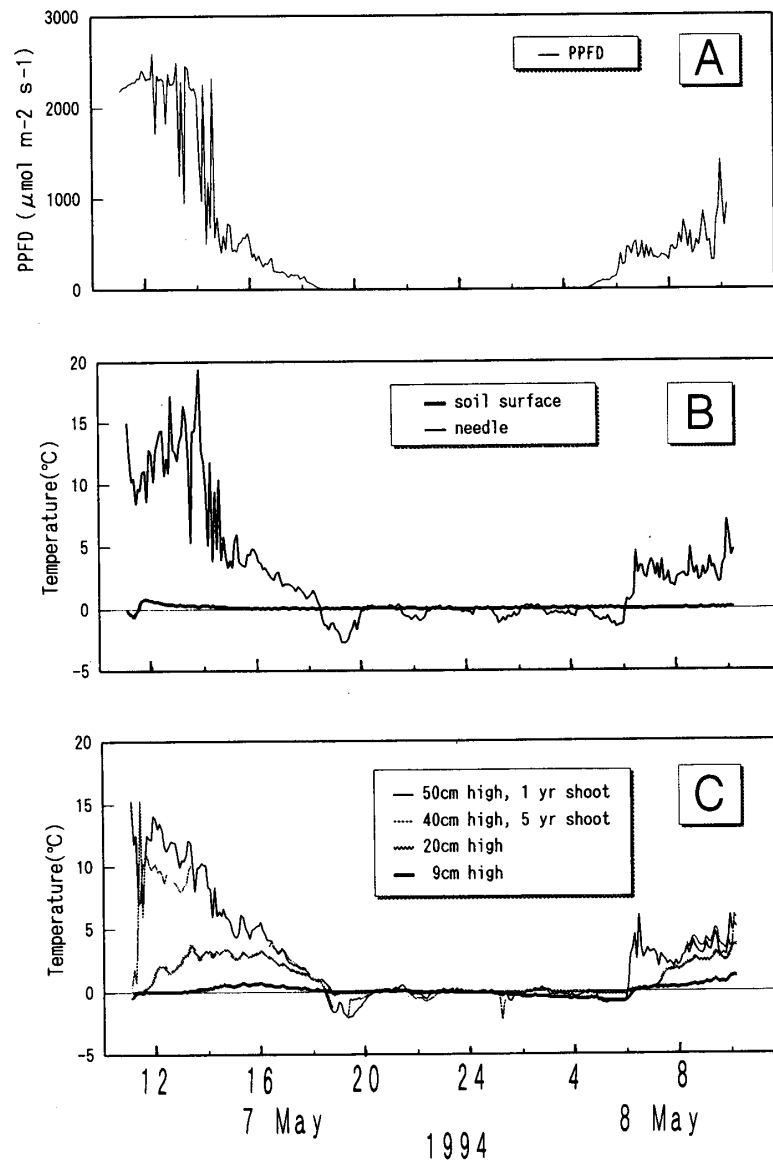


Fig. 3. Daily changes of (A) Photosynthetically active photon flux density (PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$), (B) soil surface and needle temperatures, (C) stem temperatures of *Pinus pumila* on 7 and 8 May 1994.

other hand, this situation for daily changes in soil temperature started in mid-May. At this time, snowpack appears to have melted completely. Thus, possible needle desiccation due to unfavorable water balance may occur in the period from mid-April to mid-May.

On 7 May 1994, it was clear all day and the maximum PPFD attained $2400 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3A). Stem (9 cm high) and soil temperatures under the snowpack remained near 0°C (Figs. 3C and 4). The temperature of the stem (20 cm high) just above the snow surface remained near 0°C in the morning and then increased to 3°C in the afternoon, indicating retarded heat conduction. Temperatures of needle and stems of 1 yr and 5 yr shoots increased to near 15°C in the daytime (Figs. 3B, 3C and 4). This temperature distribution of the canopy shows that water movement through the lower

Table 1. Relative water content (RWC: %) and viability (%) of needles sampled 1100 on 8 May 1994 at Murodo (2450 m); Values in parentheses are standard errors of means.

	RWC (%)	Viability (%)
<i>Pinus pumila</i>		
Exposed needles	85.5 (0.51)	86.3 (3.5)
Shaded needles	82.3 (0.73)	99.4 (0.47) ^a
Needles in snowpack	88.6 (0.59)	99.5 (0.45) ^a
<i>Gaultheria pyroloides</i>		
Exposed leaves	91.3 (0.42)	100.0 ^a
Needles in snowpack	93.4 (0.93)	100.0 ^a

^a Values in common superscripts are not statistically different ($P < 0.05$).

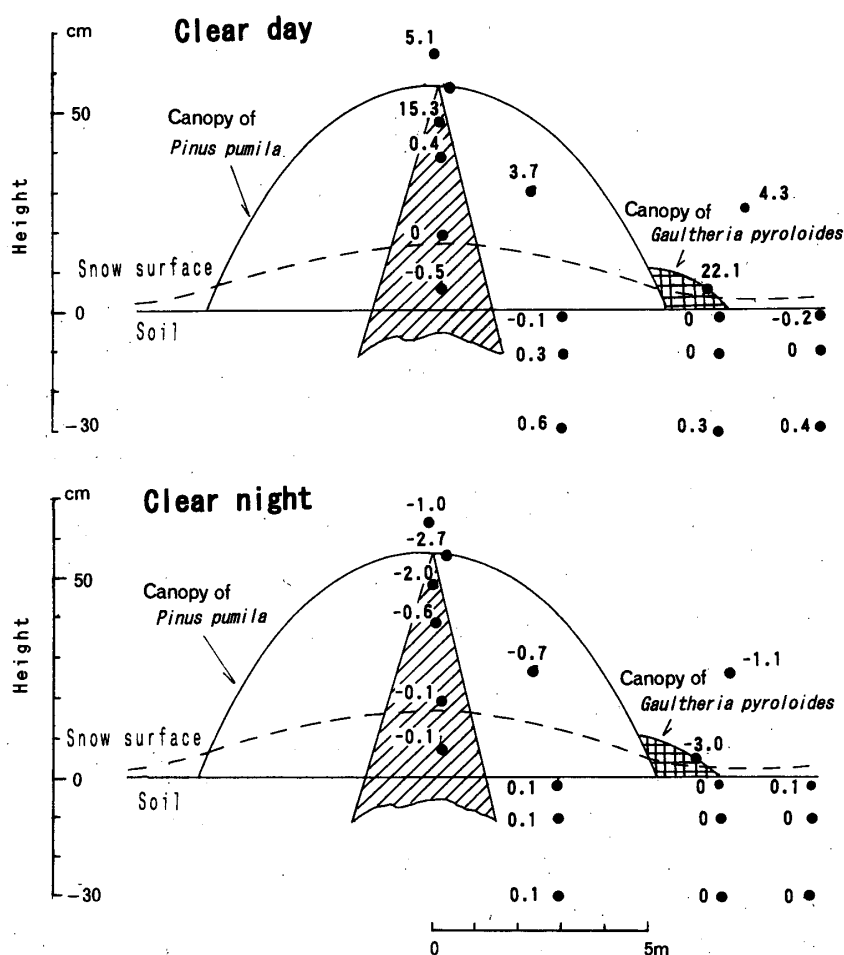


Fig. 4. Temperature distribution of a canopy of *Pinus pumila* on a clear day (1105, 7 May 1994) and at a clear night (1925, 7 May 1994); symbols of ● are points for temperature measurement; attached figures are temperatures (°C); shaded parts are stems; the size of stems is exaggerated compared to the actual ratio to the canopy size.

part of the stems is very small or zero. Thus, if needles transpire in the daytime during this season, water loss from needles should be replenished with water stored in stems of shoots younger than 5 yr old. The precise value of cumulative water loss on 7 May was

unknown. Instead, an intact shoot was enclosed with a polyethylene bag in the daytime on 7 May. The amount of collected water was 10 mg, indicating transpirational water loss.

Viability was 86% for the exposed needles, whereas the other samples were near 100% (Table 1). Relative water content (RWC) of exposed and shaded needles above the snowpack was significantly ($P < 0.05$) lower than those within the snowpack (Table 1). On 7 May, transpirational water loss from needles appears to have been near the maximum value in this season, because it was clear in the daytime. Therefore, RWC of needles collected on 8 May would be near the minimum value in this season, although part of needle water deficit would have been recovered during the night. At this time, stored water in sapwood may be much decreased compared to that in mid-April immediately after exposure of shoots.

Leaf temperature, RWC and viability of *Gaultheria pyrolloides* were higher than those of *P. pumila* (Fig. 4, Table 1).

At night, soil and stem temperatures remained near 0°C (Fig. 3B, C). Temperatures of needles and 1-yr, 5-yr shoots decreased to near -3°C from 1900 to 2000 (Figs. 3C and 4) and then they remained near 0°C. It was cloudy after 2000. If it remained clear throughout the night, temperatures of needles and shoots would have lowered at dawn.

On 8 May, it was cloudy. In the morning, PPFD was lower than 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3A). Temperatures of needles and shoots increased to only 3 to 5°C due to low PPFD (Fig. 3B, C).

5. Discussion

In the snow melting season at Mt. Tateyama, RWC and viability of exposed needles of *P. pumila* were lower than those inside the snowpack (Table 1). Relative water content (RWC) of 40 to 60% is known to be the lethal level of conifers such as genera *Abies*, *Picea*, *Pinus*, *Larix* overwintering at high altitudes (TRANQUILLINI, 1979; HADLEY and SMITH, 1983, 1986), although the lethal RWC has not yet been determined for *P. pumila*. Thus, RWC of 85.5% may be much higher than the lethal level. It is concluded that needle desiccation was not responsible for the injury. Although water movement to needles through lower parts of stems would be small or zero due to the near 0°C temperature in the daytime, stored water in younger shoots above the snowpack may be enough to replenish with the lost water and to support the high value of RWC of needles.

The possible period in which *P. pumila* at the study site suffers from unfavorable water balance may be at least from mid-April to mid-May (Fig. 2). The relation between the maximum snowpack depth and snow-melting speed would determine this possible stress period. The period may differ greatly according to topography. For example, needles of *P. pumila* may be exposed much earlier at convex sites and ridges. On the other hand, snowpack may be completely melted much later at snow-bed sites. Indeed, occurrence of *P. pumila* suffering from injury appears to be limited to habitats with the longer stress period. In such habitats, possibly, sapwood water in younger shoots may be depleted and needles may suffer from desiccation. Furthermore, at ridges, stems and shoots may be already exposed in the cold season and suffer from

freeze-thaw-induced embolism (SPERRY *et al.*, 1994) and water movement may be prevented. In such cases, needle desiccation may be the main cause of die-back.

Despite the higher leaf temperature of *G. pyroloides*, RWC and viability were higher than those of *P. pumila*. Leaves of *G. pyroloides* with dwarf cushion form would have been just exposed.

Possible cause of needle injury of *P. pumila* in this study may be freezing damage. On 7, 8 May, the daily change of needle temperature was from 15°C to -3°C. During the cold, clear night, the minimum temperature may be lower, indicating the possibility of freeze-induced damage. On the other hand, spring decrease in RWC to non-lethal level on a clear day may be adaptive to chilling temperature in the cold night, because it should cause increasing freezing resistance by lowering the osmotic potential of cells. Until further experiments for freezing resistance have been conducted, the cause must remain conjectural.

Acknowledgments

We are grateful to Prof. S. KAWANO (Kyoto University), Prof. Y. AGETA and Dr. T. OHHATA (Nagoya University), for their valuable advice; Mr. R. YOSHII (Tateyama Museum), Mr. M. YOKOZAWA and Mr. S. YONEMURA (Agricultural and Environmental Technology Institute) for their assistance during the field study. This work was supported by a Grant for Scientific Research (No. 05304053), Ministry of Education, Science and Culture, Japan. Field study was conducted by permission of Japan Environmental Agency and Tateyama District Forest Ranger Station.

References

- BAIG, M.N. and TRANQUILLINI, W. (1976): Studies on upper timberline: Morphological and anatomy of Norway spruce (*Picea abies*) and stone pine (*Pinus cembra*) needles from various habitat conditions. *Can. J. Bot.*, **54**, 1622-1632.
- HADLEY, J.L. and SMITH, W.K. (1983): Influence of wind exposure on needle desiccation and mortality for timberline conifers in Wyoming, U.S.A. *Arct. Alp. Res.*, **15**, 127-135.
- HADLEY, J.L. and SMITH, W.K. (1986): Wind effects on needles of timberline conifers: Seasonal influence on mortality. *Ecology*, **67**, 12-19.
- HIGUCHI, K., OHHATA, T. and IIDA, H. (1991): Distribution and variation of snowpack on Tateyama mountain range. Toyamaken Tateyama Hakubutsukan Itaku Kenkyu Hôkokusho (Report on Research sponsored by Tateyama Museum, Toyama Prefecture). 56 p. (in Japanese).
- LARCHER, W. (1980): *Physiological Plant Ecology*. Berlin, Springer, 303 p.
- SAKAI, A. (1982): Freezing resistance and adaptation to cold climate. Tokyo, Gakkai Shuppan Center, 469 p. (in Japanese).
- SPERRY, J.S., NICHOLS, K.L., SULLIVAN, J.E.M. and EASTLACK, S.E. (1994): Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. *Ecology*, **75**, 1736-1752.
- TRANQUILLINI, W. (1979): *Physiological ecology of the alpine timberline*. Berlin, Springer, 137 p.
- WARDLE, P.W. (1968): Engelmann spruce (*Picea engelmannii* ENGEL.) at its upper limits on the front range, Colorado. *Ecology*, **49**, 483-495.

(Received July 3, 1995; Revised manuscript accepted September 13, 1995)