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Freezing Resistance of Conifers[1])

By A. Sakai[2]) and S. Okada[3])

Introduction

Desiccation injury in winter and frost injury occuring in various seasons constitute the greatest limiting factors for growing forest trees individually or in combination. From an ecological point of view, these injuries are also known to be the most important factors affecting distribution of plants. However, no extensive survey concerning the freezing resistance of main coniferous species has been carried out.

To clarify the characteristics in freezing resistance of the main genera of conifer, and the relation between the freezing resistance and meteorological conditions of their native habitats, the freezing resistance of over 100 coniferous species native to the northern hemisphere was investigated.

Materials and Methods

Winter twigs taken from about 10 year old trees and saplings of 3 to 6 years of age which are grown in the Tokyo University Forest at Yamabe, Hokkaido, or the Hokkaido Branch of the Breeding Station of Forest Trees in Sapporo were mainly used. The mean January temperatures in Yamabe and Sapporo are about —7 and —5° C respectively. The snow cover in winter amounts to about 1 to 2 m at both stations.

Some coniferous species not wintering in Hokkaido were sent from Honshu, chiefly from the Nagano prefecture in late December to mid January. Thereafter, materials sent from Honshu were hardened at —3 and —5° C for 2 weeks in hardy species and at 0 and —3° C for 2 weeks in less hardy species respectively to enhance their freezing resistance maximum (Sakai 1970 A).

In each experiment, 3 to 5 of saplings or 1-year-old winter twigs were used. Twigs or saplings were placed in a polyethylene bag. They were kept in a cold chamber at —30 C for one hour. Thereafter, they were transferred at 2 hours intervals to successively colder chambers varying by 5 to 10° C until the desired test temperatures were reached. These twigs or saplings were kept at the test temperatures for 16 hours, and then were thawed in air at 0° C. To determine the pre-freezing temperatures (Sakai 1960, 1965) which are effective in maintaining the viability of the twigs, the twig pieces were bound with thread and pre-frozen for 6 hours at temperatures of —15 to —70° C. These pre-frozen twigs were then immersed directly in liquid nitrogen (—196° C) for 30 minutes. They were transferred to a chamber at —30° C for 2 hours before being exposed to 0° C. The frozen twigs and saplings place in polythylene bags, were kept at room temperature for 1 month. Thereafter, the freezing injury was determined by the degree of browning in each tissue. The degree of freezing resistance in twigs and saplings was represented by the lowest temperatures at which they survived freezing without injury.

Climatic zones in native habitats of conifers were divided into 7 zones based on the annual minimum temperatures (Rehder 1967). The average annual minimum of the temperatures of these zones are as follows: Zone I; exceeding —50° C, Zone II; —50 to —35°, Zone III; —35 to —20° C, Zone IV; —20 to —10° C, Zone V; —10 to —5° C Zone VI; —5 to 5° C, Zone VII; 5 to 10° C (Rehder 1967).

The results of plantation of conifers in Hokkaido were divided into 3 grades (good, bad, impossible) based on the growing tests at Yamabe and Sapporo for several years.

Results

1. Seasonal *variations* of freezing resistance in different *tissues* of Saghalien fir (Abies sachalinensis) *and Cryptomeria (Cryptomeria* japonica)

Seasonal variations of freezing resistance in different tissues of 5-year-old Saghalien fir native to Hokkaido were investigated. As shown in Fig. 1, in any season the freez-

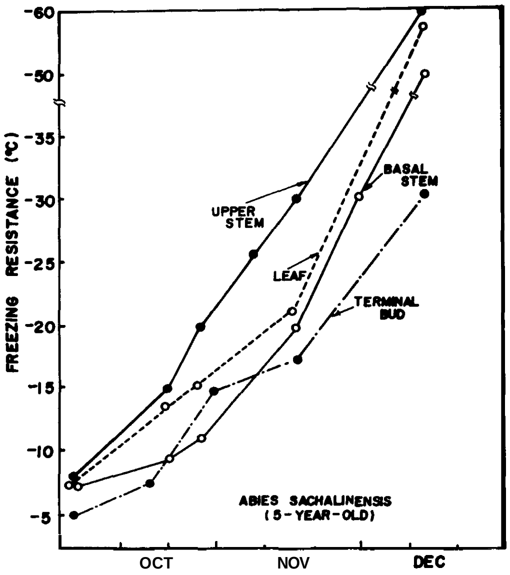

Fig. 1. — Seasonal variations of freezing resistance in different tissues of Abies sachalinensis.

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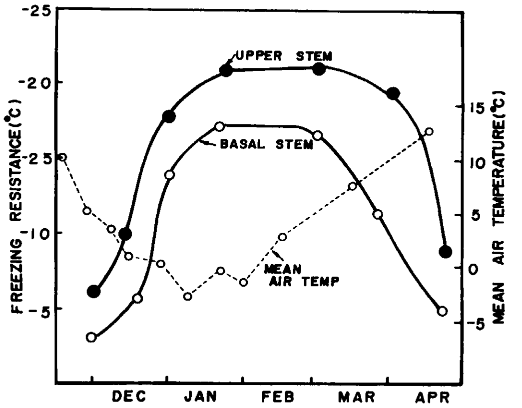

Fig. 2. — Seasonal variations of freezing resistance of upper and basal parts of a stem of *Cryptomeria japonica*.

ing resistance in the upper part of a stem was much greater than that in the basal part. The difference between the two amounted to about 10⁰ C. The same trend was also observed in spring. The terminal buds were most sensitive to freezing of the tissues and resisted freezing down to only —30⁰ C.

As shown in *Fig. 2*, the same results were obtained in cryptomeria growing near Tokyo. The basal part on a stem became frost hardy about 10 or 14 days later than the upper part in autumn and also lost its freezing resistance earlier than the latter in spring. And the freezing resistance of the upper part of a stem was invariably lower than that of the basal part.

2. Freezing resistance in winter of saplings and twigs of firs

In *Tables 1 and 2*, the freezing resistance in winter of saplings and twigs of firs are presented. In less hardy

Table 1. — Freezing Resistance of Saplings of Firs in Winter.

Species	Climatic zones	Seed source	Freezing Resistance of tissues (⁰ C) Terminal Bud	Leaf	Basal stem	Upper stem	Age of tree	Growth*** in Hokkaido
Abies balsamea	III	U.S.A.	—35	—70	—40	—50	6	Good
Abies sacchalinensis	III	Japan (Hokkaido)	—30	—70	—50	—70	6	Good
Abies veitchii	III	Japan (Nagano)	—25	—40	—50	—50	5	Good
Abies homolepis	IV	Japan (Nagano)	—25	—30	—25	—50	7	Good
Abies mariesii	IV	Japan (Nagano)	—25	—30	—15**	—30	4	Bad
Abies nordmanniana	IV	U.S.S.R. (Gruzinskaya)	—20	—30	—20**	—30	7	Bad
*Abies firma**	VI	Japan (Nagano)	—20	—25	—25**	—25	5	Bad

* Materials were sent from Nagano in late December.
** Basal part of stem suffered injury.
*** Result of plantation in Hokkaido was divided into 3 grade based on the growing tests in Tokyo University's Forest in Hokkaido and Hokkaido Branch of Breeding of Forest Trees for several years.

Table 2. — Freezing Resistance of Winter Twigs of Firs.

Species	Climatic zones	Seed source	Freezing resistance of tissues Terminal Bud	Leaf	Twig	Age of tree	Growth in Hokkaido
Abies balsamea	III	U.S.A. (Wisconsin)	—40	—70	—70	12	Good
Abies sachalinensis	III	Japan (Hokkaido)	—35	—70	—70	12	Good
Abies concolor	IV	U.S.A. (Colorado)	—35	--70	—70	12	Good
Abies veitchii	III	Japan (Nagano)	—25	—70	—70	15	Good
Abies mariesii	IV	Japan (Nagano)	—30	—50	—50	15	Bad
Abies alba	IV	Germany	—25	—30	—50	13	Good
Abies nordmanniana	IV	Caucasus	—25	—30	—50	15	Bad
Abies holophylla	V	Korea	—25	—25	—70	15	Bad
Abies homolepis	IV	Japan (Nagano)	—25	—20	—40	15	Good
Abies fraseri	V	U.S.A. (Virginia)	—30	—25	—50	12	Bad
Abies grandis	VI	Canada (British Columbia)	—20	—50	—50	16	Bad
Abies firma	VI	Japan (Nagano)	—20	—25	—40	15	Bad

Table 3. — Freezing Resistance of Saplings of Spruces in Winter.

Species	Climatic zones	Seed source	Freezing resistance of tissues (⁰ C) Terminal Bud	Leaf	Upper stem	Basal stem**	Age of tree	Growth in Hokkaido
Picea mariana	II	U.S.A. (Michigan)	—40	—70	—70	—70	6	Good
Picea glauca	II	Canada (Ontario)	—40	—70	—70	—70	6	Good
Picea engelmanni	II	U.S.A.	—35	—70	—70	—70	10	Good
Picea rubens	II	U.S.A.	—35	—70	—70	—70	6	Good
Picea glehnii	II	Japan (Hokkaido)	—30	—70	—50	—70	7	Good
Picea abies	II	Germany	—30	—50	—50	—50	4	Good
*Picea koyamai**	IV	Japan (Nagano)	—30	—50	—50	—50	4	Good
Picea bicolor var. *acicularis**	IV	Japan (Nagano)	—30	—40	—40	—40	7	Bad
Picea jezoensis var. *hondoensis**	V	Japan (Nagano)	—30	—25	—25	—40	4	Bad
Picea sitchensis	VI	U.S.A. (Alaska, Sitka)	—20	—30	—40	—40	6	Bad
*Picea maximowiczii**	IV	Japan (Nagano)	—20	—20	—30	—50	4	Bad

* Materials were sent from Nagano prefecture in late December.
** Basal part 5 to 10 cm above the ground.

Table 4. — Freezing Resistance of Winter Twigs of spruces.

Species	Climatic zones	Seed source	Freezing resistance of tissues (⁰ C) Terminal Bud	Leaf	Twig	Age of trees	Growth in Hokkaido
Picea mariana	I	U.S.A. (Alaska, Fairbanks)	—70**	—70**	—70**	—	—
Picea mariana	II	U.S.A. (New York)	—50	—70**	—70**	12	Good
*Picea glauca**	I	U.S.A. (Alaska, Fairbanks)	—70**	—70**	—70**	—	—
*Picea glauca**	II	Canada (Nova Scotia)	—50	—70**	—70**	12	Good
Picea abies	II	Germany (Schwarzwald)	—35	—70**	—70**	12	Good
Picea rubens	II	U.S.A. (New York)	—35	—60	—60	12	Good
Picea omorica	IV	Germany	—30	—70**	—70**	12	Good
Picea glehnii	II	Japan (Hokkaido)	—30	—70**	—70**	12	Good
Picea koyamai	IV	Japan (Nagano)	—30	—35	—60	10	Good
Picea bicolor var. *acicularis*	IV	Japan (Nagano)	—25	—35	—70**	10	Bad
Picea jezoensis var. *hondoensis*	V	Japan (Nagano)	—25	—30	—40	10	Bad
Picea sitchensis	VI	U.S.A. (Washington)	—20	—30	—30	10	Bad
Picea smithiana	VI	India (Nepal)	—20	—15	—30	10	Bad

* Twigs were sent from Fairbanks in January.

** Tissues resisted freezing down to —70⁰ C at least.

Table 5. — Freezing Resistance of Saplings of Pines in Winter.

Species	Climatic zones	Seed source	Freezing resistance of tissues (⁰ C) Terminal Bud	Leaf	Basal stem	Upper stem	Age of trees	Growth in Hokkaido
Pinus sylvestris	II	Germany	—90	—90	—70	—90	5	Good
Pinus strobus	III	U.S.A. (Wisconsin)	—90	—90	—70	—90	5	Good
Pinus pumila	II	Japan (Hokkaido)	—90	—90	—40	—70	6	Good
Pinus koraiensis	III	Korea	—90	—70	—50	—70	4	Good
Pinus densiflora	IV	Japan (Aomori)	—50	—20	—20*	—50	4	Good
Pinus thunbergii	V	Japan (Aomori)	—30	—20	—20*	—40	4	Bad
Pinus peuce	IV	Balkan Mts.	—30	—40	—20*	—40	5	Bad
Pinus heldreichii var. *leucodermis*	V	Bulgaria	—20	—25	—20*	—20	5	Bad
*Pinus palustris***	VII	U.S.A.	—20	—15	— 5*	—15	—	Impossible

* Basal part of stem suffered injury.

** Materials were sent from Japan main island in late December.

Table 6. — Freezing Resistance of Winter Twigs of Pines.

Species	Climatic zones	Seed source	Freezing resistance of tissues (⁰ C) Terminal Bud	Leaf	Twig	Age of trees	Growth in Hokkaido
Pinus banksiana	II	U.S.A. (New York)	—90	—90	—90	15	Good
Pinus pumila	II	Japan (Hokkaido)	—90	—90	—90	15	Good
Pinus resinosa	II	U.S.A. (Wisconsin)	—90	—90	—90	15	Good
Pinus strobus	III	U.S.A. (Wisconsin)	—90	—90	—90	15	Good
Pinus mugo	II	Spain	—30	—90	—30	15	Good
Pinus sylvestris	II	Denmark	—90	—90	—90	15	Good
Pinus contorta var. *latifolia*	II	U.S.A.	—90	—90	—90	13	Good
Pinus koraiensis	III	Japan (Iwate)	—90	—90	—90	15	Good
Pinus parviflora var. *pentaphylla*	—	Japan (Hokkaido)	—90	—90	—90	15	Good
Pinus aristata	V	U.S.A. (Colorado)	—90	—90	—90	10	Good
Pinus montana var. *rostrata*	III	France	—90	—90	—90	15	Good
Pinus peuce	IV	Balkan	—90	—90	—90	12	Good
Pinus monticola	V	U.S.A. (Idaho)	—90	—90	—90	12	Good
Pinus rigida	IV	U.S.A. (New York)	—70	—70	—70	13	Good
Pinus densiflora	IV	Japan (Aomori)	—50	—50	—50	15	Good
Pinus ponderosa	IV	U.S.A. (California)	—30	—40	—50	13	Bad
Pinus pallasiana	—	U.S.S.R.	—50	—40	—50	8	Bad
Pinus jeffreyi	V	U.S.A. (Calfornia)	—30	—30	—50	13	Bad
Pinus griffithii	V	Nepal	—25	—35	—35	8	Impossible
Pinus thunbergii	V	Japan (Akita)	—30	—25	—30	15	Bad
Pinus parviflora	V	Japan (Akita)	—30	—30	—30	11	Bad
*Pinus taeda**	VI	U.S.A. (Georgia)	—25	—10	—20	15	Impossible
Pinus elliottii	VII	U.S.A. (Florida)	—25	—10	—10	15	Impossible
*Pinus palustris**	VII	U.S.A.	—20	—15	—10	15	Impossible

* Materials were sent from Japan main island in late December.

species of firs, the basal part of a stem is apt to suffer freezing injury. A characteristic in the freezing resistance is that the leaves, twigs and stems in hardy species survived freezing down to —50 to —70° C, but their terminal and lateral buds resisted freezing down to only —40° C at most in the materials used here. The freezing resistance of spruces is shown in *Tables 3 and 4*. The terminal buds showed the lowest resistance to freezing among the tissues of spruces. However, even in less hardy spruces, no injury was observed in the basal part of the stem in midwinter.

In *Tables 5 and 6*, freezing resistance of saplings and twigs of pines is presented. Freezing resistance in pines varied greatly with species, ranging from —90 to —10° C among the materials used. In less hardy pines, the basal stem near the ground surface was found to be the most sensitive to freezing injury among their tissues.

In *Tables 7 and 8*, the freezing resistance of other important conifers are shown. The conifers except for *Tsuga canadensis, Thuja occidentalis* and 3 kinds of larch have their native habitats in mild climates. And the basal stems of their saplings are apt to suffer freezing injury.

Characteristics of freezing resistance among the genera of conifers are summarized in *Fig. 3*. The general trend is that in less hardy conifers, the basal part on the stems of the saplings is sensitive to freezing injury even in winter. It is also interesting that terminal buds of hardy pines, larches *(Table 9)* and spruces can survive freezing below —70° C, but in other conifers, even in hardy hemlocks and firs, these terminal buds resisted freezing down to only about —40° C.

As shown in *Table 9*, the freezing resistance of leaf buds of larches differed considerably from the species from —15 to —120° C, depending upon the climates of their native habitats. It was also observed that the leaf buds of larches had the lesser resistance to freezing than the twig tissues and the higher resistance than the flower buds.

3. The highest degree of freezing resistance in some extremely hardy species

Some pine trees did not suffer even when cooled down to —70° C. To investigate the highest degree of freezing resistance, twigs of 6 species of pines and *Thuja occidentalis* were further cooled down to —90° C and —120° C for 6 hours. As a result, these twigs were found to resist freez-

Table 7. — Freezing Resistance of Saplings of Some Conifers.

Species	Climatic zones	Seed source	Freezing resistance of tissues (° C)				Age of tree	Growth in Hokkaido
			Bud	Leaf	Basal stem	Upper stem		
Larix leptolepis	IV	Japan (Nagano)	—30	—	—30	—50	3	Good
Larix gmelinii var. *japonica*	II	Saghalien	—30	—	—30	—50	3	Good
Larix laricina	II	Canada	—70	—	—70	—70	4	Good
Thuja occidentalis	II	U.S.A.	—30	—90	—30	—90	6	Good
*Chamaecyparis obtusa**	V	Japan (Nagano)	—30	—30	—25**	—30	3	Bad
*Thuja standishii**	V	Japan (Aichi)	—20	—30	—25**	—50	3	Bad
Cryptomeria japonica	V	Japan (Hokkaido)	—20	—25	—20**	—25	3	Bad
*Metasequoia glyptostroboides**	—	China	—25	—	—20**	—25	3	Bad
*Pseudotsuga japonica**	VI	Japan (Tokyo)	—15	—15	—20**	—25	4	Bad
Thujopsis dolabrata var. *hondai*	IV	Japan (Hokkaido)	—15	—15	—15**	—25	4	Bad
*Cedrus deodara**	—	Nepal	—15	—15	—15**	—20	3	Impossible
*Sequoia sempervirens**	VII	U.S.A.	—10	—15	—10**	—15	4	Impossible

* Materials were sent from Japan main island in late December.
** Basal part of stem suffered injury.

Table 8. — Freezing Resistance of Winter Twigs of Some Conifers.

Species	Climatic zones	Seed source	Freezing resistance of tissues (° C)			Age of tree	Growth in Hokkaido
			Bud	Leaf	Twig		
Tsuga canadensis	IV	Canada	—35	—70	—50	40	Good
Tsuga diversifolia	IV	Japan (Nagano)	—25	—20	—30	20	Impossible
*Tsuga sieboldii**	VI	Japan (Kyoto)	—20	—20	—40	20	Impossible
Pseudotsuga menziesii	VI	U.S.A. (Washington)	—25	—20	—25	12	Bad
Thuja occidentalis	II	U.S.A.	—	—90	—90	15	Good
Thuja plicata	V	U.S.A. (Washington)	—20	—40	—25	15	Impossible
Thuja orientalis	V	Japan (Nagano)	—20	—20	—20	20	Bad
Thuja standishii	V	Japan (Nagano)	—15	—25	—25	20	Impossible
Thujopsis dolabrata var. *hondai*	V	Japan	—	—20	—20	10	Bad
Cryptomeria japonica	V	Japan (Hokkaido)	—15	—15	—15	20	Bad
Chamaecyparis obtusa	V	Japan	—20	—20	—25	20	Bad
Chamaecyparis pisifera	V	Japan	—20	—20	—20	20	Bad
Chamaecyparis lawsoniana	V	U.S.A. (California)	—15	—20	—30	15	Impossible
*Metasequoia glyptostroboides**	VII	China	—25	—	—30	15	Bad
*Sequoia sempervirens**	VII	U.S.A. (California)	—15	—20	—20	20	Impossible
*Taiwania cryptomeroides**	VII	Formosa	—15	—15	—15	20	Impossible
Cupressus macrocarpa	VII	U.S.A.	—15	—10	—10	20	Impossible
*Cupressus sempervirens**	VII	Italy	—10	—10	—15	20	Impossible
*Cupressus arizonica**	VII	U.S.A.	—10	—10	—10	20	Impossible

* Materials were sent from Japan main island in late December.

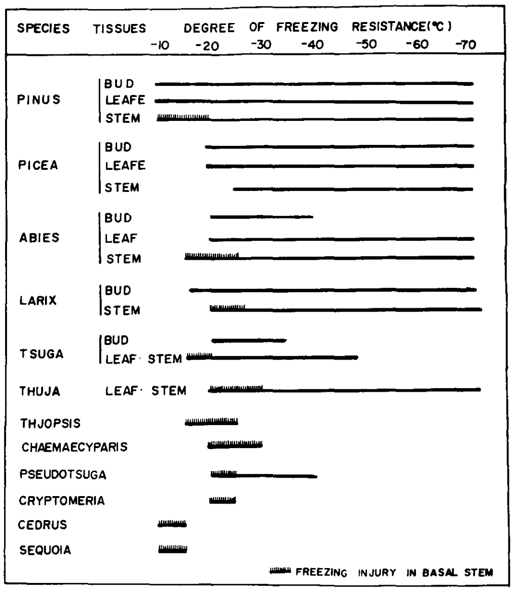

Fig. 3. — Comparison of freezing resistance of saplings in winter among the main genera of conifer.

ing even down to such super-low temperatures as —120° C *(Table 10).*

Twigs having different degrees of freezing resistance were immersed in liquid nitrogen after pre-freezing at temperatures ranging from —10 to —120° C respectively. As shown in *Table 10,* the twigs surviving freezing down to temperatures of —70 to —120° C could withstand immersion in liquid nitrogen following pre-freezing, while the twigs with a freezing resistance of only —50° C suffered freeezing injury after immersion in liquid nitrogen. The effective pre-freezing temperatures for maintaining viability after immersion in liquid nitrogen differed considerably in different species in a temperature range from —15° to about —70° C according to the degree of freezing resistance. It was also found that birch and Saghalien willow could withstand immersion in liquid nitrogen even after pre-freezing at —15° C. In all experiments, it was observed that the greater the freezing resistance, the higher the effective pre-freezing temperatures.

Discussion

1. Freezing injury of basal stem near the ground surface in saplings

Cold injury can be caused by several different environ-

Table 9. — A Relation between Freezing Resistance of Larch Species and Climates of Their Native Places (Leaf Bud).

Species	Native place	Latitude	Altitude (m)	Mean air temperature (° C) (January)	Freezing resistance (° C) of buds
Larix griffithiana	Himalaya	27 ~ 28°	2400 ~ 3600	0 ~ 4	—15 ~ —20
Larix potaninii	S.W. China	25 ~ 32°	2500 ~ 3400	1 ~ 6	—20 ~ —25
Larix leptolepis	C. Japan	35 ~ 37°	1000 ~ 2000	— 5 ~ —10	—30 ~ —40
Larix occidentalis	N.W. USA	45 ~ 52°	600 ~ 2100	— 2 ~ — 9	—30 ~ —40
Larix decidua	Europe	46 ~ 48°	2300 ~ 2500	— 7 ~ —11	—60 ~ —70
Larix gmelini	Saghalien	43 ~ 50°	50 ~ 200	—10 ~ 15	—50 ~ —60
Larix principis-rupprechtii	N. China	38 ~ 42°	2000 ~ 3000	—11 ~ —16	—50 ~ —55
Larix olegensis	Maritime province (USSR) Manchuria (China)	42 ~ 45°	500 ~ 1000	—15 ~ —20	—60 ~ —70
Larix laricina	N. USA Canada	45 ~ 60°	Plain and Swamp	—10 ~ 20	—120*
Larix var. *alaskensis*	Alaska	55 ~ 65°	Plain and Swamp	—20 ~ —25	—120*
Larix siberica	C. & W. Siberia	55 ~ 70°	Plain and Swamp	—16 ~ —25	—120*

* Twigs can survive freezing down to —120° C at least.

Table 10. — Relation between Effective Pre-freezing Temperatures and Degree of Freezing Resistance (in Midwinter).

Species	Pre-freezing temperature (° C) before immersion in liquid nitrogen										Freezing resistance (° C)*
	—10	—15	—20	—30	—40	—50	—60	—70	—90	—120	
Larix leptolepis			●	●	●	●	●	●	●	●	— 30
Abies sachalinensis			●	●	●	●	●	●	●	●	— 40
Picea glehnii			●	●	●	●	●	●	●	●	— 50
Picea alba			●	●	●	●	●	●	●	●	— 50
Pinus banksiana			●	●	o	o	o	o	o	o	—120
Pinus pumira		●	●	●	Δ	o	o	o	o	o	—120
Thuja occidentalis		●	●	●	●	o	o	o	o	o	—120
Pinus resinosa			●	●	●	Δ	o	o	o	o	—120
Pinus sylvestris			●	●	●	●	o	o	o	o	—120
Pinus strobus		●	●	●	●	Δ	o	o	o	o	—120
Pinus koraiensis		●	●	●	●	Δ	o	o	o	o	—120
Betula tauschii	●	o	o	o	o	o	o	o	o	o	—120
Salix sachalinensis	●	o	o	o	o	o	o	o	o	o	—120

o: Normal, Δ: Medium injured, ●: Serious injured or killed.
* Freezing resistance was represented by the lowest temperatures in which plants could survived without injury.

mental factors. For example, winter desiccation, late spring frost, severe cold in late fall and winter can cause injury either individually or in combination. Among them, one of the most important factors exerting a detrimental influence on growing forest trees is frost injury on the basal stem near the ground surface. In Japan, not only in the cold climates, but also in the southern mild climates frost injury of slender stems is often observed in acacia, cryptomeria, Japanese cypress, Japanese larch and Saghalien fir (Sakai, 1968 A). The frost injury of this type exercises a great negative influence upon the development of individual plants and plantations (Sakai, 1968 A). This type of frost injury has been studied by many investigators in various countries, especially by Day *et al.* (1934, 1945) and Eiche (1966). The basal stem near the ground surface is exposed to a remarkable fluctuation in temperature, especially to a sharp drop in temperature due to radiation at night (Sakai 1968 A). Also, it was found that the freezing resistance of the basal part on a stem was generally lower than that of the upper part in many forest trees, the difference between the two amounting to about 5° to 15° C. These facts suggest that the basal part on a stem is apt to suffer frost injury. In extremely hardy conifers, the difference in freezing resistance between the basal and upper parts of a stem becomes far less in winter, even in basal stems becoming resistant to freezing at temperatures as low as —50° to —70° C. However, in less hardy conifers, the freezing resistance of the basal stem even in winter is invariably much lower than that of the upper stem. In addition, the cambium and the adjacent phloem cells are most frost sensitive of the tissues on a stem. In Saghalien fir *(Abies sachalinensis,* climatic zone III), a native tree in Hokkaido, the basal stem and the buds often suffer frost injury in late spring and even early summer, and most of the cortical cells on the basal stem are killed, while the cambial initials still remaine alive and continue to differenciate in the new cortex and xylem (Sakai, 1968 A). The same fact was also observed in other seasons. These facts indicate that the cambium of hardy conifers has the highest freezing resistance of stem tissues even in spring, unlike the less hardy species native to mild climates. The senior author recently found that in Japanese and Saghalien larches, the basal stem, especially the cambium, of 1 to 2 year old seedlings is very sensitive to freezing, but in 3 to 4 year old seedlings it becomes highly resistant. As shown in *Table 2, Abies mariesii,* which is a typical subalpine conifer in Japan main island (latitude about 35 to 40° N), has a rather high freezing resistance in midwinter, while the increase of freezing resistance of the basal stem, especially the cambium is about 10 to 14 days later than that of Saghalien fir in Hokkaido. Because of this, the basal stem of the seedling often suffers frost injury in early winter in Hokkaido. The time of the bud opening of Saghalien fir is 14 to 20 days earlier than in Ezo spruce native to Hokkaido. For this reason, frost injury of the buds and the basal stem constitutes the most important limiting factor for plantation of this fir.

2. Relation between the degree of freezing resistance of conifers and the climate of their native habitats

It is a point of interest to investigate the variations in freezing resistance and ecotypes among climatic races of conifers. Especially this is so among the white and black spruce widely distributed in the United States and Canada. The winter buds of black and white spruce native to Central Alaska (College) survived freezing down to as low as —70° C at least, but those native to Canada (Nova Scotia, Chalk River) and Michigan did freezing to only —35° to —50° C. In the Pacific coastal regions of British Columbia and Washington and the adjacent islands, the following conifers grow: *Picea sitchensis, Thuja plicata, Pseudotsuga menziesii, Tsuga heterophylla, Chaemaecyparis nootkatensis, Abies grandis,* etc. However, in *Pseudotsuga* and *Thuja plicata,* the trees from the inland seed sources are known to be much hardier than those from the coastal area. Actually, *Pseudotsuga* from the inland origin is growing well even in Minnesota where the minimum temperature falls below —30° C.

Recently, the senior author found that in American larch, the leaf buds survived freezing down to —120° C, while the flower buds resisted freezing to about —60° C at most. Many trees can grow in the regions as far north as their natural range. However, it is known in many species that very little seeds produce in extremely northern part of the natural range. The freezing resistance of flower buds may be an important factor restricting the reproduction.

In a previous report (Sakai 1956), it was found that twigs of poplar *(Populus nigra)* wintering in Sapporo could survive freezing down to —150° C at least for 1 day, while the extremely hardy twigs suffered injury after continuous freezing at —30° C for 30 days. The inland areas of northern Siberia, the coldest area on earth in which the mean air temperature in winter ranges from —40 to —45° C and the extremes of temperature often go down to —55 to —60° C, support lush forests consisting of Dahurian larch, Siberian fir and spruce, birch, willow, poplar, et. The conifers native to Siberia and central Alaska are subjected to severe cold temperatures as low as —30° to —50° C for about 3 months. These conifers, even their flower buds, would probably have the ability to resist a continuous freezing at —30° to —50° C for a long time. In connection with this problem, it may be of interest to compare the ability to resist continuous freezing, especially of their flower buds, at —30° to —40° C using climatic races of the same species.

The conifers growing in climatic zones I to III form subalpine or boreal forests, and the conifers in zones V to VII constitute warm temperate forests. Black and white spruces and American larch which belong to zones I to II form the northern limit of tree growth in Canada and Alaska. Duhurian and Siberian larches, Siberian fir and spruce, Siberian pine etc., constitute the northern limit of conifers in Siberia. Conifers native to I to II have a far higher hardiness than those native to climatic zones IV—VI. An intimate relation between the freezing resistance and climates of the native habitat was observed among larch species.

The freezing resistance of some conifers native to the Himalayas such as Himalayan cedar *(Cedrus deodara),* pine *(Pinus griffithii)* and spruce *(Picea smithiana)* was found to be far less hardy than that of boreal species. It was also found that Himalayan larch *(Larix griffithii)* was the tenderest of larch species. In Nepal the coniferous zone is found at altitudes from 3,000 to 3,500 M. The timber line is nearly 3,500 M and in the higher altitudes, rhododendron and juniper form subalpine flora. In spite of such a high altitude in the Himalayas, the winter temperature is rather mild and humid and the climatic zones belong to V—VII.

In low and middle latitudes of mild climates in the northern hemisphere, the distributions of most coniferous species, especially *Picea, Larch, Tsuga* and *Abies* are now restricted in the high altitudes, possibly because of competition from the more tolerant hardwood species. In high and middle latitudes in which severe coldness prevails during winter, conifers cover widely the low lands. In the central Japan, spruces firs and Japanese larch are restricted their distribution to uplands over about 1,500M. The latitudial and altitudial distributions of conifers provides an interesting problem. To interpretate this ecological distributions of conifers, it seems necessary however to elucidate numerous interrelated physical and biological factors and paleo-ecological backgrounds.

3. Relationship between freezing and desiccation resistance

In the author's previous paper (Sakai, 1968 B, 1970 B) it was confirmed that the young conifers wintering in frozen soil and wind-swept areas were injured by desiccation due to an unbalance of water in leaves, small twigs and the upper stems which arose from the freezing of soil or stems for a prolonged period of two to three months. Further, in the winter of 1966 to 67, in the eastern part of Hokkaido, severe cold weather and a dry state prevailed throughout the winter. Besides, the snow cover was less than 5 to 10 cm in most of the plantations. Under these conditions, a large number of young forest trees such as Ezo spruce, Saghalien fir, white eastern pine, European spruce, American eastern arborvitae, especially those wintering on the southern slopes and sunny flat lands suffered untoward injury. In contrast, Scotch pine, Jack pine, eastern red pine, black spruce generally suffered slight or no injury (Sakai 1968 B, 1970 B).

It was demonstrated that a parallelism in hardy cells exists between desiccation or dehydration resistance (Siminovitch and Briggs 1953, Eguchi *et al.* 1966). Among several conifers native to Japan, the same relation can be observed. Namely, the plants with lesser freezing resistance such as Japanese cryptomeria and cypress which can survive freezing down to —20 to —25^0 C in winter, are more susceptible to desiccation injury than much hardier plants such as Saghalien fir and Ezo spruce. However, such conifers as white eastern pine and American eastern arborvitae can survive freezing below —120^0 C and even immersion in liquid nitrogen following pre-freezing to —50$^0 \approx$ —60^0 C, but they are susceptible to desiccation injury in winter under natural condition. Consequently, there seems but little parallelism between these two factors among different species. However, among the varieties of any one species, there seems to be an intimate correlation between freezing and desiccation resistance (Eguchi *et al.* 1966). Tropical willow *(Salix tetrasperma, Salix safsaf)* which were allowed to winter in Sapporo, could resist freezing down to about —40^0 C in late December (Sakai 1970 A). However, in the twigs and stems appearing above the snow surface, desiccation injury gradually proceeded from the tips of the twigs and stems appearing above the snow level were killed before late March, because the temperatures of the stems at 10 to 30 cm below the snow level remained below —4^0 C during the winter, which resulted in blocking water ascent from the root to the upper part. However, the willows native to both southern and northern Japan could withstand at the same wind-swept place (Sakai A). From these facts, winter dessiccation injury appears to constitute the greatest limiting factors for growth of plants, especially evergreen conifers.

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Summary

1. In saplings of less hardy species of conifers, the freezing resistance in the upper part of a stem was far greater than that in the basal part. On the other hand, in extremely hardy conifers, the difference in freezing resistance between the basal and upper parts of a stem became far less in winter. In general, the cambium of hardy species had the highest freezing resistance of stem tissues in winter.

2. One of the characteristics of the freezing resistance of *Abies, Picea* and *Tsuga* is that most of the terminal buds except *Picea mariana* and *Picea glauca* native to central Alaska resisted freezing to only about —40^0 C unlike their leaves and twigs.

3. All species of *Thujopsis, Chamaecyparis, Cryptomeria, Cedrus* and *Sequoia* did not resist freezing below —25^0 C.

4. Freezing resistant of *Pinus* widely ranged from —10^0 to —90^0 C, depending upon the climates of their native habitats.

5. An intimate relation between the freezing resistance of buds and the climates of their native habitats was observed in the species of larch.

In general, conifers native to severe cold climates had far higher resistance to freezing than those growing in warm climates.

6. The freezing resistance of the conifers native to the Himalayas was found to be far lesser than boreal species.

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Buchbesprechung

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2156 articles published up to 1930, including some books published between 1696 and 1837, are abstracted in 2 languages, Japanese and English, and arranged chronological order. This book covers many articles being little known to the world because of language barriers, and may be useful for forest geneticists all over the world. Historical development of Japanese forestry, which took a special course of development in view of forest genetics, could also be surveyed by looking through this book. T. Satoo