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Freezing Resistance of Broad-Leaved Evergreen Trees in the Warm-Temperate Zone[1]

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Abstract Maximal resistance to winter freezing of broad-leaved evergreen trees of the northern and southern warm-temperate zones was assessed.

Most of the evergreen species of the northern warm-temperate zone survived freezing to between −10 and −15°C. *Camellia japonica, Euonymus japonicum, Daphniphyllum macropodum, Photinia serrulata* (Japan), *Ilex aquifolium* (Europe), *Ilex opaca* (United States) and *Magnolia grandiflora* were the hardiest, resisting freezing to between −18 and −20°C.

Of the South Temperate species, a New Zealand evergreen timberline species, *Nothofagus solandri* var. *cliffortioides* was marginally hardy to −15°C and *Eucalyptus pauciflora* which forms the alpine tree limit on the mainalnd of Australia, resisted freezing at −15°C in the leaves. The hardiness of hardy evergreen species was comparable to that of warm-temperate deciduous species, which was much lower than that of the deciduous boreal temperate species. It was also observed that the evergreen species were much less hardy than the deciduous species belonging to the same genera such as *Quercus, Magnolia, Nothofagus, Prunus, Acer,* etc. Very hardy evergreen tree species, which withstand freezing below −30°C seem not to have evolved in any family, except for some shrubs of the *Ericaceae.* Thus, it seems likely that winter cold appears to be the principal factor limiting the northern boundaries of the natural ranges of broad-leaved evergreen trees.

Introduction

Very hardy coniferous forests and temperate deciduous broad-leaved forests are characteristic of the generally continental, winter-cold climates of North America (2, 5, 21) and Eurasia (3, 6, 9, 18). From an extensive study of freezing resistance of woody plants in different climates in the world, it appears that low winter temperatures rank high among the natural selection pressures that have led to evolution of ecotypes and species adapted to cold regions, and have an important part in setting the northern boundaries of the ranges of many Northern and Southern Hemisphere trees (20, 21, 22, 24). Broad-leaved evergreen trees and shrubs with large, ellipitical or

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oval, usually shiny leaves are typical of regions with a favorable temperature all the year round. Broad-leaved evergreens occur mainly in three climatic zones (Fig. 1) : in coastal regions exposed to oceanic influence and islands of the temperate zone, in the Mediterranean climatic regions with a summer drought of 1–3 months, (e. g. on the Mediterranean coast, in California, Chile, South Africa and Western Australia), and at high altitudes in wet subtropical and tropical regions.

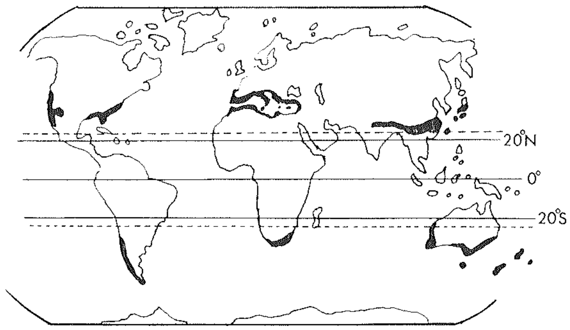

Fig. 1. Main regions of distribution of warm-temperate broad-leaved evergreen trees except for the subtropics and tropics

To understand the evolution of cold hardiness of woody plants, the relative mid-winter hardiness of broad-leaved evergreen trees from different areas both in the North and South Hemispheres was assessed.

Materials and Methods

One-year-old twig matierials were collected in mid winter in several different years, mostly from natural habitats in Japan, Korea, New Zealand, Australia and the United States. Planted materials were collected in mid-winter in Italy, New Zealand, Australia and Japan. Twigs were also taken in mid-winter from one to two-year-old seedlings of *Eucalyptus pauciflora* grown at Sapporo from seeds collected near the alpine tree limit in the Snowy Mountains of Australia. Samples collected in various countries were sent by air to Sapporo. Upon receipt, samples consisting of five uniform pieces of twigs were prepared from the material and enclosed in polyethylene bags. The freezing resistance of winter twigs can change in response to previous environmental temperature (13, 15). Thus, to overcome the possibility that the freezing resistance of the twigs could reflect recent variations in environmental temperature, including those encountered during transport, all twigs were subjected to an artificial hardening regime of 0°C for 5 days, followed by −1°C to −3°C for 14 days, and −5°C for 3 days (15, 20, 21). After hardening, most of the samples were cooled at 2 or 3°C increments at 4 hr intervals to successively colder temperatures from −5°C down to −25°C, and then at 5°C or 10°C increments at 4 hr intervals to $-50°C$ or $-70°C$, respectively. After standing at selected test temperatures for 4 hr, they were removed from the freezer and thawed in air near 0°C.

To evaluate damage, thawed evergreen twigs were placed with their bases in water in polyethylene bags at room temperature for 20 days. Thereafter, freezing injury was evaluated visually using browning as the criterion. This method allowed freezing resistance of vegetative buds, leaves and tissues of the twigs to be expressed as the lowest temperature at which little or no injury was sustained.

Results

1. *Freezing resistance of broad-leaved evergreen species growing in Mediterranean climatic regions*

Evergreen species such as *Olea europea*, *Laurus nobilis*, *Quercus suber*, and *Nerium oleander* all grow along the Mediterranean coast of Europe. The leaves of evergreen species tested mostly survived freezing to only -10 to $-13°C$ except for *Ilex aquifolium* and *Hedera helix* which occur more widely in Western Europe (3, 12) (Table 1). In the species of *Ilex* and *Quercus* tested, the leaves were much less hardy than were their twig tissues. Evergreen cherry, *Prunus laurocerasus*, growing in Yugoslavia, Bulgaria and Turkey was hardy to $-12°C$ in the leaves.

Some deciduous species belonging to the same genera as the Mediterranean evergreen species and growing in South-East Europe were much

Table 1. Freezing resistance of broad-leaved evergreen trees growing in the Mediterranean region

Species	Family	Freezing resistance (°C)				Site of collection
		Leaf	Bud	Cortex	Xylem	
Olea europaea	Oleaceae	−10	−10	−10	−15	Milano
Laurus nobilis	Lauraceae	−10	−10	−10	−10	Napoli
〃	〃	−10	−10	−10	−10	Tokyo
Quercus suber	Fagaceae	−13	−18	−20	−20	Milano
Q. ilex	〃	−13	−18	−18	−18	〃
Ilex aquifolium	Aquifoliaceae	−18	−18	−20	−23	Tokyo
Hedera helix	Araliaceae					〃
Prunus laurocerasus	Rosaceae	−12	−12[a]	−12[a]	−20	Kyoto
Quercus pubescens (D)[b]	Fagaceae	—	−25	−40	−25	Milano
Q. robur (D)[c]	〃	—	−50	−70	−35	Stockholm
Fraxinus orientalis (D)[b]	Oleaceae	—	−30	−50	−25	Poland
F. excelsior (D)[c]	〃	—	−50	−70	−30	Stockholm

D: Deciduous; a: Uninjured at $-12°C$; b: Range at South-East Europe; c: Range to northern Europe hardier than the evergreen species. However, their hardiness was much lower than the boreal deciduous species which occur widely in Northern Europe (Table 1).

Evergreen hardwood species within the *Myricaceae, Lauraceae, Fagaceae* etc. grow along the West Coast of the United States where a Mediterranean climate prevails. The leaves of evergreen species tested mostly survived freezing to only −10 to −13°C except for *Myrica californica* and *Arctostaphylos pungens* (Table 2). In general, the leaf and bud are less hardy than the twig tissues. *Arctostaphylos pungens*, which has hard and thick leaves characteristic of arid areas, survived freezing to −15°C. Deciduous *Quercus* species from the West Coast showed nearly the same order of hardiness as that of evergreen species (Table 2).

Table 2. Freezing resistance of broad-leaved evergreen trees native to the West Coast of the North America

Species	Family	Freezing resistance (°C)				Site of collection	Distribution
		Leaf	Bud	Cortex	Xylem		
Myrica californica	Myricaceae	−15	−15	−15	−15	Corvallis	Washington-California
Umbellularia californica	Lauraceae	−10	−10	−10	−10	"	Oregon-California
Quercus agrifolia	Fagaceae	−10	−10	−17	−17	Berkeley	California
Q. chrysolepis	"	−10	−10	−13	−13	"	Oregon-California
Q. wislizenii	"	−13	−15	−17	−17	"	California
Q. emoryi	"	−10	−10	−18	−18	Arizona (1600 m)	Arizona-Mexico
Q. hypoleucoides	"	−13	−13	−20	−20	" (2000 m)	"
Q. oblongifolia	"	−10	−10	−15	−15	" (1600 m)	"
Arctostaphylos pungens	Ericaceae	−15	−15	−15	−18	" (1500 m)	"
Q. douglasii (D)	Fagaceae	—	−13	−13	−13	Berkeley	California
Q. garryana (D)	"	—	−15	−18	−18	"	Washington-California
Q. kelloggii (D)	"	—	−13	−13	−13	"	Oregon-California
Platanus wrightii (D)	Platanaceae	—	−13	−13	−13	Arizona (720 m)	Arizona-Mexico

D: Deciduous

2. *Freezing resistance of broad-leaved evergreen species native to the Southeastern Atlantic Coast region in the United States*

Myrica, Quercus, Magnolia, Osmanthus, Prunus and *Acer* are genera containing typical broad-leaved evergreen species. The leaves of evergreen species tested were marginally hardy to −10°C except for *Ilex opaca* and *Magnolia grandifolia* (Table 3). *Ilex opaca* occurs from central Florida to

Table 3. Freezing resistance of broad-leaved evergreen trees from the Southeastern Atlantic Coast in the United States

Species	Family	Freezing resistance (°C)				Site of collection
		Leaf	Bud	Cortex	Xylem	
Gordonia orlando	Theaceae	−10	−15	−15	−15	Orland (Florida)
Myrica cerifera	Myricaceae	−10	−10	−10	−18	〃
Magnolia grandiflora	Magnoliaceae	−15	−20	−18	−18	Greensville (Mississippii)
〃	〃	−20	−20	−20	−20	Tokyo
Ilex opaca	Aquifoliaceae	−20	−20	−20	−18	〃
〃	〃	−20	−20	−20	−20	Missouri
Quercus virginiana	Fagaceae	− 8	−10	−10	−10	Orland
Q. myrtifolia	〃	−10	−13	−15[a]	−15[a]	〃
Prunus caroliniana	Rosaceae	− 5	−15	−15	−15	〃
Acer floridanum	Acevaceae	− 8	−10	−13	−15	〃
Kalmia latifolia	Ericaceae	−30[a]	−30[a]	−30[a]	−30[a]	Tokyo
Rhododendron maximum	〃	−50	−60	−70	−30	Sapporo
R. catawbiense	〃	−50	−60	−70	−30	〃
Stewartia ovata (D)	Theaceae	—	−25	−25	−30	Sapporo
Q. nigra (D)	Fagaceae	—	−15	−15	−15	Orland
Q. chapmanii (D)	〃	—	−15	−20	−20	〃
Q. laurifolia (SE)	〃	—	−15	−15	−18	〃

D: Deciduous; SE: Semievergreen; a: Uninjured at the lowest temperature indicated

as far north as Massachusetts and southwestward to southeastern Missouri (5). *Magnolia grandifolia* is planted as far north as New Jersey on the Atlantic Coast. The leaves of evergreen species of *Acer* and *Prunus* were marginally hardy to −8°C. Deciduous species of Quercus growing along the Southeast Coast showed nearly the same degree of hardiness as evergreen species. *Stewartia pseudo-camellia,* a deciduous species of *Theaceae,* was much hardier than the evergreen *Camellia* and *Cleyera* species (Table 3). *Rhododendron maximum* and *Kalmia latifolia* which are very commonly associated, were the hardiest of the broad-leaved evergreen species tested in North America (Table 3). They occur mostly in the Appalachians (up to about 2000 m) and adjacent territory from northern Georgia to Southern New York State (5, 11).

3. *Freezing resistance of evergreen species of the South temperate zone*

Evergreen broad-leaved forests prevail in the South temperate zone where climates are far more equable than is usual at similar latitudes in the Northern Hemisphere. And the nearly total absence of deciduous hardwoods is characterized by the South temperate zone (20).

Table 4. Freezing resistance of broad-leaved evergreen trees of the South temperate zone

Species	Family	Freezing resistance (°C) Leaf	Bud	Cortex	Xylem	Site of collection
Nothofagus fusca	Fagaceae	−8	−10	−10	−13	Christchurch
N. moorei	"	−8	−8	−8	−12	"
N. solandri var. *cliffortioides*	"	−13	−15	−15	−15	New Zealand (1370 m)
Eucalyptus cinerea	Myrtaceae	−8	−8 (F. B. −8)	−12	−12	Tokyo
E. coccifera	"	−13	−13	−13	−13	"
E. pauciflora	"	−15	−15	−18	−23	Australia (1760 m)
"	"	−16	−20	−20	−20	" (1900 m)
Melaleuca armillaris	"	−5	−5	—	−5	Canberra
Banksia marginata	Proteaceae	−10	−10	−10	−10	"
B. integrifolia	"	−8	−8	—	−10	"
Protea compacta	"	−8	−8	−8	−8	Shizuoka (Japan)
Nothofagus antarctica (D)	Fagaceae	—	−22	−22	−22	Chile (subalpine)
N. gunnii (D)	"	—	−17	−17	−17	Tasmania (subalpine, 1000 m)
Hoheria glabrata (D)	Malvaceae	—	−15	−17	−17	New Zealand (Arthur pass, 900 m)

D: Deciduous; F. B.: Flower bud

Maximal resistance to winter freezing of trees of the South temperate zone, especially subalpine trees of Australasia was assessed. A New Zealand evergreen timberline species, (20) *Nothofagus solandri* var. *cliffortioides* was marginally hardy to −15°C (Table 4). Of the *Eucalyptus* species, *E. pauciflora* which forms the alpine tree limit on the mainland of Australia was the hardiest, resisting freezing to −15°C in the leaves (22). Other high altitude angiosperm species tested mostly survived freezing to only −10 or −15°C. Most of the tree species which grow in low altitudes were marginally hardy to −10°C. Deciduous, subalpine *Nothofagus antarctica* of South America was the hardiest, resisting freezing to −22°C. The other deciduous aubalpine *Nothofagus gunii* in Tasmania and deciduous subalpine species *Hoheria glabrata* in New Zealand were both hardy only to −15 or −17°C.

4. *Freezing resistance of broad-leaved evergreen trees in East Asia*

The mesophytic broad-leaved evergreen forests extend from central Japan westwards to the south side of the Himalaya mountains in a large belt across southern China. The warm-temperate or partly subtropical zone between 1000 m and 3000 m altitude in the East Himalaya is dominated by warm-temperate evergreen broad-leaved forest with many epiphytes. *Quercus semecarpifolia*, was the hardiest of the Himalaya's evergreen broad-leaved trees tested, except for *Rhododendron* species, a finding in keeping with the fact that it is the only evergreen oak ascending to altitudes of 3000 m in both the Himalaya and Southwest China (23, 26). Freezing resistance of evergreen species native to the Himalaya and China tested was marginally hardy only to −15°C, except for *Photinia serrulata* and *Ilex chinensis* (Table 5).

Table 5. Freezing resistance of broad-leaved evergreen trees in Himalaya and China

Species	Family	Freezing resistance (°C)				Site of collection
		Leaf	Bud	Cortex	Xylem	
Castanopsis siderophyllum	Fagaceae	−10	−10	−10	−10	Kunmin[a] (China)
Quercus lanuginosa	〃	− 8	− 8	−10	−10	Nepal (2250 m)
Q. semecarpifolia	〃	−13	−15	−15	−15	Nepal (3000 m)
Machilus duthiei	Lauraceae	−13	−13	−13	−13	Nepal (2800 m)
M. yunnanensis	〃	−10	−10	−10	−10	Kunmin[a]
Neolitsea umbrosa	〃	−13	−13	−13	−13	Nepal (2700 m)
Ilex chinensis	Aquifoliaceae	−18	−18 (F. B. −15)	−20	−20	Tokyo
I. dipyrena	〃	−10	−13	−13	−13	Nepal (2600 m)
Photinia serrulata	Rosaceae	−18	−20	−20	−20	Tokyo
Camellia reticulata	Theaceae	−13	−13	−13	−15	Kunmin[a]
Osmanthus fragrans	Oleaceae	−13	−13	−13	−13	Tokyo

a : Planted trees in Institute of Botany, Kunmin ; F. B. : Flower bud

The dominant members of the warm-temperate forests in Japan are *Castanopsis cuspidata* var. *sieboldii* and *Machilus thunbergii*. In southern parts, *Cinnamomum camphora*, *Quercus gilva* and *Q. acuta* are often intermingled with them, while close to the northern boundaries, other evergreen oak species such as *Q. glauca*, *Q. salicina*, *Q. myrsinaefolia* and *Q. sessilifolia* are dominant. As chief lower evergreen trees or shrubs, *Camellia japonica*, *Aucuba japonica*, *Eurya japonica* and *Neolitsea sericea* are also frequent. Along the south coast in Korea, the same warm-temperate species as in Japan occur. Freezing resistance of warm-temperate evergreen species in Japan and Korea is summarized in Table 6.

Small trees such as *Euonymus japonica* and *Daphniphyllum macropodum* which extend north to southern Hokkaido were the hardiest evergreen warm-temperate trees in Japan, resisting freezing to −20 to −22°C (Table 6). *Camellia japonica* occurred right up to the northern growth limit of trees, which extends as far north as about 40°50′N along the sea coast, and was hardy to −18°C in the leaves. Some *Quercus* species and *Camellia japonica* occuring near the top of Mt. Tsukuba (876 m alt. 36°20′N), which is located near the growth limits of many evergreen species, also

Table 6. Freezing resistance of broad-leaved evergreen species of the warm-temperate zone in Japan and Korea

Species	Family	Freezing resistance (°C)				Site of collection
		Leaf	Bud	Cortex	Xylem	
Cinnamomum camphora	Lauraceae	−13	−13	−13	−13	Tokyo
Machilus thunbergii	〃	−10	−10	−10	−12	Iwate[a]
〃	〃	−13	−13	−15	−15	Henzan[a] (Korea)
Neolitsea sericea	〃	−10	−8	−10	−12	Tokyo
Ligustrum japonicum	Oleaceae	−17	−17	−17	−17	Fukushima[a]
Osmanthus ilicifolius	〃	−15	−17	−17	−20	Mt. Tsukuba (700 m)[a]
Ilex integra	Aquifoliaceae	−15	−15	−15	−15	Tokyo
Castanopsis cuspidata	Fagaceae	−15	−15	−15	−15	Mr. Tsukuba (580 m)[a]
var. *sieboldii*	〃	−15	−15	−15	−15	Yusu (Korea)
Pasania edulis	〃	−12	−12	−15	−17	Tokyo
Quercus glauca	〃	−15	−15	−15	−18	Iwaki[a]
Q. myrsinaefolia	〃	−18	−18	−18	−20	Kuwanju[a] (Korea)
Q. phillyraeoides	〃	−15	−15	−15	−20	Mito
〃	〃	−18	−18	−18	−20	Kuwanju (Korea)
Camellia japonica	Theaceae	−18	−18 (F. B. −15)	−20	−20	Aomori[a]
〃	〃	−18	−18 (F. B. −15)	−20	−20	Mt. Tsukuba (850 m)
Cleyera japonica	〃	−15	−15	−15	−15	Mito
Euonymus japonicus	Celastraciae	−22	−22	−25	−22	〃
Daphnyniphyllum macropodum	Euphorbiaceae	−20	−20	−20	−20	Mt. Tsukuba (550 m)
Rhododendron brachycarpum	Ericaceae	−70	−70	−70	−30	Sapporo[b]
R. metternichii hondoense	〃	−70	−70	−70	−30	Matsumoto (2000 m)[b]
Pieris japonica	〃	−23	−23	−23	−23	Mt. Tsukuba (800 m)
Fagus crenata (D)	Fagaceae	—	−27	−30	−27	Hiroshima (800 m)
Quercus acutissima (D)	〃	—	−30	−40	−25	〃 (800 m)
Q. variabilis (D)	〃	—	−20	−20	−20	Kyoto
〃	〃	—	−30	−30	−25	Peking
Stewartia Pseudo-camellia (D)	Theaceae	—	−25	−25	−25	Kyoto
Lindera obtsusiloba (D)	Lauraceae	—	−17	−20	−20	Hiroshima (800 m)

a: Northern growth limit; b: Subalpine zone in cool temperate region; D: Deciduous; F. B.: Flower bud showed the same degree of hardiness. However, most of the warm-temperate evergreen species were hardy to −10 or −15°C at most (Table 6). Deciduous species which belong to *Fagaceae* and *Theaceae* and which grow in warm- and cool-temperate zones were much hardier than these evergreen species.

Rhododendron brachycarpum which occurs in subalpine regions of Honshu and extends north to Hokkaido, was the hardiest among the broad-leaved evergreen species, except dwarf shrubs in Japan, resisting freezing to −70°C even in the leaves (Table 6).

Evergreen species belonging to the same genera as the temperate deciduous species occur along the warm Pacific sea coast and in the subtropical areas in Japan. Most of these evergreen trees were marginally hardy to −10°C in their leaves (Table 7).

Table 7. Freezing resistance of broad-leaved evergreen species extending to the warm seacoast from subtropics in Japan, which belong to the same genera as the temperate deciduous species

Species	Family	Freezing resistance (°C)				Site of collection
		Leaf	Bud	Cortex	Xylem	
Acer oblongum	Aceraceae	− 8	−10	−15	−15	Okinawa
Diospyros morrisiana	Ebenaceae	−10	−10	−10	−10	Ise
Fraxinus griffithii	Oleaceae	− 5	−10	−10	−10	Okinawa
Ligustrum liukiuense	〃	− 5	−15	−15[a]	−15[a]	〃
Mallotus philippensis	Euphorbiaceae	− 7	−10	−12	−10	〃
Prunus spinulosa	Rosaceae	− 7	− 7	− 7	− 7	〃
P. zippeliana	〃	−10	−10	− 8	−10	Irozaki
Rosa laevigata	〃	−10	−17	−15	−17	Kochi
Vaccinum wrightii	Ericaceae	−10	−10	−10	−10	Okinawa
Viburnum suspensium	Carpifoliaceae	− 7	− 7	−10	−10	〃

a : Uninjured

Finally, leaf hardiness distribution of the broad-leaved evergreen trees and shrubs used in the present study is summarized in Fig. 2.

Some of the trees which range widely in the tropics of South East Asia extend to the Rhukyu islands, northwards to Yaku and Tanega islands which are the northern limit of the frost free area in Japan (Fig. 3, F Line). Tropical evergreen trees such as four mangrove species, *Ficus microcarpa, Malanolepis multiglandulosa* and *Diospyros ferra* do not tolerate freezing even at −3°C, and the northern limits of their natural ranges are limited to frost free areas (17, 18). *Ficus wightiana, Scheffera arboricola* and *Syzygium buxifolium,* which are widely distributed in tropical and subtropical areas and extend to the warm sea coast in south-western Japan were hardy to −3°C (17, 18). Most of the evergreen tree species range

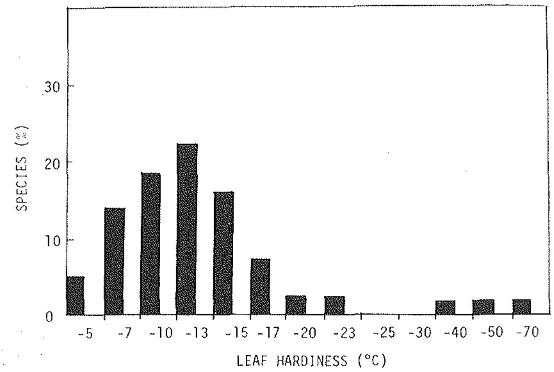

Fig. 2. Leaf hardiness distribution of the broad-leaved evergreen trees and shrubs. Species (%) of ordinate was expressed as percentage of the number of species with indicated hardiness to the total number of species evaluated hardiness in the present study.

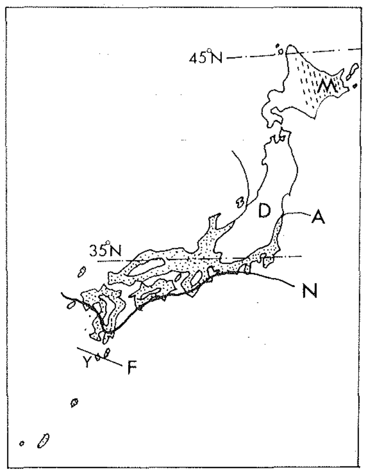

Fig. 3. Tree vegetation in Japanese archipelago. F: Northern limit of frost free region of Japan; N: Northern limit of natural ranges of broad-leaved evergreen trees extending from the tropics and subtropics in East Asia to Rhukyu, Yaku and Tanega islands, and further northeastward to the Pacific Sea Coast; A: Northern limit of natural ranges of most of the warm-temperate evergreen trees; Y: Yaku Island; T: Tanega Island; D: Cool-temperate deciduous forest; E: Warm-temperate broad-leaved evergreen forest; M: Mixed broad-leaved deciduous and coniferous forest

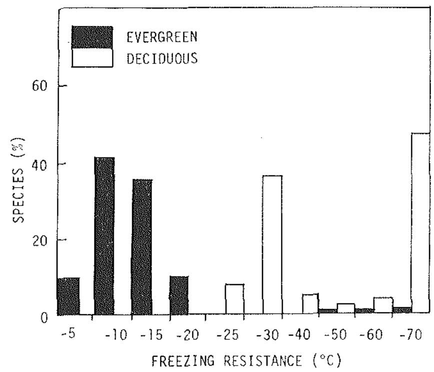

Fig. 4. Hardiness distributions of twig cortex of hardy broad-leaved evergreen and boreal temperate deciduous trees growing in Japan. Species (%) of ordinate was expressed as the percentage of the number of species with indicated freezing resistance to the total number of evergreen (43 species) or deciduous (43 species) species which were evaluated hardiness, respectively.

from Rhukyu, Taiwan and South or South-western China to the warm Pacific sea coast in Japan (Fig. 3, N Line), where the extreme minimum temperatures range between −5 and −7°C. These evergreen trees survived freezing to around −8°C (17, 18). Almost all of the warm-temperate evergreen trees ranging near the northern limit of their natural range (Fig. 3, A Line) were marginally hardy to −18 or −20°C at most. Their natural range coincides with the mean temperature of about 2°C in the coldest month, which is roughly comparable to about −15°C in the extreme temperature (17, 18). In preliminary experiments, we observed that the wintering acorns from some evergreen oaks were marginally hardy to between −10 and −13°C. In Japan, hardy temperate deciduous forests (Fig. 3) are distributed further northeast into Hokkaido or inland mountanous areas (6, 17, 18). Hardiness distributions of temperate deciduous and evergreen broad-leaved trees in Japan are shown in Fig. 4. From these results winter minimal temperatures appear to be the principal factor limiting the northern boundaries of the natural ranges of hardy broad-leaved evergreen trees in Japanese archipelago.

Discussion

In general, warm-temperate broad-leaved evergreen trees are characterized by slow growth and summer-drought resistance, unlike the rapid-growing and water-requiring deciduous broad-leaved trees. Evergreen Mediterranean elements compete with summergreen deciduous species whenever winter is mild enough to permit the existence of evergreens and where summer brings sufficient rain for the deciduous elements (10). If the summer is consistently dry, as it is in the Mediterranean climate and the other summer-arid areas in North America, the deciduous elements are gradually ousted by drought-resistant hard-leaved trees (10). Summer drought causes greather hardship to the deciduous soft-leaved woody plants. Also, hard-leaved evergreen trees are in position to make up for the lack of summer productivity in late autumn and spring, and even in winter at temperatures above 0°C, provided that their evergreen leaves are hardy enough to withstand sub-freezing temperatures. On the other hand, where the summer is consistently wet, the deciduous trees thrive in such luxuriance that they overgrow the evergreens, which even if well-provided with water grow slowly. The South temperate forests even in far southern latitudes are characterized by the nearly total absence of deciduous hardwoods. It seems likely that in the highly temperate climates characterized by very low seasonal ranges of temperature, high precipitation well distributed through the year and mild winter, deciduous tree species probably could not have competed as effectively with broad-leaved evergreens which could grow more continuously through the year (1).

In monsoon areas, in the North temperate zone, broad-leaved evergreen forests are exclusively confined to oceanic winter-mild areas as seen in Japan (6) and the United States (2, 5). With increasing latitude the broad-leaved evergreen species, except for dwarfs on forest floors, decrease considerably in number and in diversity as deciduous hardwoods increase to form the dominants of floras at mid or northern latitudes. Iversen (7) concluded that the eastern boundary of *Ilex* and *Hedera* which are marginally hardy to −20°C, is 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. These facts strongly suggest that winter cold temperatures are among the important factors setting the northern boundaries of the natural ranges of many evergreen hardwoods.

Warm-temperate evergreen trees are characterized by susceptibility to winter desiccation (4, 8, 9, 14, 16, 25) in soil frozen areas, though most of them are resistant to summer drought. It is known that the ability to absorb water by roots abruptly decreases at temperatures below 5°C in citrus plants (8) or 3°C in tea plants (4). Such plants are very susceptible to dehydration from winds and winter sunshine. On Mt. Tsukuba (876 m alt. 36°26′N) located in the range of warm-temperate forest zone in Japan, evergreen hardwoods occur on the south-facing slopes where the soil remains unforzen, while only deciduous hardwoods range on the north-facing slopes where the soil usually remains frozen for one month or more, and north-westerly winds sweep throughout winter. In the Himalayan mountains, an uppermost evergreen oak forest, *Quercus semecarpifolia* occurs only on the south-facing slopes at around 3000 m altitude where the soil remains unfrozen even in mid winter, while on the other hand, deciduous hardwoods occur on the north-facing slopes where the soils freeze in the same area (unpublished data).

These facts suggest that winter desiccation (25) seems to be an important factor governing the natural range of many broad-leaved evergreen trees.

Ericaceae seems to be the only family which has evolved very hardy evergreen shrubs, belonging to the genera of *Rhododendron* and *Kalmia* except dwarfs, resisting freezing below −40°C in the leaves which range to subalpine in Eurasia and North America (11). However, most of the rhododendrons are marginally hardy to −20°C or more even in rhododendrons near the timber lines in Himalayan mountains (23). Very hardy rhododendrons can resist winter drought by rolling down the leaves at subfreezing temperatures which is a particularly effective way of reducing the transpiring surface of wintering leaves.

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