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Cold Hardiness in the Genus Rhododendron

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Abstract. **Cold hardiness of 101 *Rhododendron* genotypes was assessed. In hardy rhododendrons, the difference in hardiness between floral primordia and other tissues or organs was greater than in the less hardy species. All rhododendrons tested were divided into 4 hardiness divisions: very hardy, semihardy, hardy, and tender. In all hardiness divisions, the vegetative buds, leaves, and stem cortex were hardiest, whereas the floral primorida were least hardy, with a lowest survival temperature (LST) of −35°C or higher. The majority of the very hardy division of rhododendrons, such as *R. brachycarpum* D., *R. catawbiense* Michx., and *R. maximum* L., belong to the ponticum series. In general, rhododendrons from cold regions were hardier than those from warm regions. The hardiness of the floral primordia of rhododendrons growing near the timberline (3900 m alt.) of East Himalaya and the high altitudes of the northwestern Yunnan area were similar (−20° to −23°). These were less hardy than those found in the subalpine forests of Japan and eastern North America, probably due to moderate temperature and high humidity during the winter in eastern Himalaya and northwestern Yunnan.**

The genus *Rhododendron* is comprised of about 850 species ranging in size from tiny, mat-like growths of several centimeters tall to trees up to about 15 m or more. The genus *Rhododendron* originated in a limited district of southwest China which covers northwestern Yunnan, southeastern Tibet, and western Szechwan (9, 22). About 320 species of rhododendron, including the most primitive species, grow here, suggesting that this area is the greatest natural center of the genus. Rhododendrons also inhabit a vast area of southeast Asia, stretching from northwestern Yunnan to Malaysia, Indonesia, and New Guinea. About 280 species of rhododendrons are native to Malaysia. Ninety percent of the world's rhododendrons are concentrated in Southwest China and Southeast Asia.

About 30 species of rhododendrons may have migrated westward to the Himalayas from the concentrated district of northern Yunnan, southeastern Tibet, and western Szechwan. Several species are found in Asia Minor and Europe. *Rhododendron lapponicum* (L.) Wahlenb., which has a tiny, mat-like habit grows in the circumpolar regions of Scandinavia and also occurs in Canada and the mountain ranges of the northeastern United States. Native rhododendrons are diminishing in eastern China. Their range extends northeastward into northeast China, Korea, and east Siberia. About 30 species inhabit the islands of Japan. Some dwarf rhododendrons are also found in Kamchatka, the Bering Strait area, and western Alaska. About 25 rhododendron species are native to North America. The mountain ranges of North Carolina in the eastern United States provide optimum growing conditions for rhododendrons, which grow with vigor and luxuriance not seen elsewhere in nature.

Little information is available on the winterhardiness of rhododendrons (14, 17, 18, 19, 21). The purpose of this study was to understand cold hardiness with respect to distribution of the genus *Rhododendron* by assessing the relative winterhardiness of 69 rhododendron species and 32 cultivars from around the world.

Materials and Methods

Dormant one-year-old twigs of 69 species and 32 cultivars were collected from mature rhododendron plantings in Sapporo (Sapporo Agriculture Center, nursery of the Institute of Low Temperature Science, Hokkaido Univ.) in midwinters of 1978–1983. In early February of 1984, about 20 species and cultivars were collected at Greer's Garden (Eugene, Ore.). Three Vireya species were sent to Sapporo from Greer's Garden in 1979. Ten species of Himalayan rhododendrons were collected in late January and mid-December of 1979 at Langtong valley (3300 m alt.) and at Shyangboche (39000 m alt.) near the forest limits, respectively. These twigs were shipped to Sapporo in a refrigerated container at 0°C. The senior author also collected some from near the timberline (3500 m alt.) at Mt. Wilhelm, Papua, New Guinea in late August of 1980. In some instances, more than one collection location of a species was tested. After collecting or receiving the samples, the samples were acclimated to their maximum level by the following procedure. Three to 5 uniform twig sections 5 to 10 cm long cut from each twig sample with flower buds were enclosed in sealed polyethylene bags. These small bags were placed in a large polyethylene bag with snow to prevent desiccation during hardening and freezing procedures. They were then subjected to an artificial hardening regime of −1° for 7 days, −3° for 14 days, −5° for 5 days, and −10° for 1 day.

After hardening, the temperature of the hardiest twigs were lowered at about 5°C increments daily to −20° and then at 2.5° increments at 4 hr intervals to successively colder temperatures. Less hardy materials were cooled at 2.5° increments at 2 or 4 hr intervals to −20°. After retaining at selected test temperatures for 16 hr or 2 hr for tender materials, frozen twigs were removed from the freezer and thawed in air at 0°. To evaluate damage, thawed evergreen twigs and leaves were placed in polyethylene bags saturated with water vapor, and the basal end of each deciduous twig was placed in water at room temperature for 20 days. Thereafter, samples were dissected, visual observations of tissue discoloration were made and freezing injury was evaluated using oxidative browning of injured tissues as the criterion. Observations were made on dormant vegetative buds and flower buds, leaves, cortex (including cambium), and xylem. Hardiness of these tissues and organs was expressed as the lowest survival temperature (LST). The LST was the lowest test temperature at which little or no injury was observed, except in the case of flower buds, where LST represented the minimum test temperature at which greater than 40% of the buds survived.

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Table 1. Freezing resistance of rhododendron species.

Hardiness divisions and species (series)	Lowest survival temperature (°C)					Collecting locality	Distribution
	Flower bud	Leaf	Vegetative bud	Cortex	Xylem		
Very hardy (−40°C)							
R. brachycarpum D. Don (Ponticum)	−30	−60	−60	−60	−35	Sapporo	C. & N. Japan (2500 m alt. 35°N)
RT. catawbiense Michx.(Ponticum)	−30	−60	−60	−60	−40	Sapporo	E. United States (1900 m. alt.)
R. dauricum L. (Dauricum)	−30	−50	−60	−60	−40	Sapporo	N.E. China, Hokkaido
R. mucronulatum Turcz. (Dauricum)	−30	---	−50	−50	−40	Sapporo	N.E. China, Japan
R. maximum L. Pursh. (Ponticum)	−27	−60	−60	−60	−35	Sapporo	N.E. United States
R. carolinianum Rehd. (Carolinianum)	−27	−40	−50	−50	−35	Sapporo	S.E. United States
R. carolinianum Rehd. 'Album'	−30	−35	−35[z]	−35[z]	−35	Eugene (Oregon)	
R. metternichii Sieb. et Zucc. (Ponticum)	−25	−50	−50	−50	−35	Sapporo	W. Japan
R. metternichii var. *hondoensis* Nakai (Ponticum)	−25	−50	−60	−60	−35	Matsumoto (C. Japan)	C. & W. Japan
R. metternichii var. *pentamerum* Maxim (Ponticum)	−24	−50	−50	−60	−30	Sapporo	N. Japan
R. makinoi Tagg. Makino (Ponticum)	−23	−40	−50	−50	−27	Sapporo	C. Japan (400–600 m)
R. yakushimanum Nakai (Ponticum)	−23	−40	−50	−50	−27	Sapporo	Yakushima (30° 50′N, 1000–1800 m alt.)
R. yakushimanum Nakai (Ponticum)[y]	---	−40	−40	−40	−27	Sapporo	Yakushima (1500 m alt.)
R. yakushimanum Nakai (Ponticum)[y]	−23	−30[z]	−40[z]	−30[z]	−30	Eugene	
R. smirnowii Trautv. (Ponticum)	−23	−30	−40	−40	−30	Sapporo	Cocasus, Asia Minor
Hardy (−39° to −30°C)							
R. ponticum L.	−23	−35	−30	−30	−30	Sapporo	Asia Minor, Caucasus, Balkans
R. micranthum Turcz. (Micranthum)	−23	−25	−30	−30	−25	Sapporo	Szechwan, Kansu (2000–2500 m alt.)
R. ferrugineum L. (Ferrugineum)	−23	−30	−25	−35	−30	Sapporo	Alps of Europe (1500–2000 m alt.)
R. campylocarpum Hook. f. (Tomsonii)	−20	−25	−30	−25	−25	Sapporo	Nepal, Sikkim (3300–4000 m alt.)
R. wallichii Hook. f. (Campanulatum)	−20	−28	−30	−30	−25	Nepal (3900 m alt.)	Nepal, Sikkim (3300–4000 m alt.)
R. hodgsonii Hook. f. (Falconeri)	---	−25	−30	−25	−25	Nepal (3900 m alt.)	Nepal, Bhutan (3300–3900 m alt.)
R. campanulatum P. Don (Campanulatum)	−20	−25	−30	−30	−25	Nepal (3900 m alt.)	Nepal, Bhutan (2800–2900 m alt.)
Semihardy (−29° to −20°C)							
R. macrophyllum G. Don	−20	−20	−25	−25	−20	Kyoto (Japan)	British Columbia, W. United States
R. macrophyllum G. Dm[y]	−22	−20	−25	−23	−20	Newport (Oregon)	N.W. United States
R. morii Hayata (Barbatum)	−23	−23	−23	−23	−23	Taichun (2000 m alt.)	Taiwan
R. wardii W.W. Sm. (Thomsonii)	−20	−20	−27	−27	−23	Eugene	Yunnan, Tibet (3000–4000 m alt.)
R. chapmanii Gray. (Caloriarum)	−20	−18	−20	−20	−20	Yokohama (Japan)	Florida
R. cinnabarinum Hook (Cinnabarinum)	−18	−18	−18	−20	−20	Nepal (3000 m alt.)	Nepal, Sikkim (3000–6000 m alt.)
R. griffithianum Wight. (Griffithianum)	−20	−23	−23	−23	−23	Sapporo	Nepal, Sikkim (2100–2800 m alt.)
R. discolor Franch. (Fortuner)	−18	−20	−20	−20	−20	Sapporo	Szechwan (1300–2000 m alt.)
R. yunnanese Franch. (Triflorium)	−15	−18	−20	−25	−25	Sapporo	Yunnan, Burma (2200–3000 m alt.)
R. augustinii Hemsl. (Triflorium)	−15	−15	−20	−20	−20	Sapporo	Yunnan (1500–2700 m alt.)
R. augustinii Hemsl. (Triflorium)[y]	−18	−20	−20	−20	−20	Eugene	
R. fortunei Lindl. (Fortunei)	−15	−18	−25	−23	−23	Sapporo	E. China

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Table 1. Continued

Hardiness divisions and species (series)	Lowest survival temperature °C) Flower bud	Leaf	Vegetative bud	Cortex	Xylem	Collecting locality	Distribution (altitude)
Tender (−19°C)							
R. barbatum Wall. (Barbatum)	−18	−18	−18	−18	−18	Nepal	Nepal (3000–3400 m alt.)
R. griersonianum Balf. Griersonianum	−17	−15	−17	−17	−17	Eugene	Yunnan, N. Burma (2100–2800 m alt.)
R. racemosum Franch. (Scabrifolium)	−17	−15	−18	−18	−18	Sapporo	Yunnan (1700–3700 m alt.)
R. lutescens Franch. (Triflorum)	−13	−13	−18	−18	−18	Kyoto	Yunnan, Szechwan (600–3000 m alt.)
R. arboretum var. *cinnamomeum* Hook. f. (Arboreum)	−13	−13	−13	−13	−13	Nepal (2800 m alt.)	Nepal (1500–2800 m alt.)
var. *campbelliae* Hook. f. (Arboreum)	−10	−10	−10	−10	−10	Nepal (2200 m alt.)	Nepal (1500–2500 m alt.)

[z] Uninjured at an indicated temperature.
[y] Obtained from another source.

In rhododendrons, flower primordia in dormant flower buds and living cells in the xylem survive freezing stress by deep supercooling and avoiding ice crystallization. Avoidance is typical of some other woody genera, including *Prunus* (4, 7, 23, 25), *Vaccinium* (6), *Malus* (24), *Pyrus* (24, 26) and many conifers, deciduous trees and shrubs native to the eastern deciduous forests in the United States and similar climatic regions around the world (5, 12, 13, 16). Plant tissues that deep supercool survive freezing temperatures as long as they remain unfrozen but are killed at the moment they freeze. In contrast, vegetative buds, leaves, and cortical tissues of Rhododendron and most other woody genera supercool only a few degrees and survive freezing by tolerating ice formation in these tissues (1, 2, 3, 4, 6, 7, 16, 19, 20, 24, 26).

Survival temperature of flower buds from Himalayan and Japanese rhododendrons was compared by differential thermal analysis (DTA). This method detects exotherms from the heat of fusion of water given off when flower primordia freeze. A copper-constantan thermocouple was inserted in an excised flower bud through the outer scale. Each flower bud was wrapped with aluminum foil and cooled at a rate of about 0.06°C/min (27).

Results

Cold hardiness of rhododendron species. Table 1 presents the cold hardiness of 32 species of rhododendrons. Differences in hardiness were found ranging from −10° to −60°C for the species tested. The rhododendron species were divided into 4 major divisions based on the freezing resistance of both the cortex and vegetative buds, where at least one of the tissues survived the following temperatures: 1. very hardy species, −40° to −60°; 2. hardy species, −30° to −39°; 3. semihardy species, −20° to −29°; and 4. tender, 0 to −19°.

Generally, major differences in the survival temperature of the tissues were found in the hardy and semi-hardy species and little or no differences in the tender species. The flower bud and xylem were least hardy, ranging from −10° to −30°C and −10° to −40°, respectively, whereas the leaves, vegetative bud, and cortex were hardiest, ranging from −10° to −60° for all species studied. In the very hardy rhododendrons, the hardiness of the flower buds, xylem, leaves, vegetative buds, and cortex ranged between −23° to −30°, −27° to −40°, −35° to −60°, −50° to −60°, and −50° to −60°, respectively. As much as 35° difference in hardiness was found between the flower buds and vegetative buds and cortex of *R. metternichii* Sieb.

Similar differences in hardiness occurred between tissues of the hardy species. The freezing resistance of the various tissues were: flower buds, −20° to −23°C; xylem, −25° to −35°; leaves, −25° to −40°; vegetative buds, −25° to −40°; and cortex, −25° to −40°. In contrast to the very hardy species, the largest range of survival temperatures of the flower bud and the vegetative bud and cortex in the semi-hardy species was −12° which occurred in *R. ferrugineum* L.

The hardiness of the various tissues of the semihardy species of rhododendrons was similar, ranging from −10° to −27°C, with the largest difference being only 10° (*R. fortunii* Lindl.). In many of the species in this division, all 5 tissues examined were hardy to the same temperature.

It is notable that a major number of the hardiest rhododendron species belong to the Ponticum series. An exception is *R. macrophyllum* G. (hardy from −20° to −25°C), native to the west coast of the United States and British Columbia. Two other series with very hardy species were Dauricum and Carolinianum.

The distribution of the rhododendron species studied is reported in Table 1. The LST's of most species were directly related to the severity (freezing temperatures) of the native climate or collection site. The hardy species, e.g., *R. brachycarpum* (range widely in the subalpines of central to northern Japan), grows in cold climates, and the less hardy species, e.g, *R. arboreum* Hook. (range 1500–2800 m alt at Nepal) grows in warmer climates.

In addition to the data on LST's reported in Table 1, the DTA profiles of flower buds between *R. wallichii* (Himalayan rhododendron occurring at the tree line, 3900 m alt) and *R. brachycarpum* (native to northern Japan were compared (Fig. 1). Exotherms from *R. wallichii* occurred at a much higher temperature (−20°C) than those from *R. brachycarpum* (−30°), thus verifying the previous results (Table 1).

Cold hardiness of dwarf rhododendrons. Freezing resistance of dwarf rhododendrons is presented in Table 2. Similar differences in hardiness between tissues were found among the dwarf rhododendrons. In contrast to the other rhododendrons, the dwarf rhododendrons were all quite hardy, with 13 out of the 15 species studied classified as very hardy. Most of the dwarf rhododendrons, belong to Lapponicum Series of *Rhododendron*, range in the alpines and subalpines of the Himalayas, north-

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Table 2. Freezing resistance of dwarf rhododendrons.

Hardiness divisions and species (series)	Lowest survival temperature (°C)					Collecting locality	Distribution (altitude)
	Flower bud	Vegetative Leaf	bud	Cortex	Xylem		
Very hardy (−40°C)							
R. camtschaticum Pall. (Camtschaticum)	−34	---	−60	−60	−40	Sapporo	Kamtschatka, shores of Okhotsk Sea, Hokkaido
R. parvifolium Adams (Lapponicum)	−32	−60	−60	−60	−50	Sapporo	N.E. China, Sakhalin, Hokkaido
R. aureum Franch.	−27	−60	−60	−60	−50	Sapporo	C. & N. Japan
R. impeditum Balf. f. & W.W. Sm (Lapponicum)	−25	−50	−50	−50	---	Sapporo	Yunnan (3300–3900 m alt.)
R. fimbriatum Hutch. (Lapponicum)	−25	−30	−40	−40	−40	Eugene	Szechwan (3600 m alt.)
R. dasypetalum (Lapponicum)	−25	−50	−50	−50	−35	Sapporo	Yunnan (3200–4000 m alt.)
R. anthopogon D. Don (Anthopogon)	−23	−50	−50	−50	−40	Nepal (3900 m alt.)	Nepal, Kashmir (3000–4800 m alt.)
R. anthopogon D. Don (Anthopogon)[y]	---	−30[z]	−30[z]	−30[z]	−30[z]	Eugene Oregon	
R. setosum D. Don (Lapponicum)	−23	−50	−50	−50	−50	Nepal (3900 m alt.)	E. Nepal to S.E. Tibet (3300–4800 m alt.)
R. setosum D. Don (Lapponicum)[y]	−23	−35	−35	−40	−40	Eugene	
R. fastigiatum Franch. (Lapponicum)	−24	−40	−40	−40	−30	Sapporo Yunnan (3100–4100 m alt.)	
R. fastigiatum Franch. (lapponicum)[y]	−20	−25[z]	−40	−40	−27	Eugene	
R. intricatum Franch. (Lapponicum)	−23	−35	−40	−50	−35	Sapporo	Szechwan, Yunnan (3600–4500 m alt.)
R. scintillans Balf. f. & W.W. Sm. (Lapponicum)	−20	−40	−40	−40	−35	Sapporo	Yunnan (3300–4200 m alt.)
R. russatum Balf. f. & Forr. (Lapponicum)	−20	−40	−40	−40	−30	Sapporo	Yunnan (3300–4000 m alt.)
R. lepidotum Wall. (Lepidotum)	−18	−40	−30	−40	−30	Nepal (3450 m alt.)	Nepal to Yunnan (2400–4500 m alt.)
R. lepidotum Wall (Lepidotum)[y]	−20	−50	−50	−50	−40	Nepal (3900 m alt.)	
Hardy (−39° to −30°C)							
R. keiskei Miq. (Triflorum)	−23	−25	−30	−30	−25	Sapporo	Japan (600–1800 m alt.)
Semihardy (−29° to −20°C)							
R. forestii Balf. f. ex Dielo var. *repens* Balf. f. & Forr. (Neuriflorum)	−20	−20	−20	−20	−23	Eugene	Yunnan, Tibet (3000–4300 m alt.)

[z] Uninjured at an indicated temperature.
[y] Obtained from another source.

western Yunnan, southeastern Tibet, and western Szechwan and low altitudes in northern cold regions of far east Asia and the circumpolar regions. The following hardy species of rhododendrons were found growing widely in cold areas: Dwarf deciduous rhododendron, *R. camtschaticum* Pall. ranges from Hokkaido, the shorts of the Okhotsk sea, and eastward to the Bering Straits and western Alaska; *R. parvifolium* Adams grows in Hokkaido, northeast China and Russian Far East; *R. aureum* Franch. range in the alpine or subalpine regions of Hokkaido, northeast China and east Siberia. The subterranean stems of *R. aureum* collected from Mt. Kurodake (1500 m alt.) in Hokkaido were very hardy, surviving freezing to −30°C (data not presented). Other hardy dwarf rhododendrons were *R. impeditum* Balf. f. and W.W. Sm., *R. intricatum* Franch. which occur at altitudes between 3300 m and 4300 m of southwestern China. Himalayan alpine rhododendrons, *R. setosum* D. Don, *R. anthopogen* D. Don, *R. lepidotum* Wall. occur in open places near forest limits (about 3900 m) to 5000 m (near the snow line). The hardiness of these rhododendrons was similar to those of the high altitudes of northwestern Yunnan areas.

Cold hardiness of azalea. The range of survival temperatures of azalea is similar to those observed in the rhododendrons (Table 3). As with rhododendrons, the hardiness of the azalea species is related to their distribution, e.g., the hardy species originate from the cold climates and the less hardy species from the warm climates. The following are some examples of the relations between the origin and the LST: *R. viscosum* L., *R. arborescens* Pursh., and *R. canadense* L., which are native to northeastern United States and Canada were hardiest among the azalea series; *R. schlippenbachii* Maxim., *R. japonicum* A. Gray, and *R. albrechii* Maxim. of northeast China, central and north Japan, and north Japan, respectively, were also either very hardy or

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Table 3. Freezing resistance of azalea.

Hardiness divisions and species (series)	Lowest survival temperature (°C)					Collecting liability	Distribution
	Flower bud	Leaf	Vegetative bud	Cortex	Xylem		
Very hardy (−40°C)							
R. viscosum (L.) Torrey	−30	---	−50	−60	−40	Sapporo	E. United States
R. viscosum (L.) Torrey[y]	−25	---	−40[z]	−40[z]	−40[z]	Sapporo	
R. arborescens (Pursh) Torrey	−30	---	−40	−60	−40	Sapporo	E. United States
R. canadense (L.) Torr. Rhodora canadensis	−30	---	−40[z]	−40[z]	−40[z]	Eugene	Quebec, Maine
R. japonicum (A. Gray) Surin	−25	---	−40	−50	−40	Sapporo	C. & N. Japan
Hardy (−39° to −30°C)							
R. schlippenbahii (Maxim.)	−28	---	−35	−35	−30	Sapporo	N.E. China
R. albrechtii Maxim.	--	---	−35	−35	−30	Sapporo	N. Japan
R. kiusianum Makino	−23	−30	−30	−30	−25	Sapporo	Japan (Kyushu, 1300–1700 m alt.)
R. yedoense Maxim. ex Regel var. *poukhanense* Lev	−25	−30	−30	−30	−30	Seoul	Korea
R. kaempferi (Planch.) Wils. −23	−25	−25	−30	−30	Sapporo	Japan (Kyushu)	
Semihardy (−29° to −20°C)							
R. occidentale Torr. & A. Gray	−20	---	−25	−25	−23	Sapporo	W. United States
R. occidentale Torr. & Gray[y]	−23	---	−30	−25	−25	Eugene	
R. linearifolium Siebold & Zucc. var. Macrosepalum (Maxim.)	−20	−20	−25	−25	−27	Sapporo	S.W. Japan
R. simsii Planch.	−18	---	−25	−25	−25	Sapporo	Yunnan (1000–2600 m alt.)
R. ripense Makino	−15	−20	−20	−20	−20	Hamamatsu (Japan)	S. Japan
Tender (−19°C)							
R. scabrum G. Don	−13	−15	−15	−15	−15	Hamamatsu	Ryukyu
R. tashiroi Maxim.	−13	−15	−15	−15	−15	Hamamatsu	Ryukyu, S.W. Japan
R. eriocarpum (Hayata) Nakai	−13	−15	−15	−15	−15	Hamamatsu	S. Japan, S.E. China

[z] Uninjured at an indicated temperature.
[y] Obtained from another source.

hardy; *R. kiusianum* Makino, one of the best native Japanese azalea, inhabits an altitude of 1300 to 1700 m in Kyushu, a southwestern island of Japan. Its flower buds were hardy to −23°C; the flower buds of *R. simsii* Planch., the most important species among azaleas (found growing widely at lower altitudes in Yunnan) survived freezing to −18°; *R. scabrum* G. Don, *R. tashiroi* Maxim., and *R. eriocarpum* Hayata, which inhabit the mild climates of Ryukyu (subtropic), Yaku island, and southwestern Kyushu, were hardy to −13° and −15°.

Freezing resistance of rhododendron cultivars. Freezing resistance of cultivars is summarized in Table 4. The degree of hardiness and the hardiness differences among the cultivars were similar to those reported for the species (Table 1). It is notable that most of the hardy cultivars belong to *R. catawbiense* hybrids (from −23° to −60°C), and *R. carolinianum* (from −25° to −50°). The hybrids produced from either *R. griersonianum* or *R. griffithianum* were not very hardy, ranging between −20° and −23°.

Freezing resistance of Malaysian rhododendron (Vireya). Three species of rhododendrons were collected at the tree limit (3500 m alt.) of Mt. Wilhelm from Papua, New Guinea, where the daily average air temperature is around 6°C and the environment is wet throughout the year. The freezing resistance of the leaves, vegetative buds, and cortex was between −3° to −6° and the xylem to −10° for all the 3 species (Table 5). All tissues of *R. kawakami*, an epiphyte from Taiwan, survived freezing to −10°. Two Vireya species obtained from the lower altitudes in Malaysia were injured by a slight freezing (−4°), even after hardening at 5° to 0°.

Discussion

Marked altitudinal and geographical variations were observed in the winterhardiness of the open-pollinated progenies from 84 mother trees of 477 clones of Sakhalin fir growing in natural stands at Hokkaido, Japan (8). The mean freezing resistance of these progenies was highly correlated with the severity of the winter temperature of the natural distributional ranges. These results suggest that the natural selection of freezing resistance may have occurred corresponding to climactic variation pattern. Intraspecific differences in freezing resistance among climactic races have been reported in many plants (10, 19, 34). These findings suggest that intraspecific differences in the hardiness

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Table 4. Freezing resistance of cultivars of rhododendrons.

Hardiness divisions and cultivars	Lowest survival temperature (°C)					Collecting locality
	Flower bud	Leaf	Vegetative bud	Cortex	Xylem	
Very hardy (−40° to −60°C)						
America[z]	−27	−50	−60	−60	−30	Sapporo, Japan
P.J.M.[y]	−27	−50	−50	−40	−40	Sapporo
P.J.M.[x]	−27	−30	−40	−40	−35	Eugene, Oregon
Album Elegans[z]	−27	−40	−50	−50	−35	Sapporo
English Roseum[z]	−27	−40	−50	−50	−35	Sapporo
Dora Amateis[y]	−27	−40	−40	−40	−35	Sapporo
President Lincoln[z]	−25	−40	−40	−40	−30	Sapporo
Fastuosum Flore Pleno[z]	−25	−35	−40	−40	−35	Sapporo
Ramapo[y]	−25	−40	−40	−40	−35	Sapporo
Ramapo[y]	−25	−35	−40	−40	−30	Sapporo
Nova Zembra[z]	−25	−35	−40	−40	−30	Sapporo
Hardy (−30° to −39°C)						
Dora Amateis[y]	−30	−30	−35	−35	−35	Eugene
Nova Zembra[z]	−27	−30	−30	−30	−30	Eugene
Cheer[z]	−25	−25	−30	−30	−25	Sapporo
Catawbiense Grandiflorum[z]	−25	−25	−30	−30	−25	Sapporo
Lee's Dark Purple[z]	−23	−35	−35	−35	−25	Sapporo
Prince Camille de Rohan	−20	−25	−35	−35	−25	Sapporo
Blue Diamond (Fastigiatum hybrid)	−20	−25	−30	−30	−25	Sapporo
Semihardy (−20 to −29°C)						
Purple Splendor (Ponticum hybrid)	−25	−25	−27	−27	−27	Corvallis
Christmas Cheer	−23	−23	−25	−25	−20	Sapporo
Ruby Bowman[w]	−23	−20	−25	−25	−23	Eugene
Scarlet Wonder	−23	−23	−25	−25	−23	Sapporo
Scarlet Wonder[x]	−20	−23	−25	−25	−25	Eugene
Blue Diamond[x]	−20	−23	−25	−25	−25	Eugene
Pink Pearl[w]	−20	−25	−25	−25	−20	Sapporo
Album Novem	−20	−25	−25	−25	−20	Corvallis
Hallelujah[w]	−20	−23	−23	−23	−23	Eugene
Trude Webster	−20	−23	−20	−20	−20	Eugene
Elizabeth[w]	−20	−20	−25	−25	−20	Sapporo
Elizabeth[x]	−17	−15	−20	−20	−20	Eugene
Vulcan[v]	−20	−20	−20	−20	−20	Eugene
Hino Crimson (Azalea)	−20	−20	−23	−23	−23	Eugene
Unknown Warrior	−17	−20	−17	−23	−20	Eugene
Unique	−17	−15	−25	−25	−25	Sapporo
Unique[x]	−17	−15	−20	−20	−20	Eugene
President Roosevelt	−17	−15	−20	−20	−17	Sapporo
Tender (o° to −19°C)						
Thor	−13	−15	−25	−25	−20	Sapporo

[z] catawbiense hybrid.
[y] calorinianum hybrid.
[x] Obtained from another source.
[w] griffithianum hybrid.
[v] griersonianum hybrid.

of rhododendrons may also be a result of climatic adaptation. Although most of the samples were collected from planted rhododendrons in Sapporo, and the seed origin is obscure, marked differences in freezing resistance of rhododendrons relate well with their area of distribution. This association was supported with the results from the few species obtained from their point of origin, which showed a close relationship of freezing resistance to the temperature conditions of the distribution area.

In all species tested, the floral primordia that did not survive freezing below −35°C was the least hardy. These data concur with the results of Iwaya-Inoue and Kaku (19). The xylem was slightly hardier than the floral buds. Generally, the hardiest tissues were the vegetative buds, leaves, and cortex that survived temperatures of −50° or lower in hardy species. Rhododendron floral primordia survive low temperatures by supercooling (11, 14, 19, 21) or extraorgan freezing (17, 18, 30). It was also observed that low temperature exotherms are reduced further when the flower buds acclimate or when they are cooled slowly and that the water in the floral primordia migrates to the ice formed within the bud scales via vascular system (17, 18).

The hardy rhododendron species grow in the severely cold

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Table 5. Freezing resistance of tender Malaysian rhododendrons.

Species	Lowest survival temperature (°C)					Collecting locality	Distribution
	Flower bud	Leaf	Vegetative bud	Cortex	Xylem		
R. kawakami	---	−10	−10	−10	−10	Tokyo	Taiwan
R. atropurpurain sleum.[z]	---	− 5	− 5	− 5	−10	Papua New Guinea (3600 . alt.)	Papua New Guinea
R. womersleyil sleum.[z]	---	− 4	− 6	− 6	−10	Papua New Guinea (3600 m alt.)	Papua New Guinea
R. gultherifolium sleum.[z]	---	− 3	− 3	− 3	−10	Papua New Guinea (3500 M alt.)	Papua New Guinea
R. javanicum[y] (Blume) J. Benn.	---	X	X	X	X		Malaysia (800–2400 m alt.)
R. ravum[y]	---	X	X	X	X		Malaysia (1600–3500 m alt.)

[z] Samples were collected on 22 to 23 Aug. 1980.
[y] Samples were sent from Greer Garden, Oregon and planted in a greenhouse for one year.
[x] Injjured freezing at −4°C for 3 hr.

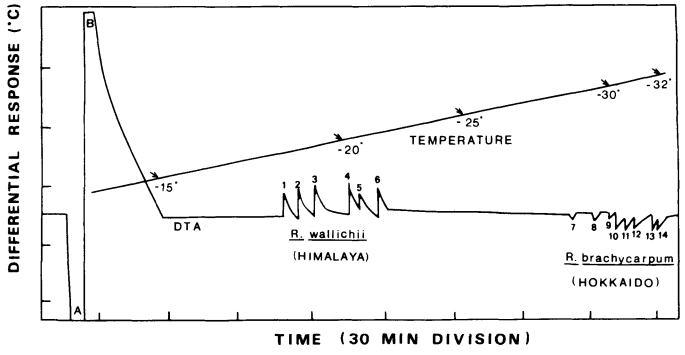

Fig. 1. DTA profile of excised winter flower buds of *R. wallichii* **(B)** collected at East Himalaya (3900 m) and of *R. brachycarpum* **(A)**, respectively. Exotherms (1–6) and (7–14) correspond to freezing of flower buds of *R. wallichii* and *R. brachycarpum*, respectively. Each flower bud was wrapped in aluminum foil and the positive and negative thermocouple were inserted in each flower bud. Cooling rate: 0.06°C/min.

areas of eastern North America and northern far east Asia. In North America, the hardy species are found at the high altitudes in the Appalachian mountain ranges and northward to New Hampshire, Maine, and Nova Scotia. In eastern Asia, the hardiest rhododendrons grow in the alpines or subalpines of central and northern Japan. The mean temperature in midwinter at the 2000 m altitudes in central Japan (about 36° N) or 1500 m altitude in Hokkaido at which *R. brachycarpum* is found is estimated to be −12° or −14°C. This temperature is roughly comparable to that of the 2000 m altitude in the Allegheny mountains in the United States where *R. catawbiense* occurs. The distribution range of several hardy dwarf rhododendrons occur widely in Hokkaido, Sakhalin, Northeast China, northward to East Siberia.

In the warm temperate zone, between 1000 m and 2400 m altitude, of the East Himalayas (27° 50′N), the predominant vegetation is broad-leaf and coniferous evergreen forests and epiphytes. Evergreen oak, *Quercus semicarpifolia*, covered by mosses, ferns, and epiphytes is quite common on south faces, even at altitudes as high as 3000 m. The coniferous forest is mainly Abies and Tsuga at the higher altitudes and is usually accompanied by rhododendrons. *Abies spectabilis* occurs at high altitudes, dominating the forest up to timberline (3900 m alt.). The winter temperatures at the timberline of Shyangboche (36° 30′N) are as follows: mean temperature (−4.4°C), daily minimum temperature (−11.2°), and extreme minimum temperature (−15.8°) (33). These temperatures are comparable to that of Karuizawa (36° 30′N, 990 m alt) located in central Japan (33). These areas are also quite humid during the winters (33). The rhododendrons distributed in these mild climates are less hardy than those growing in the colder areas. The flower buds of Himalayan rhododendrons, even those found at timberline, tolerated temperatures of only −20° to −23°C.

The climates and tree vegetations at northwestern Yunnan, southeastern Tibet, and western Szechwan resemble those of the East Himalaya. This region has deep, narrow, and steep valleys through which 5 great rivers flow. This area is uniquely isolated geographically which probably accounts for the high proportion of endemic species and diversity of vegetation. In addition to rhododendrons, this area has a large number of coniferous species (2500 to 4300 m alt.) (35). With increasing elevation, the climate gradually becomes more humid and colder. The rhododendrons are found at altitudes between 3300 and 4300 m altitude which forms the secondary layer in the coniferous forest. The flower buds of rhododendrons at the high altitudes showed nearly the same range of hardiness as those growing at the Himalayas.

The climates of eastern Himalayas and the northwestern Yunnan area are characterized by a relatively narrow annual range of temperature and high rainfall in the summer, and rather high humidity and moderate temperatures in the winter, similar to the conditions of the southern oceanic climate. Thus, rhododendrons growing at the high altitudes of Himalayas and northwestern Yunnan are very sensitive to high summer heat and high humidity conditions. These rhododendrons are easily cultivated in New Zealand, Tasmania, England, and the northern west coast of the United States. In contrast, most of the rhododendrons from the lower altitudes in southwest Japan, southeast china, and the east coast of the United States tolerate summer heat and high humidity.

Azaleas have evolved within areas with hot summer and dry winter conditions. *R. metternichii, R. yakushimanum*, and *R. makinoi*, which are native to western Japan, are tolerant to summer heat as well as winter cold (29).

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The leaves of *Rhododendron* are very hardy, surviving −40°C or below. This characteristic is unique to the genus *Rhododendron* (31). Hardy rhododendrons, except *R. arboreum* and related species, resist winter dehydration by rolling down the leaves at subfreezing temperatures, thus reducing transpiration. In the snowy wind-swept areas, the leaves, small twigs, and buds protruding above the snow level are often damaged by winter desiccation (28, 32). In these cold areas, where the mean temperature is around −3°C or below, the water ascent from root to upper parts of stems is completely blocked. The combination of accelerated transpiration rates due to sunshine and/or dry winds, and frozen soil is, therefore, a major cause of desiccation damage (15, 23). Effective methods of preventing winter drought for cultivated rhododendrons are shading and mulching (22).

The freezing resistance of the cultivated varieties of rhododendrons suggests that the varieties originating from hardy species, e.g., Catawbiense hybrids are generally hardier than those from less hardy species, e.g., griersonianum hybrids (Table 4). This information should be useful to plant breeders interested in developing hardy varieties of rhododendrons.

Literature Cited

1. Anderson, J.A., L.V. Gusta, D.W. Buchanan, and M.J. Burke. 1983. Freezing of water in citrus leaves. J. Amer. Soc. Hort. Sci. 108:397–400.
2. Ashworth, E.N. 1982. Properties of peach flower buds which facilitate supercooling. Plant Physiol. 70:1475–1479.
3. Ashworth, E.N. and D.J. Rowse. 1982. Vascular development in dormant *Prunus* flower buds and its relationship to supercooling. HortScience 17:790–791.
4. Ashworth, E.N., D.J. Rowse, and L.H. Billmyer. 1983. The freezing of water in woody tissues of apricot and peach and the relationship to freezing injury. J. Amer. Soc. Hort. Sci. 108:299–303.
5. Becwar, M.R., C. Rajaschekar, K.J. Hanson, and M.J. Burke. 1981. Deep undercooling of tissue water and winter hardiness limitations in timberline flora. Plant Physiol. 68:111–114.
6. Biermann, J., C. Stushnoff, and M.J. Burke. 1979. Differential thermal analysis and freezing injury in cold hardy blueberry flower buds. J. Amer. Soc. Hort. Sci. 104:444–449.
7. Cain, D.W., E.R. Olien, and R.L. Andersen. 1980. Comparative freezing patterns of bark and xylem of 'Siberian C' and 'Red Haven' peach twigs. Cryobiology 17:495–499.
8. Eiga, S. and A. Sakai. 1984. Altitudinal variation in freezing resistance of Sakhalin fir (*Abies sachalinensis*). Can J. Bot. 62:156–160.
9. Fen, K.M. 1981. Rhodendron in Yunnan. Yunnan Peoples' Pub. and NHK Pub. Assoc. Tokyo.
10. Flint, M.L. 1972. Cold hardiness of twig of *Quercus rubra* L. as a function of geographic origin. Ecology 53:1163–1170.
11. George, M.F. and M.J. Burke. 1977. Supercooling in overwintering azalea flower buds. Plant Physiol. 59:326–328.
12. George, M.F., M.J. Burke, H.M. Pellett, and A.G. Johnson. 1974. Low temperature exotherms and woody plant distribution. HortScience 9:519–522.
13. George, M.F., S.G. Hong, and M.J. Burke. 1977. Cold hardiness and deep supercooling of hardwoods: its occurrence in provenance collections of red oak, yellow birch, black walnut, and black cherry. Ecology 58:674–680.
14. Graham, P.R. and R. Mullin. 1976. A study of flower bud hardiness in azalea. J. Amer. Soc. Hort. Sci. 101:7–10.
15. Havis, J.. 1965. Desiccation as a factor in winter injury of rhododendrons. J. Amer. Soc. Hort. Sci. 86:764–769.
16. Hong, S. and E. Sucoff. 1980. Units of freezing of deep supercooled water in woody xylem. Plant Physiol. 66:40–45.
17. Ishikawa, M. and A. Sakai. 1981. Freezing avoidance mechanisms by supercooling in some Rhododendron flower buds with reference to water relation. Plant Cell Physiol. 22:953–967.
18. Ishikawa, M. and A. Sakai. 1982. Characteristics of freezing avoidance by supercooling in comparison with freezing tolerance. In: P.H. Li and A. Sakai (eds.), Plant cold hardiness and freezing stress, Vol. 2. Academic Press, New York.
19. Iwaya-Inoue, M. and S. kaku. 1983. Cold hardiness in various organs and tissues of *Rhododendron* species and the supercooling ability of flower buds as the most susceptible organ. Cryobiology 20(3):310–317.
20. Kaku, S., M. Iwaya-Inoue, and K.D. Jeon. 1983. Effects of temperature on cold acclimation and deacclimation in flower buds of evergreen azaleas. Plant Cell Physiol. 24(3):557–564.
21. Kaku, S., M. Iwaya, and M. Kunishige. 1980. Supercooling ability of Rhododendron flower buds in relation to cooling rate and cold hardiness. Plant Cell Physiol. 21:1205–1216.
22. Leach, D.G. 1963. Rhododendron of the world. Scribners, N.Y.
23. Parker, J. 1963. Causes of winter desiccation in transpiration and photosynthesis in some evergreens. Forest Sci. 9:158–166.
24. Quamme, H.A. 1976. Relationship of low temperature exotherms to apple and pear production in North America. Can. J. Plant Sci. 56:493–500.
25. Quamme, H.A., R.E.C. Layne, and W.G. Ronald. 1982. Relationship of supercooling to cold hardiness and the northern distribution of several cultivated and native *Prunus* species and hybrids. Can. J. Plant Sci. 62:137–148.
26. Rajashekar, C., M.N. Westwood, and M.J. Burke. 1982. Deep supercooling and cold hardiness in genus *Pyrus*. J. Amer. Soc. Hort. Sci. 107:968–972.
27. Sakai, A. 1970. Freezing resistance in willows from different climates. Ecology 51:485–491.
28. Sakai, A. 1970. Mechanism of desiccation damage of conifers wintering in soil-frozen areas. Ecology 51:657–664.
29. Sakai, A. 1974. Freezing resistance of evergreen and deciduous broad-leaved trees in Yakushima. Japan. Soc. Ecol. 24:116–122.
30. Sakai, A. 1979. Freezing avoidance mechanism of primordial shoots of conifer buds. Plant Cell Physiol. 20:1381–1390.
31. Sakai A. 1980. Freezing resistance of broad-leaved evergreen trees in the warm-temperate zone. Low Temp. Sci. Ser. B 38:1–14.
32. Sakai, A. and K. Otsuka. 1970. Freezing resistance of Alpine plants. Ecology 51:665–671.
33. Sakai, A. and S.B. Malla. 1981. Winter hardiness of tree species at high altitudes in the East Himalaya, Nepal. Ecology 62:1288–1298.
34. Smithberg, M.H. and C.J. Weiser. 1968. Pattern of variation among climatic races of red-osier dogwood. Ecology 49:495–505.
35. Wang, C.W. 1961. The forest trees of Chinese with a survey of grass-land and desert vegetation. Harvard Univ. Cambridge, Mass.

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