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Freezing Tolerance of Evergreen and Deciduous Broad-Leaved Trees in Japan with Reference to Tree Regions¹

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Abstract Dormant one-year-old twigs collected from mature trees growing under different climates in mid-winter were artificially hardened to overcome the differences due to the site of collection and to increase cold hardiness maximally. Evergreen broad-leaved trees which extend to the warm Pacific sea coast in Japan from the tropics and subtropics in East Asia survived freezing only between -3 and -8°C . Warm-temperate evergreen broad-leaved trees which range from southern China to the northern Kanto District in Japan were hardy between -7 and -18°C . Most of the hardy deciduous trees which have northern limits of their natural ranges in northern Honshu and southern Hokkaido were hardy to -30°C and in these trees little or no difference was observed in hardiness among their cortex, buds and xylem. However, in most of the more widely distributed deciduous tree species, which extend to inland Hokkaido, Sakhalin, Northeastern provinces in China and Maritime provinces in USSR, the buds and cortex survived freezing even below -70°C , though the xylem sustained injury between -30 and -40°C .

In general, tree species from colder climates were found to be much hardier than those from mild climates in Japan. And the same trend was observed in the same species from different provenances. From these results, winter minimal temperatures appear to be the principal factor limiting the northern boundaries of the natural ranges of many trees species, especially less hardy evergreen broad-leaved trees.

Introduction

The Japanese archipelago lies approximately between 24° and 46°N latitude east of continental Asia. The islands of Japan have several markedly different climatic regions ranging from severe cold to subtropical. These range mainly from south to north along the islands. Monsoon climate is also characteristic in Japan and there is, in general, ample precipitation for the growth of plants. Thus, temperature is the dominant factor determining both the climatic and vegetational zones in Japan. Fig. 1 shows the

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3 major tree regions in Japan, which are designated as warm-temperate evergreen broad-leaved forest (G), cool-temperate broad-leaved deciduous forest (D), and sub-cold mixed deciduous and coniferous forest (M) (Fig. 1). The subtropical zone in Japan includes the long chains of small islands of Ryukyu islands. However, most of the natural vegetation has been lost.

Variations in temperature, moisture and soils are the principal determinants of where plants grow. The ability to survive sub-freezing temperatures, cold hardiness, is almost certainly an important factor in the distribution of many tree species (10, 17, 35).

Cold hardiness of Japanese Alpine plants (32) and conifers (30, 31), and trees in North America (35) and New Zealand (34) with reference to their regions of adaptation have been reported by the present author and his coauthors. However, only a limited amount of information is available on the cold hardiness of Japanese tree species.

This study has examined the relative mid-winter hardiness of broad-leaved trees from the major tree regions of Japan since 1968. The present study is an investigation of mechanisms of wintering and physiological adaptation of trees growing under sub-freezing temperatures.

Materials and Methods

Dormant one-year-old twigs of about 110 species were collected, mainly from mature trees, during the winters of 1968 to 1977. Many of the samples were personally collected by the author. Hardiness was evaluated at least 2 or 3 times in the same species in different years. Twigs were also sent by air to the Institute of Low Temperature Science, Sapporo, from Seoul and Vladivostock.

Five twig pieces, 10 cm long were cut from each twig sample and used in the hardiness evaluation. Since the freezing tolerance of winter twigs can change in response to previous environmental temperature (25), all twigs were subjected to an artificial hardening regime which consisted of holding samples at -3°C for 2 weeks, -5°C for 3 days to induce maximum hardiness and to overcome differences associated with sites of collection and handling procedures (22, 35). Less hardy evergreen twigs were hardened

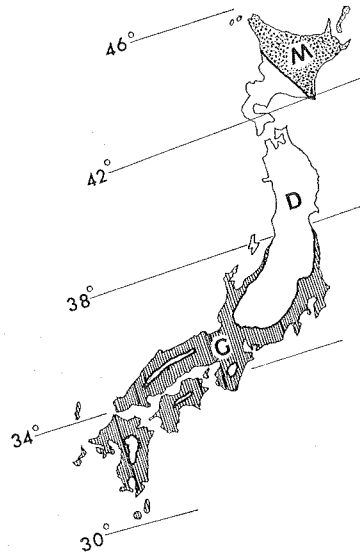


Fig. 1. Vegetation map of Japan.

G: Warm-temperate evergreen broad-leaved forest, D: Cool-temperate broad-leaved deciduous forest, M: Mixed deciduous and coniferous forest.

at temperatures between -1 and -3°C for 15 days at least. After hardening the twigs, enclosed in polyethylene bags, were frozen at -5°C in the cold room for 1 hr, and then cooled at 2.5°C increments for evergreen species or 5.0°C increments for hardy deciduous species at about 2 hr intervals to successively colder temperatures to -40°C . They were then further cooled to -70°C at 10° increments at 2 hr intervals. At selected test temperatures, twig samples were held for 4 hrs, removed and thawed in air at 0°C .

After thawing deciduous twigs were placed in water at room temperature, and evergreen twigs were placed in water in polyethylene bags in the green house for 2 or 3 weeks to evaluate viability. Browning was mainly used as the criterion for rating injury. The lowest survival temperatures at which no injury was sustained were expressed as freezing tolerance of leaves, vegetative and flower buds, and of cortex and xylem of twigs.

The occurrence of exotherms in excised twig pieces (2 cm long) was investigated by differential thermal analysis (DTA). A copper-constantan thermocouple was inserted in the pith of a twig piece. Another thermocouple, connected in series with the first, was inserted into another twig sample which had been previously dried in an oven. The twig piece with the inserted thermocouple was placed in an aluminum vessel (0.5 cm diameter, 5 cm long). DTA profiles were mainly obtained with a DTA apparatus of Shinkū Riko Co. which can be cooled at different cooling rates between 30 and -100°C . In another method the twig piece and bud with the inserted thermocouple were placed in a thermos flask, 7.3 cm diameter, 20 cm high, and the flask was directly transferred to the freezer held at about -42°C .

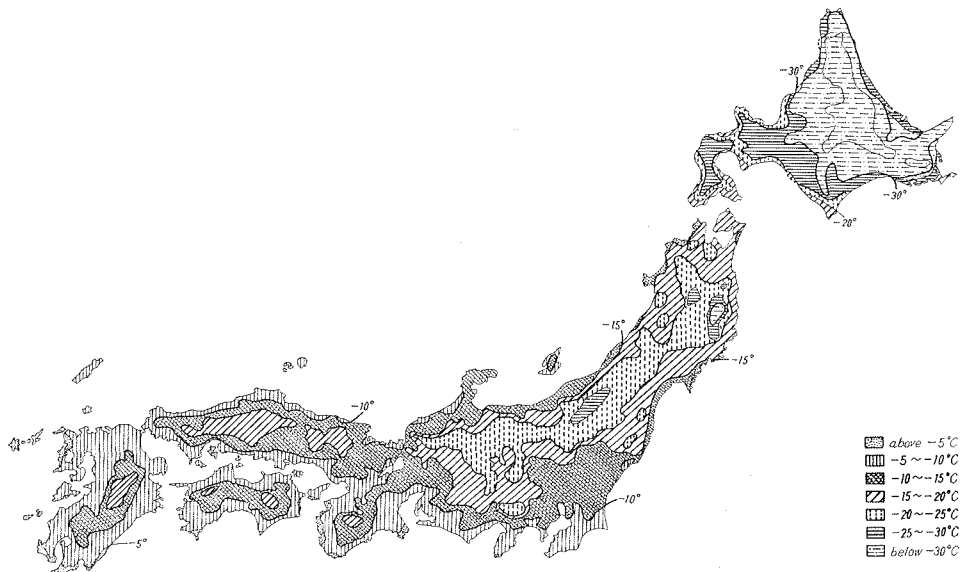


Fig. 2. Isotherms of extreme minimum temperatures in Japan. Based on records for 35 years at 1,555 meteorological stations¹.

The cooling rate was $0.3^{\circ}\text{C}/\text{min}$ between -20 and -30°C . The temperature of the bud or twig sample was determined by an additional thermocouple and recorded.

Isotherms of extreme minimum temperatures in Japan were presented in Fig. 2.

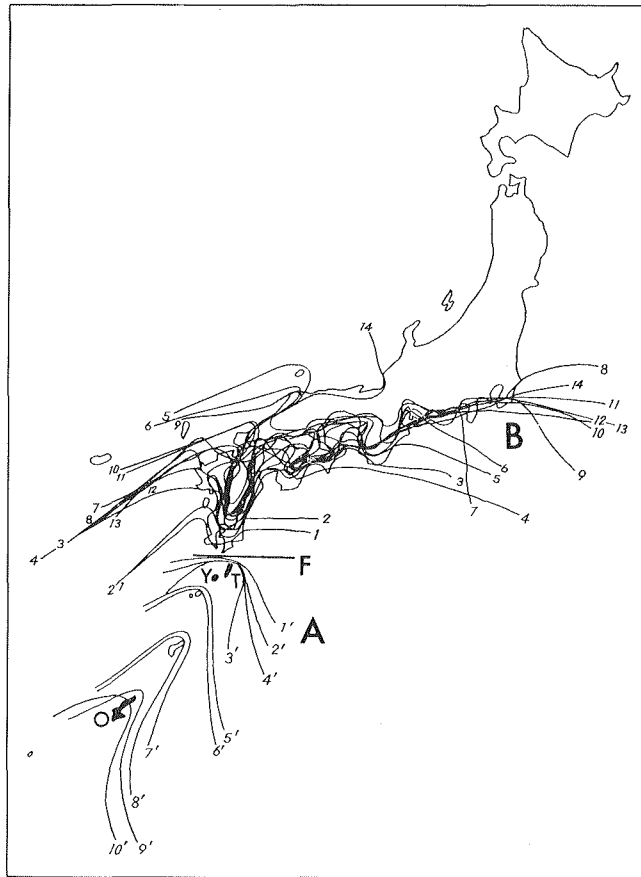


Fig. 3. Northern limits of natural ranges of evergreen broad-leaved trees extending from tropics and subtropics in East Asia to Ryukyu, Yaku and Tanega Islands (A) and further extend northeastward to the warm Pacific sea coast (B). F: Northern limit of frost free area in Japan. Y: Yaku Island, T: Tanega Island. Northern ranges are based on Hatsujima⁶, Horikawa^{7,8} and Kurata¹²⁻¹⁵.

A: 1', *Ficus microcarpa*, 2', *Hibiscus tiliaceus*, 3', *Kandella Candel*, 4', *Clerodendron inerme* var. *neriifolium*, 5', *Ficus virgata*, 6', *Pandanus tectorius* var. *liukiensis*, 7', *Bruguiera conjugata*, 8', *Excoecaria agallocha*, 9', *Melanolepis multiglandulosa*, 10', *Rhizophora stylosa*.

B: 1, *Schefflera octophylla*, 2, *Syzygium buxifolium*, 3, *Ficus superba* var. *japonica*, 4, *Turpinia ternata*, 5, *Litsea japonica*, 6, *Eurya emarginata*, 7, *Diospyros morrisiana*, 8, *Gordenia grandiflora*, 9, *Michelia compressa*, 10, *Prunus zippeliana*, 11, *Elaeocarpus sylvestris*, 12, *Helicia cochinchinensis*, 13, *Actinodaphne lancifolia*, 14, *Myrica rubra*.

Results

1. Freezing tolerance of tropical trees extending to Yaku and Tanega islands from tropical Asia

Some of the trees which range widely in the tropics of Asia extend to the Ryuku islands (6) and Yaku and Tanega islands (Fig. 3). Mangrove species cover muddy tidal marshes of lagoons and estuaries. Of the 6 species, *Kandella candel* is distributed as far north as Yaku and Tanega islands, the northern limit of the frost free area in Japan (Fig. 3). Leaves and twigs of mangrove species, *Kandella Candel*, *Burgulera conjugata*, *Rhizophora stylosa*, and *Thespesia populnea*, could not survive freezing at -3°C for 1 hr, except for the leaves of *Kandella Candel* which did not freeze at -3°C due to its high cell concentration. *Ficus microcarpa* and the other 6 tropical species were all killed by freezing at -3°C for 1 hr. Thus, these species, which range from tropical Asia to the Ryukyu islands and Yaku and Tanga islands, don't tolerate freezing and the northern limits of their natural ranges are limited to the frost free area.

Table 1. Freezing tolerance of evergreen broad-leaved trees extending to Yaku, Tanega and Ryuku Islands from tropics in East Asia

Species	Freezing tolerance		Locality of twig collection	Distribution
	Leaf	Twig		
<i>Kandella Candel</i>	X	X	Yaku, Okinawa Is.	Yaku, Tanega Is. —Tropics in S. East Asia
<i>Ficus microcarpa</i>	X	X	"	" — "
<i>Burgiera conjugata</i>	X	X	Okinawa Is.	Amami-Oshima Is. — "
<i>Rhizophora stylosa</i>	X	X	"	Okinawa Is. — "
<i>Hibiscus tiliaceus</i>	X	X	"	Yaku Tanega Is. — "
<i>Thespesia populnea</i>	X	X	"	Okinoerabu Is. — "
<i>Pandanus tectorius</i> var. <i>liukiuensis</i>	X	X	"	Tokara Is. — "
<i>Ficus virgata</i>	X	X	"	" — "
<i>Melanolepis multiglandulosa</i>	X	X	"	Okinawa Is. — "
<i>Diospyros ferra</i> var. <i>buxifolia</i>	X	X	"	" — "

X: Injured at -3°C . Leaves of *Kandella Candel* did not freeze at -3°C due to its high cell concentration, but sustained injury at -5°C .

2. Freezing tolerance of evergreen trees extending to warm sea coast areas in Japan from tropics and subtropics in East Asia

Ficus wightiana, *Scheffiera octophylla*, *Syzygium buxifolium*, etc., which are widely distributed in the tropics and subrtopics in East Asia,

extend to the southwestern warm sea coast areas of Kyushu, Shikoku and Honshu. These twigs were hardly to -3°C unlike *Ficus microcarpa* (Table 2). Evergreen tree species which range from Ryukyu, Taiwan and southern China to the warm Pacific sea coasts in Japan eastwards to Izu and Boso peninsulas (Fig. 3, B), survived freezing between -5 and -8°C (Table 2).

Table 2. Freezing tolerance of evergreen broad-leaved trees extending to warm Pacific sea coast areas from subtropics and tropics in East Asia

Species	Freezing tolerance ($^{\circ}\text{C}$)			Locality of twig collection	Distribution
	Leaf	Bud	Twig		
<i>Ficus superba</i> var. <i>japonica</i>	X	-3	-3	Yaku Is., Irozaki	S. west warm coast in Japan —tropics in S. East Asia
<i>Schefflera arboricola</i>	X	-3	-3	Yaku Is., Kagoshima	Far Southern Kyushu —S. E. Asia
<i>Syzygium buxifolium</i>	-3	-5	-5	Okinawa Is.	" — "
<i>Turpinia ternata</i>	-5	-5	-7	Kagoshima	Shikoku, Kyushu —Ryukyu Taiwan
<i>Actinodaphne lancifolia</i>	-7	-7	-7	"	S. west warm coast —Taiwan
<i>A. longifolia</i>	-10	-7	-7	Yaku Is. (200 m)	Warm sea coast —Ryukyu Taiwan
<i>Distylium racemosum</i>	-10	-10	-10	Irozaki	" — "
<i>Diospyros morrisiana</i>	-5	-5	-5	Kagoshima	" — Taiwan S. China
<i>Elaeocarpus sylvestris</i>	-7	-7	-7	Irozaki	" — "
<i>Glochidion hayatae</i>	—*	-7	-10	Yaku Is., Irozaki	Ryukyu—S. E. Aais
<i>Helicia cochinchinensis</i>	-8	-7	-7	Kumamoto	" — Taiwan S. China S. E. Asia
<i>Litsea japonica</i>	-10	-8	-8	Irozaki	" — Ryukyu
<i>Myrica rubra</i>	-10	-10	-8	"	" — Taiwan S. China S. E. Asia
<i>Prunus zippeliana</i>	-10	-10	-8	"	" — "

* Deciduous tree, X; Injured at -3°C .

3. Freezing tolerance of warm-temperate evergreen broad-leaved trees

The typical composition of forests of the warm-temperate zone is a mixed community of very many broad-leaved evergreen species, dominated by *Quercus*, *Castanopsis*, and *Machilus* in the upper canopy, and succeeded by a complex vertical profile containing several distinct tree layers.

Most of the genera and species in this forest zone are East Asiatic elements and indicate a very close relationship between the flora of Japan and that of the China-Himalayan region.

Freezing tolerance of warm-temperate evergreen trees is shown in Table 3. The northern limits of their natural ranges are summarized in Fig. 4. Most of the warm-temperate evergreen trees survived freezing between -10 and -15°C . Differences were associated with the altitudes and latitudes of their natural ranges. *Camellia japonica*, which extends as far north as

about 40°50'N, survived freezing between -18 and -20°C . A considerable variation in hardiness was observed in the *Camellia* from different provenances. It is very interesting that warm-temperate evergreen tree species native to Okinawa island were found to be hardy between -5 and -10°C in low altitudes (data not presented).

Less hardy deciduous trees which have nearly the same natural range as warm-temperate evergreen trees, survived freezing from -5 to -17°C (data not presented).

Table 3. Freezing tolerance of evergreen broad-leaved trees of the warm-temperate zone in Japan

Species	Freezing tolerance ($^{\circ}\text{C}$)				Locality of twig collection
	Leaf	Bud	Cortex	Xylem	
<i>Cinnamomum camphora</i>	-10	-8	-10	-12	Tokyo
<i>C. japonicum</i>	-10	-10	-10	-12	Kashima (Ibaragi)
<i>Neolitsea sericea</i>	-8~-10	-8	-10	-15~-17	Tokyo
<i>Machilus thunbergii</i>	-10	-8	-10	-12	"
"	-12	-10	-10	-12	Funakoshi (Iwate)
<i>Pasania edulis</i>	-10	-12	-15	-15~-17	Tokyo
<i>Castanopsis cuspidata</i> var. <i>sieboldii</i>	-13	-13	-13	-15	Mt. Tsukuba (580 m)
<i>Ligustrum japonicum</i>	-15	-15	-15	-17	Iwaki (Fukushima)
<i>Osmanthus ilicifolius</i>	-15	-17	-17	-20	Mt. Tsukuba (700 m)
<i>Ilex integra</i>	-15	-15	-15	-18	Tokyo
<i>Cleyera japonica</i>	-15	-15	-15	-15~-17	"
<i>Ternstroemia japonica</i>	-17	-17	-17	-20	Iwate
<i>Q. gilva</i>	-10	-10	-13	-13	Kyoto
<i>Q. salicina</i>	-15	-15	-15	-15	Mt. Tsukuba (680 m)
<i>Q. phillyraeoides</i>	-15	-15	-15	-20	Naka (Ibaragi)
"	-17	-17	-17	-20	Kuwanju (Korea)
<i>Q. myrsinaefolia</i>	-15	-15	-15	-15~-17	Mt. Tsukuba (550 m)
"	-18	-18	-18	-20	Kuwanju (Korea)
<i>Q. glauca</i>	-15	-15	-15	-18	Iwaki (Fukushima)
<i>Q. acuta</i>	-15	-17	-17	-20	Mt. Tsukuba (840 m)
<i>Q. sessilifolia</i>	-15	-15	-15	-18	Tokyo
<i>Eurya japonica</i>	-15	-15	-17	-17	Mt. Tsukuba (840 m)
<i>Illicium religiosum</i>	-20	-20	-18	-20	"
<i>Camellia japonica</i>	-18~-20	-18 (-17*)	-20	-20	Natsudomari Pen. (Aomori)
"	-18~-20	-18 (-17)*	-20	-20	Mt. Tsukuba (850 m)
"	-15	-15 (-15)*	-15	-20	Irozaki
"	-15	-15 (-15)*	-15	-20	Tokyo
<i>Daphniphyllum macropodum</i>	-20	-20	-20	—	Mt. Tsukuba (550 m)
<i>Pieris japonica</i>	-22	-22	-25	—	"

* Flower bud

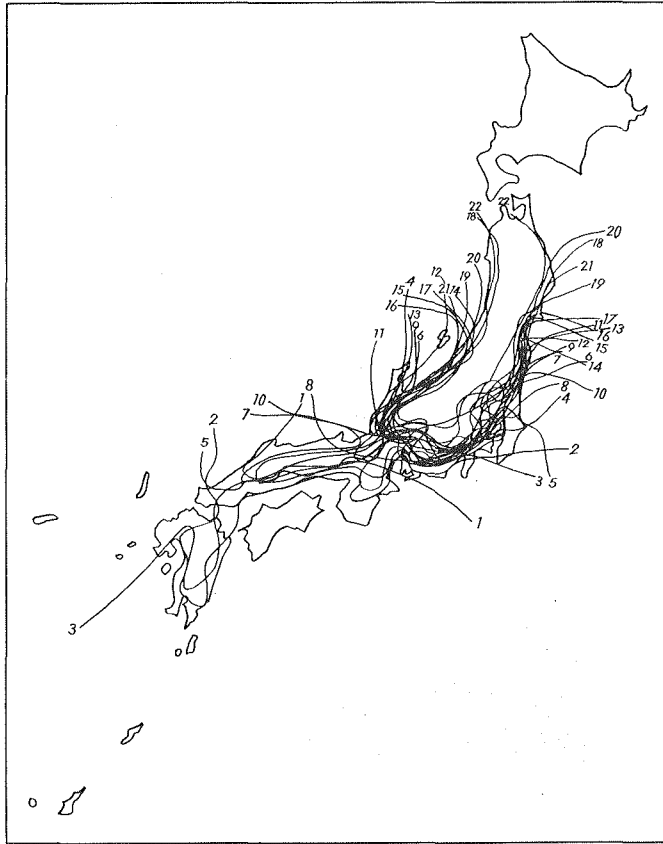


Fig. 4. Northern limits of natural ranges of warm-temperate evergreen trees.

1, *Machilus japonica*, 2, *Quercus phillyraeoides* 3, *Photinia glabra*, 4, *Cinnamomum japonicum*, 5, *Q. gilva*, 6, *Cleyera japonica*, 7, *Ternstroemia japonica*, 8, *Cinnamomum camphora*, 9, *Q. sessiliflora*, 10, *Q. glabra*, 11, *Daphniphyllum macropodum*, 12, *Castanopsis cuspidata* var. *sieboldii*, 13, *Ligustrum japonicum*, 14, *Q. salicina*, 15, *Neolitsea sericea*, 16, *Q. myrsinaefolia*, 17, *Q. acuta*, 18, *Machilus thunbergii*, 19, *Ilex integra*, 20, *Eurya japonica*, 21, *Illicium religiosum*, 22, *Camellia japonica*.

Northern limits of natural ranges are based on Horikawa^{7,8} and Kurata¹²⁻¹⁵.

4. Freezing tolerance of cool-temperate deciduous trees

The cool-temperate vegetation zone contains the primary part of Japanese flora, and is rich in distinct endemic genera and species. Cool-temperate deciduous trees are divided into two groups by the northern limits of their natural ranges.

Cool-temperate deciduous trees are much hardier than warm-temperate evergreen trees. Most of the hardy deciduous trees which have the northern limits of their natural ranges in northern Honshu and southern Hokkaido (Fig. 5) survived freezing to only about -30°C . Only a slight difference in

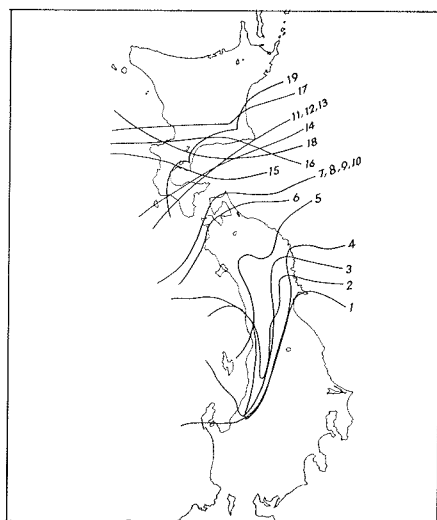


Fig. 5. Northern limits of natural ranges of cool-temperate deciduous trees which extend to northern Honshu and southern Hokkaido.

1, *Acer crataegifolium*, 2, *Celtis sinensis* var. *japonica*, 3, *Q. acutissima*, 4, *Acer carpiniifolium*, 5, *A. rufinerve*, 6, *Albizia julibrissin*, 7, *Stylax japonica*, 8, *Rhododendron japonicum*, 9, *Zelkova serrata*, 10, *Wisteria floribunda*, 11, *Clethra barbinervis*, 12, *Pterocarya rhoifolia*, 13, *Deutzia crenata*, 14, *Prunus grayana*, 15, *Fagus crenata*, 16, *Castanea crenata*, 17, *Q. serrata*, 18, *Aesculus turbinata*, 19, *Carpinus laxiflora*.

Northern limits of natural ranges are based on Horikawa^{7,8} and Kurata¹²⁻¹⁵.

the hardiness was observed among cortex, buds and xylem (Table 4). However, in most of the more widely distributed deciduous species which extend to inland Hokkaido, Sakhalin, Northeastern provinces in China and the Maritime provinces in USSR, the buds and cortex of the twigs survived freezing below -70°C , though the xylem sustained freezing injury below -40°C (Tables 5, 6). In some extremely hardy genera such as *Populus*, *Salix*, *Betula* and *Tilia*, the xylem also survived freezing to the temperature of liquid nitrogen.

In most of the tree species in both evergreen and deciduous trees, flower buds were much less hardy than vegetative buds (Table 7).

5. DTA profiles of evergreen and deciduous broad-leaved trees

Typical DTA profiles of winter twigs of warm-temperate evergreen trees are shown in Fig. 6. The temperature at the initiation of freezing of the winter twigs, which reflects the amount of super-cooling in the spontaneously nucleating samples, varied from -7 to -12°C . The first major exotherm (A) followed immediately after the initiation of freezing. The second low temperature exotherm (E) initiated between -18 and -20°C in *Camellia sasanqua* and *Quercus phyllyraeoides* (Fig. 6). In xylem sections from which living bark of twigs had been removed, the first exotherm (A)

Table 4. Freezing tolerance of hardy deciduous trees extending to northern Honshu and southern Hokkaido

Species	Freezing tolerance (°C)			Locality of collection
	Bud	Cortex	Xylem	
<i>Acer rufinerve</i>	-30	-40	-25	Morioka
<i>A. carpiniifolium</i>	-25	-50	-25	Miyoshi (Hiroshima)
<i>A. palmatum</i> var. <i>matsumurae</i>	-25	-40	-25	Morioka
"	-30 (F.B -25)	-30	-30	Mt. Yamizo (800 m)
<i>Aesculus turbinata</i>	-40	-50	-40	Yamabe (Hokkaido)
<i>Castanea crenata</i>	-30	-40	-30	Hakodate
<i>Celtis jessoensis</i>	-27	-30	-30	Sapporo
<i>C. sinensis</i> var. <i>japonica</i>	-20	-25	-25	Tokyo
<i>Clethra barbinervis</i>	-25	-25	-25	Mt. Yamizo (800 m)
<i>Carpinus tschonoskii</i>	-25	-25	-25	Daigo (Ibaragi)
<i>C. japonica</i>	-20	-25	-25	"
<i>C. laxiflora</i>	-25	-30	-25	"
"	-30	-30	-30	Miyoshi (Hiroshima)
<i>C. cordata</i>	-30	-30	-30	Daigo (Ibaragi)
"	-40	-30	-30	Yamabe (Hokkaido)
<i>Corylus heterophylla</i> var. <i>thunbergii</i>	-40	-40	-30	Morioka
<i>Fagus crenata</i>	-27	-27	-27	Mt. Tsukuba (750 m)
"	-27	-27	-30	Hakodate
<i>Lindera umbellata</i>	-20 (F.B -15)	-15	-15	"
<i>Pterocarya rhoifolia</i>	-70	-70	-70	Sapporo
<i>Quercus aliena</i>	-30 (F.B -25)	-30	-30	Miyoshi (Hiroshima)
<i>Q. acutissima</i>	-25 (-30)**	-30	-30	Morioka
<i>Q. serrata</i>	-25	-25	-25	Miyoshi (Hiroshima)
<i>Stewartia pseudocamellia</i>	-25	-25	-25	Sapporo
<i>Styrax japonica</i>	-30	-30	-30	Mt. Yamizo (800 m)
<i>Zelkova serrata</i>	-30	-30	-27	Hakodate
"	-30	-50	-30	Seoul

FB: Flower bud; ** Lateral buds.

Table 5. Freezing tolerance of very hardy deciduous trees of cool-temperate zone in Japan

Species	Freezing tolerance (°C)			Locality of twig collection	Northern limits of natural ranges
	Bud	Cortex	Xylem		
<i>Acer japonicum</i>	-30 (-70)*	-60	-30	Miyoshi (Hiroshima)	Hokkaido
<i>A. mono</i>	-35 (-60)*	-70*	-35	Yamabe (Hokkaido)	Maritime Province (M. P.), Sakhalin, N. E. China
<i>Alnus hirsuta</i>	-70	-70	-35	"	"
<i>A. maximowiczii</i>	-70	-70	-35	Sapporo	"
<i>Cercidiphyllum japonicum</i>	-70	-70	-40	Nakagawa (Hokkaido)	Hokkaido
<i>Cornus controversa</i>	-70	-70	-40	Yamabe	Sakhalin, M. P., N. E. China
<i>Corylus heterophylla</i>	-70 (♀ -70)	-70	-40	"	"
<i>C. sieboldiana</i> var. <i>mandshurica</i>	-70	-70	-40	"	"
<i>Fraxinus mandshurica</i> var. <i>japonica</i>	-50 (F.B -35)	-70	-40	"	"
<i>Juglans mandshurica</i> subsp. <i>sieboldiana</i>	-50 (-70)*	-50	-40	"	Sakhalin
<i>Kalopanax septemlobus</i>	-70*	-70*	-35	"	Sakhalin, M. P., N. E. China
<i>Magnolia obovata</i>	-50 (F.B -30)	-70	-30	Nakagawa	Hokkaido
<i>Phellodendron amurense</i> var. <i>sachalinense</i>	-70	-70	-35	Yamabe	Sakhalin
<i>Prunus padus</i>	-70 (F.B -40)	-70	-35	"	Sakhalin, M. P., N. E. China
<i>P. sargentii</i>	-30 (70-)* (F.B -35)	-70	-35	"	Sakhalin
<i>P. ssiiori</i>	-35 (-70)* (F.B -35)	-70	-35	"	"
<i>Quercus crispula</i>	-35 (-50)*	-70	-35	"	"
<i>Sorbus alnifolia</i>	-70	-70	-35	Nakagawa	Sakhalin, M. P., N. E. China
<i>S. commixta</i>	-70	-70	-35	"	Sakhalin
<i>Ulmus davidiana</i> var. <i>japonica</i>	-70 (F.B -25)	-70	-40	Sapporo	Sakhalin, M. P., N. E. China
<i>U. laciniata</i>	-70	-70	-35	Yamabe	"
<i>Betula ermani</i>	-70	-70	-70	Yamabe	"
<i>B. platyphylla</i> var. <i>japonica</i>	-70	-70	-70	"	"
<i>Maackia amurensis</i>	-50 (-70)*	-70	-70	"	"
<i>Populus maximowiczii</i>	-70	-70	-70	"	"
<i>P. sieboldii</i>	-70	-70	-70	"	Hokkaido
<i>Salix sachalinensis</i>	-70	-70	-70	Sapporo	Sakhalin
<i>Tilia japonica</i>	-70	-70	-70	Yamabe	Hokkaido
<i>T. maximowicziana</i>	-70	-70	-70	"	"

* Lateral bud, F. B: Flower bud.

Table 6. Freezing tolerance of very hardy deciduous trees of cool-temperate zone in Northeast Asia

Species	Freezing tolerance (°C)			Locality of twig collection	Distribution
	Bud	Cortex	Xylem		
<i>Acer barbinerve</i>	-60	-70	-35	Seoul	N. E. China, Ussuri, Maritime province (USSR), Korea
<i>A. mandshurica</i>	-30 (-50)*	-70	-40	"	"
<i>A. mono</i>	-30 (-50)*	-70	-30	Vladivostok	"
<i>A. tegmentosum</i>	-40 (-50)*	-70	-30	Seoul	"
<i>A. triflorum</i>	-30 (-50)*	-70	-40	"	N. E. China, Korea
<i>Alnus hirsuta</i>	-70	-70	-35	"	N. E. China, Ussuri, Maritime province, Korea
<i>Fraxinus mandshurica</i>	-40 (-70)*	-70	-45	Vladivostok	"
<i>Juglans mandshurica</i>	-70	-70	-40	"	"
<i>Maackia amurensis</i>	-70 (F.B -70)	-70	-60	Seoul	"
<i>Phellodendron amurense</i>	-70	-70	-40	Vladivostok	"
<i>Quercus mongolica</i>	-50 (-70)*	-70	-35	"	"
<i>Ulmus pumila</i>	-70	-70	-40	Seoul	"
<i>U. laciniata</i>	-70	-70	-40	Vladivostok	"
<i>Betula ermani</i>	-70	-70	-70	"	"
<i>B. davurica</i>	-70	-70	-70	"	"
<i>B. costata</i>	-70	-70	-70	Seoul	"
<i>B. platyphylla</i>	-70	-70	-70	"	"
<i>B. schmidtii</i>	-70	-70	-70	"	"
<i>Populus maximowiczii</i>	-70	-70	-70	"	"
<i>Tilia amurensis</i>	-70	-70	-70	"	"
<i>T. mandshurica</i>	-70	-70	-70	"	"

* Lateral buds, F.B: Flower bud.

Table 7. Freezing resistance of flower buds

Species	Freezing resistance (°C)				Locality of twig collection
	Vegetative bud	Flower bud	Cortex	Xylem	
<i>Aesculus turbinata</i>	-60	-25~-30	-60	-30	Sapporo
<i>Cornus kousa</i>	-30	-20	-30	-30	Tokyo
<i>Corylopsis spicata</i>	-20	-20	-30	-30	Sapporo
<i>Deutzia crenata</i>	-50	-25~-30	-40	-40	"
<i>Forsythia intermedia</i>	-40	-25	-50*	-30	"
<i>Hamamelis japonica</i>	-40	-30	-60*	-30	"
<i>Camellia sasanqua</i>	-15	-7	-15	-17	Tokyo
<i>C. reticulata</i>	-10	-5	-10	-15	"
<i>Prunus campanulata</i>	-15	-8	-20	-20	"
<i>P. padus</i>	-70*	-40	-70*	-40	Sapporo
<i>P. sargentii</i> var. <i>kurilensis</i>	-30 (-70)**	-25	-70*	-30	"

* Survived at the lowest test temperatures indicated.

** Lateral bud.

became much smaller than in the intact twigs, but the second exotherm (E) remained the same size (Fig. 6-2). These results suggest that the second broad exotherm (E) results from the freezing of the xylem and pith. It was also observed that the second exotherms occurred at nearly the same temperatures that resulted in the death of the xylem ray parenchyma cells. Thus, it may be considered that the xylem survives subfreezing by supercooling. Nearly the same DTA profiles were obtained in the twigs of many warm-temperate evergreen trees and some warm-temperate deciduous trees such as *Lagerstroemia indica* (Fig. 7-1), and *Albizia julibrissin*.

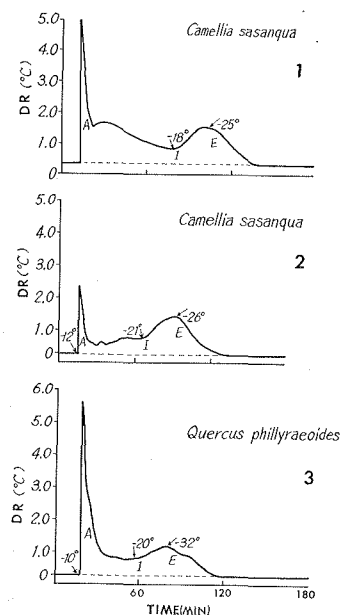
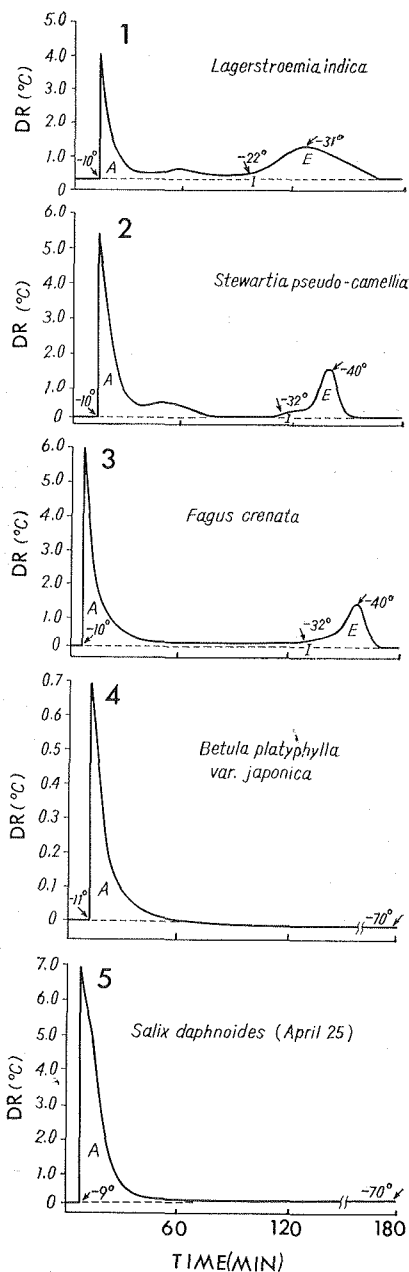


Fig. 6. DTA profiles of winter twig of warm-temperate evergreen trees.

DR: Differential response, A: The first exotherm resulting from freezing of the living bark, E: The second exotherm resulting from freezing of the xylem and pith. I: Initiation of the second exotherm. 2: DTA profile of xylem and pith of a twig stripped off the living bark.

Fig. 7. DTA profiles of twigs of deciduous trees

DR: Differential response, A: The first exotherm, E: Low temperature exotherm, 5: In the twig collected on April 25, any low temperature exotherm associated with xylem injury did not appear on the DTA profile.



In many cool-temperate deciduous trees, the second low temperature exotherm appeared in their twig xylem between -30 and -40°C . Typical DTA profiles of hardy deciduous twigs are shown in Fig. 7. At nearly the same temperature, xylem ray parenchyma cells sustained freezing injury. However, no low temperature exotherm was detected in very hardy deciduous trees such as *Populus*, *Salix*, *Betula* and *Tilia*, which were observed to survive freezing below -70°C . Willow twigs in mid autumn and early spring sustained freezing injury between -20 and -35°C . However, no low temperature exotherm was detected on the DTA profile. These facts suggest that in these very hardy twigs the xylem survived subfreezing by tolerating extracellular freezing, and that in these species, winter minimal temperatures do not appear to be the principal factor governing geographic distributions.

Discussion

In studying the hardiness of about 150 hardy angiosperms from all over the world, the author has observed xylem injury at temperatures between -30 and -40°C , although the vegetative bud and twig cortex are much hardier, resisting freezing even below -70°C (21). Thus, in these very hardy deciduous trees, xylem is the least hardy tissue of a twig.

Quamme et al (18) have found that exotherms near -40°C in mid-winter apple twigs caused injury to the xylem ray parenchyma cells and that the injury to the xylem invariably occurred only when twigs were cooled below the temperature of the low temperature exotherm. Using DTA, pulsed nuclear magnetic resonance spectroscopy and low temperature microscopy, George and Burke (4) clearly demonstrated that the low temperature exotherm in xylem of Shagbark hickory results from the freezing of cellular water in a manner predicted for supercooled dilute aqueous solutions, and that this supercooled water is extremely stable at -38°C and the freezing occurs intracellularly in the xylem ray parenchyma (4).

Low temperature exotherms observed in plant tissue always occurred at approximately -40°C or above (5, 18). Thus, there is a low temperature limit of this frost avoidance mechanism. This temperature corresponds to the homogeneous nucleation temperature of water.

In the willows native to the tropics and sub-tropics, *Salix tetrasperma* in southeast Asia, and *S. safsaf* throughout Africa (25), the cortex survived freezing between -20 and -70°C depending upon their native regions, and the xylem sustained injury between -15 and -35°C . No exotherm associated with xylem injury was, however, detected. The same result was obtained both in fall and spring in the less hardy twigs of very hardy *Salix sachalinensis*, native to cold climates in Japan. These results suggest that willow twigs all survive subfreezing by tolerating extracellular freezing. One question has not been answered, how can twig xylem of some genera tolerate freezing to very low temperatures? Low temperature exotherms may be

related in some way to phylogenetic features, probably to the wood morphology.

Recent evidence suggests that deep supercooling may indeed play a significant part in freezing resistance of some hardwood xylem (4, 11, 18), overwintering floral primordia (3, 28) in some genera of angiosperms, and winter primordial shoots of many genera of gymnosperms (27). However, in many woody plants, the most important living tissues and organs are cambium (9, 10, 24), phloem and vegetative buds. And these tissues and organs, of both evergreen and deciduous trees, principally survive subfreezing by tolerating extracellular freezing.

Cool-temperate hardwoods in Japan are classified into two groups, hardy and very hardy, based on the northern limits of their natural ranges. A great difference was not observed in the ability to avoid freezing of the hardwood xylem between these groups. However, a conspicuous difference was noted in the tolerance of freezing by cortical tissues and vegetative buds. The hardy deciduous trees which have northern limits of their natural ranges in southern Hokkaido and northern Honshu were marginally hardy to -30 and -40°C . However, most of the very hardy deciduous trees which extend to far northern areas tolerate freezing below -70°C and even the temperature of liquid nitrogen. These facts suggest that freezing tolerance of living bark and vegetative buds appears to be the principal factor for survival of cold climates by deciduous trees.

The freezing tolerance of evergreen broad-leaved trees is characterized by the susceptibility of vascular tissue in leaf petioles to injury. The vegetative buds, leaves, cambium and phloem are also less hardy, seldom surviving freezing to -20°C except for small shrubs and hardy *Rhododendron* species, though these xylem survive between -15 and -22°C by supercooling. The same trends have been observed in other warm-temperate evergreen broad-leaved trees native to Pacific and southeastern coast regions in the United States, Mediterranean coast, Himalayan mountains and southern China (unpublished).

The distribution of most trees is generally determined quite preponderantly by the temperature during the growing season, if precipitation is sufficient for the plant. However, the temperature requirements in the growing season and the ability to resist winter cold differs greatly among species. Thus, the principal factors governing climatic boundaries of plants are also different among plant species.

Iversen (10) concluded on the basis of his wide range experiments of wintering and the post-glacial history in northwestern Europe of *Hedera*, *Ilex* and *Viscum* that the eastern boundary of *Ilex* and tree-climbing *Hedera* which are marginally hardy to -20°C , are not determined principally by the length of the growing season and summer heat, unlike *Viscum*, but by the winter cold itself, presumably the minimum temperatures of the severe winters that occur at certain intervals. In evergreen broad-leaved trees in

Japan, cold hardiness appears to be a decisive factor setting the limits of their natural ranges.

These warm-temperate evergreen trees are susceptible to winter desiccation (23, 26) in frozen soil areas, though most of them are resistant to summer drought. Winter desiccation is an important limiting factor in frozen soil areas (23, 26). Sub-tropical willows growing in wind swept areas in Sapporo were alive in late December (Sakai 1970), but twigs above the snow level were killed by winter desiccation by late March because they remained frozen (below -3°C) 10 to 30 cm below the snow level during the winter, resulting in a blockage of water ascent. Little or no winter desiccation was, however, observed on willows native to southern or northern Japan grown at the same location (25). Most boreal conifers are also very resistant to severe winter desiccation (26). It is well known that there is a parallelism between winter desiccation and freezing tolerance in many hardy plants. A similar relation was observed among Japanese *cryptomeria* grown local areas, which differ in hardiness (2).

From an ecological point of view, the freezing resistance of regenerative organs such as flower buds and cones is highly important. Flower buds have generally far less resistance than vegetative buds (29, 33). Many trees could extend beyond the present northern limits of their natural ranges if sexual reproductions were possible. Unfortunately only limited information on the freezing resistance of flower buds is now available (29, 33).

Forty-two native evergreen woody species in New Zealand, where only a few deciduous trees are endemic, were selected to represent the range of temperature-related ecological gradients in New Zealand. Their hardiness was compared with that of trees native to Japan, which, though similar in size, topography and latitude to New Zealand, differs in lying close to a continental land mass. Most New Zealand evergreen broad-leaved tree species were observed to survive freezing temperatures of -5 to -12°C . The four hardiest conifers, which are sub-alpine, survived freezing only between -15 and -22°C , which is equivalent to the hardiness of warm-temperate evergreen trees in Japan (34). Nearly the same trend was observed in tree species native to Australia (unpublished). Also, a selection of evergreen and deciduous trees native to eastern Australia and south America cultivated in Christchurch, New Zealand, exhibited a range of freezing tolerance similar to that of New Zealand species (34). These results suggest that the mildness of South temperate winters is reflected in the comparatively low freezing tolerance in New Zealand and other Southern Hemisphere plant materials. Even in the Northern Hemisphere, most of the broad-leaved evergreen trees and less hardy deciduous trees are confined to the mild winter climates (34). On the other hand, very hardy deciduous broad-leaved trees and very hardy conifers cover widely the cool-temperate and sub-cold climatic zones (30, 31, 35).

There is a considerable interest in intraspecific differences in freezing

tolerance among ecotypes and climatic races of widely ranging species (16, 34, 35, 36, 37). Many studies on intraspecific difference in cold hardiness have reported that, almost without exception, tree species from colder provenances were hardier than warmer ones, and the frost injury by trees from southern or warmer sources was due to improper (late) onset of cold acclimation as well as to an insufficient inherent ability to harden. Intraspecific variations in hardiness generally appeared to be closely related to the winter minimum of their native habitats.

These results suggest that winter cold is certainly a prime factor in the natural selection pressures which have led to the evolution of frost hardy ecotypes and species. Although winter low temperature is only one of many environmental stresses and tolerance to midwinter minimum temperatures is only one of several types of winter hardiness, the close relationship between the two suggests that cold hardiness has played a significant role in plant distribution. Studies on freezing tolerance in midwinter should prove useful in plant introduction programs and should contribute to our understanding of plant adaptations to natural selection stresses.

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