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Freezing Resistance of Herbaceous Plants¹

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Abstract About 30 species of herbaceous plants were mainly collected in Sapporo in early December. These plants were artificially hardened at -3°C for 20 or 30 days to increase their hardiness before determining the hardiness. *Elymus mollis* has the greatest freezing resistance of the species tested; the leaf and rhizome survived freezing down to -20°C . The rhizomes and crowns or winter buds of the following species, *Ranunculus acris*, *Plantago asiatica*, *Poa pratensis*, *Phleum pratense*, *Linaria vulgaris* survived freezing to -15°C . In general the herbaceous plants with adventitious roots and rhizomes have much greater hardiness than those with tap roots, and they have high ability to regenerate new roots from basal stems and rhizomes. The winter hardiness of less hardy species is characterized by the susceptibility of the roots or rhizomes to injury, which did not survive freezing below -5°C . Most of the seeds of *Rumex obtusifolius* and *Oenothera lamarckiana*, which have water content about 40% (fresh weight), germinated after freezing to -20°C .

Introduction

Many herbaceous plants are distributed in alpine and circumpolar regions as woody plants are (1). In herbaceous plants, winter hardiness of rhizomes, crowns, roots and seeds appears to be the principal factor limiting their natural ranges. We reported that most crowns of alpine perennial herbaceous plants survived freezing to the temperatures as low as -30 to -50°C (4). Most weeds of the herbaceous plants are so aggressive that they have colonized in wide ranges in the world. However, little or no information on the freezing resistance of herbaceous plants is available. To understand cold adaptation of herbaceous plants, winter hardiness was studied on plants wintering in Sapporo.

Materials and Methods

About 30 species of herbaceous plants wintering on our campus, or near Sapporo were collected in the period from December 1st to 12th, 1972. The meteorological data in the first ten days of December, 1972 are presented in Table 1. About 30 herbaceous species were used in this study.

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Table 1. Climatic data in Sapporo

	In the first ten days of December, 1972	Mean air temperature in January*
Mean air temperature	2.5	-5.1
Mean daily maximum	5.7	-1.1
Mean daily minimum	-0.4	-9.5

* 29 years (1941 to 1970)

Sapporo (latitude: 43°03'N, altitude: 17.2 m)

After washing the soil from around the roots, collected plants were enclosed in polyethylene bags. Since the freezing resistance of winter plants can change in response to previous environmental temperature (3), all plants were subjected at -3°C for 20 or 30 days to increase their hardiness and to overcome differences associated with sites of collection and hardening procedures. Frozen samples at -5°C were cooled at 5°C increments at daily intervals to successively colder temperatures to -30°C or below. At selected test temperatures, samples were held for 16 hrs, removed and thawed in air at 0°C . After thawing plants were placed at about 10°C for 10 days to evaluate viability. In some plants held at 10°C for 10 days, it was difficult to evaluate their viability with browning. Therefore, these plants were planted in sand in green house for one month to evaluate their viability and to observe their recovery. The lowest survival temperatures at which little or no injury was sustained were expressed as freezing resistance of each organ or tissue.

Results

1. Freezing resistance of herbaceous plants with a tap root

Freezing resistance of herbaceous plants with a tap root is shown in Table 2. The freezing resistance of these plants is characterized by the susceptibility of the tap roots to injury. Those plants sustaining injury to

Table 2. Freezing resistance of herbaceous plants with a tap root

Species		Freezing resistance ($^{\circ}\text{C}$)		
		Leaf	Leaf primordia	Tap root
<i>Sonchus oleraceus</i>	N	- 5	- 7	- 5*
	H	-15*	- 5*	- 5*
<i>Taraxacum platycarpum</i>	N	-10	-10	-10
	H	-10	- 7	- 7*
<i>Oenothera lamarckiana</i>	N	-20	-15	-10
	H	-15	-15	-10*
<i>Rumex obtusifolius</i>	N	- 7	- 7	- 7*
	H	- 7	- 7	- 7

* Injured at the temperature indicated

N: Before hardening; H: After hardening

tap roots cannot retain their viability as an individual plant, even though other organs and tissues remained alive, because these tap roots don't have the ability to regenerate new roots. Thus, their winter survival appears to be limited by the freezing resistance of tap roots.

2. Freezing resistance of annual herbaceous plants with fibrous roots

Freezing resistance of annual herbaceous plants with fibrous roots is shown in Table 3. *Sonchus oleraceus*, *Senecio vulgaris*, *Erigeron annuus* were marginally hardy to -5°C and little or no increase was observed after hardening. In perennial herbaceous plants such as *Plantago asiatica*, *Ranunculus acris*, *Dactylis glomerata*, *Lolium perenne* and biennial plants, *Poa annua*, the root was the least hardy organ. However, those plants sustaining injury to roots regenerated new roots from the segments in basal stems of which tissue was also well hardened. In *Poa annua*, *Plantago asiatica*, *Ranunculus acris*, the roots were also well hardened. However, in *Plantago lanceolata*, the hardening effect was negligible.

Table 3. Freezing resistance of herbaceous plants with fibrous roots

Species		Freezing resistance ($^{\circ}\text{C}$)		
		Leaf	Leaf primordia	Root
<i>Sonchus oleraceus</i>	N	-5	-7	-5*
	H	-5*	-5*	-5*
<i>Senecio vulgaris</i>	N	-5	-10 (Bud)	-5
	H	-7*	-7*	-7*
<i>Erigeron annuus</i>	N	-7	-7	-5
	H	-10	-10	-7*
<i>Plantago lanceolata</i>	N	-10	-7	-5
	H	-7*	-7*	-7*
<i>Plantago asiatica</i>	N	-10	-10	-5
	H	-10	-15	-15 (-15)***
<i>Ranunculus acris</i>	N	-7	-7	-5 (-7)***
	H	-15	-15	-13 (-15)***
<i>Poa annua</i>	N	-7	-7	-5* (-7)***
	H	-10	-13	-7 (-13)***
<i>Dactylis glomerata</i>	N	-10	-5**	-5* (-5)***
	H	-10	-10**	-7* (-10)***
<i>Lolium perenne</i>	N	-10	-10**	-5
	H	-7	-13**	-7* (-13)***

* Injured at the temperature indicated

** Small tiller bud

*** The lowest minimum temperature at which plants regenerated new root

N: Before hardening; H: After hardening

In the herbaceous plants with fibrous roots, the winter hardiness of the roots or basal stems from which roots are regenerated is most important.

3. Freezing resistance of herbaceous plants with rhizomes

Freezing resistance of herbaceous plants with rhizomes is summarized

in Table 4. In these plants, roots are easily regenerated from the rhizomes, basal stems and other tissues, and most of the rhizomes have very hardy buds. In *Petasites japonicus*, *Artemisia princeps*, *Solidago gigantea*, *Rudbeckia laciniata* which all belong to *Compositae*, the rhizomes and roots were marginally hardy to -7°C and only a slight hardiness increase was observed after hardening. On the other hand, most of the plants tested which belong to *Gramineae*, such as *Elymus mollis*, *Phragmites communis*, *Elytrigia*

Table 4. Freezing resistance of herbaceous plants with rhizomes

Species	Freezing resistance ($^{\circ}\text{C}$)						Development of new adventitious roots**
	Leaf	Leaf primordia	Winter bud	Rhizome	Root		
<i>Lactuca repens</i>	H		-10	-7	-5*	-5	
<i>Vicia japonica</i>	H		-10	-10		-10	
<i>Equisetum arvense</i>	H		-13 ^a , -10 ^b	-7		-7	
<i>Petasites japonicus</i>	N		-7 ^c , -5 ^d	-5	-5*	-5	
	H		-7 ^c , -7 ^d	-5	-5*	-7	
<i>Artemisia princeps</i>	N		-7	-5	-5		
	H		-7	-7	-7	-7	
<i>Solidago gigantea</i>	N		-10	-7	-5*	-5	
	H		-13	-7	-7	-7	
<i>Rudbeckia laciniata</i>	N	-10	-5	-5	-5*	-5	
	H	-7	-7	-7	-5*	-7	
<i>Rumex acetosella</i>	N	-5	-5	-5			
	H	-7	-7*	-7*			
<i>Linaria vulgaris</i>	N		-7	-7			
	H		-15	-15			
<i>Glehnia littoralis</i>	N		-13	-5			
	H		-15	-15			
<i>Miscanthus sinensis</i>	N	-15	-5*	-5*	-10	-10	
	H	-15	-5*	-5*	-10	-10	
<i>Phragmites communis</i>	N	-13	-10	-5	-5	-5	
	H	-15	-13	-15	-13	-7*	
<i>Elymus mollis</i>	N	-15	-10	-15	-10	-5	
	H	-20	-20	-20	-20	-13	
<i>Elytrigia repens</i>	N	-10	-10	-5	-5	-5	
	H	-7*	-15	-15	-15	-7	
<i>Phytolacca esculenta</i>	N	-10	-5	-5	-5	-5*	
	H	-7	-10	-10	-10	-7	
<i>Festuca drundinacea</i>	N	-10	-5	-5	-5	-5	
	H	-13	-7	-7	-7	-7*	
<i>Poa pratensis</i>	N	-10	-10	-5	-5	-5	
	H	-15	-17	-15	-13	-7*	
<i>Phleum pratense</i>	N	-18	-10	-13	-10	-10	
	H	-15	-15	-15	-17	-13	

* Injured at the temperature indicated

** The lowest minimum temperatures at which new adventitious roots developed from rhizomes and basal stems

a: Fertile buds; b: Vegetative bud; c: Flower bud; d: Leaf bud

N: Before hardening; H: After hardening

repens, *Phleum pratense*, *Poa pratensis* were greatly hardened and their rhizomes and buds were hardy to -13 to -20°C . However, in *Miscanthus sinensis*, the buds and leaf primordia were much less hardy, though the rhizomes and roots resisted freezing to -10°C . *Phytolacca esculenta* has a tuberous root on which many winter buds located. These buds and tuberous roots were not hardened. *Glehnia littoralis*, a seashore plant, occurs on the Japan Sea coast near Sapporo. The rhizomes extend to as deep as 1 m and there are many buds on the upper rhizomes. These rhizomes and buds were hardy to -15°C . *Lactuca repens* occurring on the same sand beach, has long rhizomes which expand several meters laterally, which resisted freezing to -10°C at least. Fertile and vegetative buds of *Equisetum arvense* survived freezing to -13 and 10°C , respectively. The rhizome and roots were hardy to -7°C .

Herbaceous plants collected in late January in Mito (latitude 36°N) were sent to Sapporo by air and were then hardened. Most of the samples were less hardy plants (Table 5). Four species were evaluated for hardiness in both Sapporo and Mito. However, only a slight difference was observed between them.

Table 5. Freezing resistance of herbaceous plants wintering in Mito

	Freezing resistance ($^{\circ}\text{C}$)				
	Leaf	Leaf primordia	Winter bud	Rhizome	Root
* <i>Artemisia vulgaris</i> var. <i>indica</i>	-5	-15	-10	-10	-5 (-10)**
<i>Capsella bursa-pastris</i>	-10	-7			-7
<i>Cerastium schizopetalum</i>	-10	-7		-13	-5 (-7)**
<i>Cirsium japonicum</i>	-5	-5			-5
<i>Gnaphalium multiceps</i>	-5	-5			-5
<i>Lamium amplexicaule</i>	-7	-7			-5
<i>Lepidum virginicum</i>	-10	-10			-5
<i>Oenanthe stolonifera</i>	-7	-7			-5 (-7)**
<i>Oxalis corniculata</i>	-5	-5		-7	-5
* <i>Poa annua</i>	-10	-7	-10		-7 (-10)**
<i>Potentilla freyniana</i>	-10	-5			-5
* <i>Senecio vulgaris</i>	-10	-10			-7
* <i>Sonchus asper</i>	-5	-5			-5
* <i>Stellaria media</i>	-5	-7		-10	-5
<i>Veronica didyma</i> var. <i>lilacina</i>	-5	-5			-5

Samples wintering in Mito (latitude: 36°N ; altitude: 29 m) were sent to Sapporo by air and were then hardened at -1°C for 14 days and -3°C for 7 days. The mean air temperature in Mito is 3.3°C

* The winter hardiness of the same species was evaluated in Sapporo.

** Adventitious roots developed from the plants frozen at the temperature indicated

The temperature fluctuations of different organs of a wintering plant *Oenothera lamarckiana* were measured with copper-constantan thermocouples and recorded. The leaf temperature near the ground level was the lowest (Table 6) and it was exposed to a remarkable fluctuation in temperature, especially when the plant was not covered with snow. Plant temperature is considerably affected by the height or the depth above or below the ground (2).

Table 6. Temperatures of different organs of *Oenothera lamarckiana*, which is wintering as rosette

Site of determination	Daily minimum temperature (°C)	
	December 12 1972 (Clear)	January 6 1973 (Clear)
Air temperature	-10.5	-13.0
Leaf surface	-12.7	- 2.0
Ground surface beneath the leaf	- 5.6	0.7
Leaf primordia	- 4.1	0.1
Root (5 cm below the surface)	- 4.1	0.1
Root (10 cm below the surface)	- 0.9	0.8
Snow cover (cm)	0	13

Temperature was determined with 0.2 mm copper-constantan thermocouple and recorded.

Freezing resistance of seeds from some herbaceous plants which have water contents from 35 to 40% was determined. Seeds were soaked in water at 10°C for 16 hr or at 0°C for 16 hr to raise their water content. Most of the moist seeds of *Rumex obtusifolius* and *Oenothera lamarckiana* germinated after freezing to -20°C for 1 day (Table 7). The seeds of *Hieracium* sp. and *Lepidium* sp. were collected at Yakutsk, East Siberia by the junior author and were soaked in water at 3°C for 3 days. Most

Table 7. Freezing resistance of moist seeds of some herbaceous plants

Freezing temperature (°C)	<i>Rumex obtusifolius</i>		<i>Oenothera lamarckiana</i>		
	A* (W.C: 36% FW)	B*	A (W.C: 34% FW)	B	C
- 5	91**	—	94	—	—
-10	90	—	96	—	—
-20	—	-40	74	97	100
-25	32	—	—	86	—
-30	—	—	—	—	—

* Method of water absorption

** Germination rate (%)

A: Soaked in water at 10°C for 16 hr; B or C: Soaked in water at 0°C for 24 hr (B) and for 10 days (C)

of these seeds germinated after freezing to -20°C for one day. These facts suggest that moist seeds of some herbaceous plants resist freezing to -20°C at least.

Discussion

In the tundra areas near Point Barrow, Alaska, mean air temperature in summer ranges from 3 to 4°C , and the soil remains melted only 20 to 30 cm below the ground level. However, the tundra area has abundant herbaceous plants, chiefly *Papaver redicatum*, *Potentilla emarginata*, *Pedicularis sudetica*, *Saxifraga*, *Luzula nivalis*, *Eriophorum polystachym*, *Petasites*, etc. (1). In midwinter the mean air temperature in Point Barrow ranges from -30 to -35°C and reach extremes of around -50°C . The temperatures at 50 to 100 cm below the surface of snow drifts are about -20 to -25°C , and those of frozen soil at 25 cm below the surface of bare tundra reach about -25°C . All plants wintering in a frozen state on the tundra thus encounter temperatures around -20 to -25°C , probably for several months (4, 6).

Some herbaceous alpine plants such as *Saxifraga laciniata*, *Potentilla miyabei*, *Primula cuneifolia*, *Pentstemon frutescens* were collected at 1900 m on Mt. Kurodake, Hokkaido. The crowns of these plants survived freezing to around -30 to -50°C and roots were hardy to -25°C (4). Maximum depth of the snow cover there was about 50 cm in late December. A minimum air temperature of about -43°C was recorded. Minimum temperatures of the frozen soil at 5- and 10-cm depths were -24 and -22°C respectively during the winter of 1968 and 1969 (4). The *Iris* sp. collected from the forest floor under Dahurian larch trees near Yakutsk by the junior author was hardy to -70°C in leaves and to -25°C in roots. These results suggest that the maximum hardiness of rhizomes and roots is around -25°C .

Studies on intraspecific differences in freezing resistance of trees among ecotypes and climatic races of widely ranging species indicate that almost without exception, trees from northern or colder provenances were more resistant than southern or warmer ones (5, 8). Climatic stresses are certainly prime factors in the natural selection pressure which have led to the evolution of adapted ecotypes and species. Thus, comparative study on intraspecific differences in hardiness of herbaceous plants which range widely in different climates is required.

Although this study dealt with winter hardiness, cold injury can be caused by several different environmental factors, e. g. late spring or early frosts, severe cold in late fall, winter and early spring, and winter desiccation. These stresses can cause injury either individually or in combination. Many reports suggest that the winter injury sustained by woody plants from southern sources was probably due to improper onset of cold acclimation rather than to an insufficient inherent ability to harden (8).

The freezing resistance of less hardy herbaceous plants is characterized by the susceptibility of crown, rhizome and root to injury. In hardy plants, these organs become more hardy, resisting freezing to -10 to -15°C . Also, hardy herbaceous plants are characterized by the ability to regenerate new roots from the rhizomes, basal stems, etc. In the ecological view, though the winter hardiness of these organs is important to winter safely for these plants, the depth of these organs from the ground level by which they could avoid effectively severe cold (7), and wintering of seeds are highly important. Many herbaceous plants, especially most weeds, have colonized over a wide range from circumpolar to tropics. To understand fully their strategy for cold adaptation, studies on timing of cold acclimation and winter hardiness of these plants as well as studies of how and where these seeds winter seems to be essential.

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