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Freezing Resistance of the Leaf of Pteridophyta Native to Hokkaido with Special Reference to the Phenology of the Leaf[1]

Toshiyuki SATO and Akira SAKAI[2]
佐藤利幸・酒井　昭

Abstract Freezing resistance of the leaf of 65 species of Pteridophyta native to Hokkaido was assessed with special reference to the phenology of the leaf. Average maximal freezing resistance of leaves of winter green, evergreen, semi-evergreen and summer green Pteridophyta were −33, −32, −19 and −2°C respectively. Leaves of the first, the second and most of the third Pteridophyta resisted freezing between −10 and −40°C in December, while leaves of the first three Pteridophyta were cold acclimated, more or less, from September to December. Meanwhile, as for the fourth one namely summer green ferns, their leaves were least or much less resisting to −5°C at most in mid-November, though the freezing resistance of their rhizomes increased; their leaves showed little or no increase in acclimation; leaves of many of them remain green before damaged by severe frost. One of the main factors limiting the phenology of their leaves seems to be winter cold; thus most of them are well adapted to cold climates by enhancing the freezing resistance of rhizomes, as has been suggested by data of ferns sampled in a temperate climates warmer than Hokkaido.

Introduction

About 130 species of Pteridophyta occur in Hokkaido. About 100 out of them are Pterophytina species different in habitats and distributional ranges (Sato unpublished), 67 species of which are summer green ferns, constituting a dominant life form of the ferns in Hokkaido (2), to the cold climates of which they have adapted themselves phenologically. It is known that winter frost injures leaves of evergreen ferns in warm temperate regions sometimes around natural northern boundaries and that *Coniogramme intermedia* and *Stegnogramma pozoi* change their life form from evergreen to summer green as they move from warm to cool temperate regions. Recently we also demonstrated that the freezing resistance of the rhizome considerably depends upon the habitat at which a fern occurs (4) and that gametophytes are stronger in freezing resistance than sporophytes in the life cycle of ferns native to Hokkaido (3, 5). In this connection, the freezing resistance

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[2] The Institute of Low Temperature Science, Hokkaido University, Sapporo, 060

of the leaf of the 65 species of Pteridophyta was assessed to look into the phenological adaptations in their life histories, as there is little or no information on it (4, 5).

Materials and Methods

In each distributional range demarcated between two successive natural boundaries, percentages of evergreen and summer green species of Lomariopsidaceae, Dryopteridaceae, Thelypteridaceae and Athyriaceae, which occur fairly commonly in Hokkaido, were expressed respectively against the total number of evergreen and summer green species, as are referred to Tagawa (7) and Shimura (6) and modified by the senior author (Fig. 1).

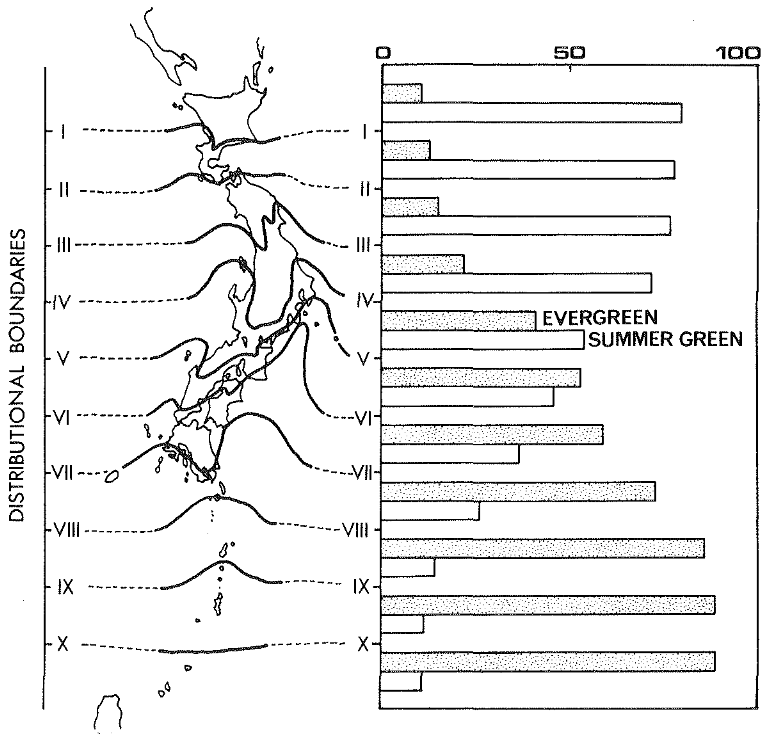

Fig. 1. Distributions of summer green and evergreen ferns in the Japanese Archipelago. DISTRIBUTIONAL BOUNDARIES: Main northern distributional boundaries referred to Sato and Sakai (1). Abscissa (%) was expressed as the percentage of the number of specific summer green (or evergreen) ferns against the total number of all ferns in each distributional range.

Phenology of the leaf of mature sporophytes was observed at about 350 different places in Hokkaido for four years beginning 1977. Based on the method previously reported (2), the degree of unfolding of a leaf was expressed as the pecentage of the area occupied by it against the total area to be occupied by the leaf at the unfolded stage ; the degree of decaying of a leaf was expressed likewise.

As shown in Fig. 2, *Polypodium fauriei*, a winter green fern, unfolds its leaf during late July and August, which decays during next June and July after retaining the green leaf in winter. *Struthiopteris niponica*, an evergreen fern, unfold its leaf during June and July, which decays from next July to October. *Polystichum retroso-paleaceum*, a semi-evergreen fern, unfolds its leaf during late May and June, which decays from October to Next June. The most popular life form of ferns growing in Hokkaido is the summer green such as *Lunathyrium pycnosorum*, whose leaf unfolds during late May and June and decays during October.

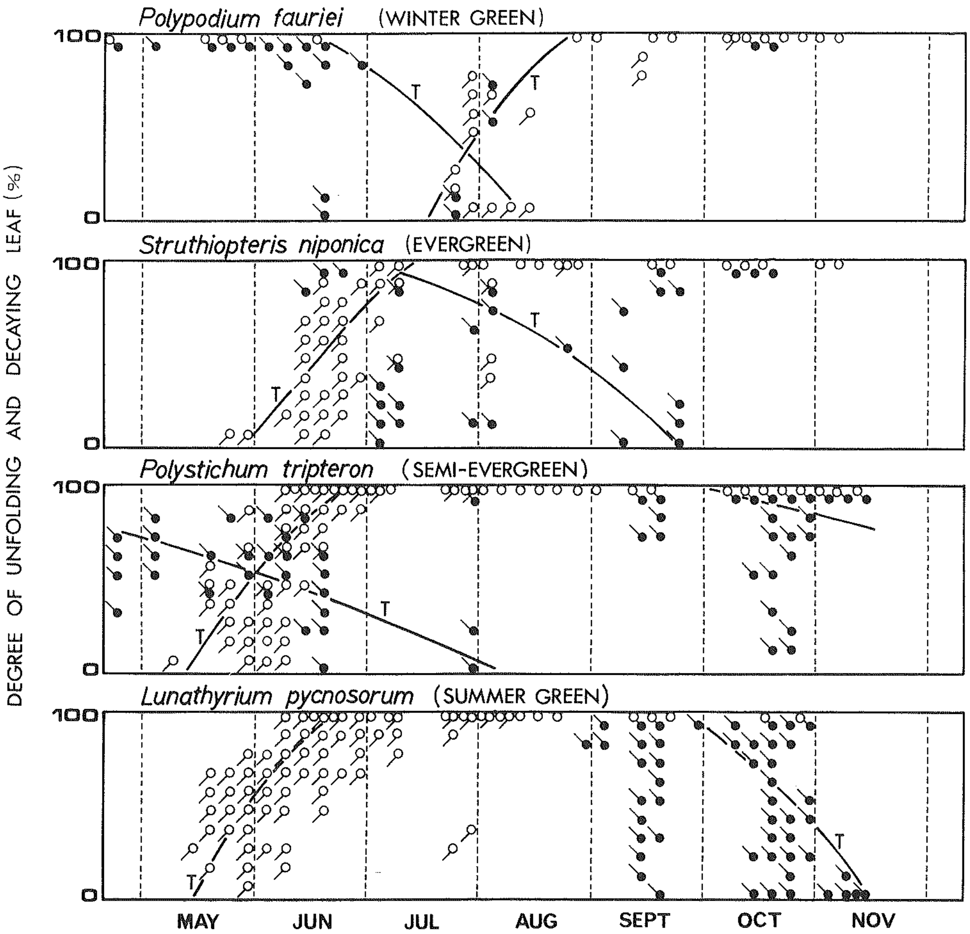

Fig. 2. Phenology of the leaf of some ferns in Hokkaido. ⚲ : Unfolding ; ⚲ : decaying. Degrees of unfolding and decaying were based on the method reported previously by Sato and Sakai (2). T : Phenology of the leaf at Mt. Teine

Table 1. Maximal freezingresistance of the leaf of Pteridophyta native to Hokkaido

Life form	Species	Freezing resistance (°C)	Life form	Species	Freezing resistance (°C)
Winter green	*Polypodium fauriei*	−40	Summer green	*Dryopteris austriaca*	−5
	Pleurosoriopsis makinoi	−40		*Dryopteris coreano-montana*	−5
	Sceptridium multifidum	−20		*Dryopteris monticola*	−5
Ever-green	*Equisetum hyemale*	−40		*Dryopteris laeta*	−5
	Lycopodium chinense	−40		*Polystichum microchlamys*	−5
	Lycopodium obscurum	−40		*Adiantum pedatum*	−5
	Lycopodium clavatum	−40		*Woodsia polystichoides*	−5
	Lycopodium annotinum	−40		*Stegnogramma pozoi*	−5
	Lycopodium complanatum	−40		*Cystopteris fragilis*	−5
	Selaginella helvetica	−40		*Matteuccia struthiopteris*	−3
	Selaginella shakotanensis	−40		*Equisetum arvense*	−3
	Lepisorus ussuriensis	−40		*Woodsia* sp.	−3
	Arachniodes mutica	−40		*Lunathyrium pycnosorum*	+
	Polypodium virginianum	−40		*Lunathyrium pterorachis*	+
	Dryopteris saxifraga	−40		*Athyrium brevifrons*	+
	Pyrrosia tricuspis	−40		*Athyrium vidalii*	+
	Lycopodium serratum	−30		*Athyrium deltoidofrons*	+
	Polystichum craspedosorum	−30		*Athyrium yokoscense*	+
	Asplenium incisum	−25		*Athyrium niponicum*	+
	Mecodium wrightii	−25		*Athyrium rupestre*	+
	Polypodium vulgare	−25		*Phegopteris polypodioides*	+
	Asplenium scolopendrium	−22.5		*Matteuccia orientalis*	+
	Struthiopteris niponica	−20		*Osmunda cinnamomeum*	+
	Arachniodes standishii	−12.5		*Osmunda japonica*	+
	Cyrtomium falcatum	−12.5		*Cornopteris crenulatoserrulata*	+
	Plagiogyria matsumureana	−10		*Thelypteris quelpaertensis*	+
Semi-ever-green	*Dryopteris fragrans*	−40		*Dennstaedtia wilfordii*	+
	Dryopteris crassirhizoma	−22.5		*Onoclea sensibilis*	+
	Dryopteris sabaei	−20		*Coniogramme intermedia*	+
	Polystichum braunii	−20		*Equisetum palustre*	+
	Polystichum tripteron	−17.5			
	Arachniodes miqueliana	−15			
	Polystichum retroso-paleaceum	−15			
	Dryopteris tokyoensis	−12.5			
	Dryopteris amurensis	−12.5			

+ : Sustained freezing injury at −3°C.

Freezing resistance was assessed with 65 species for five months starting September in 1977, 1978 and 1979. Most of the species were collected at Mt. Teine (alt. 300–500 m) near Sapporo, and some at more than ten locations in Hokkaido, where after they were transplanted in the nursery of the Institute of Low Temperature Science, Hokkaido University. Some excised leaves enclosed in polyethylene bags were frozen at $-5°C$ for a day. They were then cooled at the rate of about 5°C per 2-hr successively down to a specific temperature, the lowest being $-40°C$, at which they were allowed to stand for 12-hr at least; then they were removed from the freezer and were thawed in the air at 0°C. To evaluate the freezing resistance, thawed materials were placed in polyethylene bags at a room temperature at about 20°C for 3 to 5 weeks. The leaf which continued to retain the green colour as a whole was evaluated as having survived. Such a treatment, whereby freezing resistance was expressed as the lowest temperature at which the materials remained alive.

Results

Maximal freezing resistance of the leaf of 65 species is shown in Table 1.

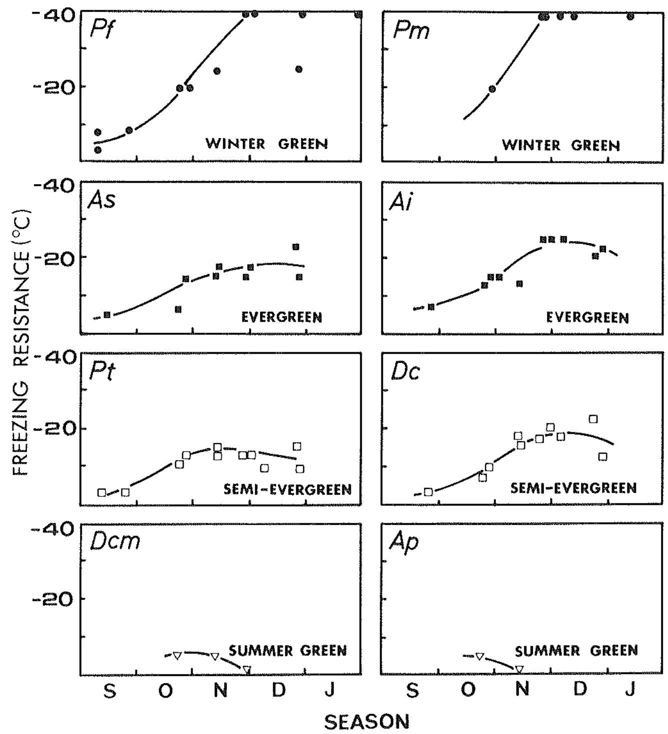

Fig. 3. Seasonal change in freezing resistance of the leaf. *Pf*: *Polypodium fauriei*; *Pm*: *Pleurosoriopsis makinoi*; *As*: *Asplenium scolopendrium*; *Ai*: *Asplenium incisum*; *Pt*: *Polystichum tripteron*; *Dc*: *Dryopteris crassirhizoma*; *Dcm*: *Dryopteris coreano-montana*; *Ap*: *Adiantum pedatum*

Only three of them are winter green ferns, two of them, *Polypodium fauriei* and *Pleurosoriopsis makinoi* having a freezing resistance below $-40°C$ in December. Most of Lycopodiacea species of 23 evergreen species of Pteridophyta resisted freezing down to $-40°C$; other evergreen species resisted freezing from -10 to $-40°C$. Almost all of the semi-evergreen species resisted freezing between -12.5 and -22.5; however, *Dryopteris fragrans* which occurred on cliffs, resisted freezing to $-40°C$. As for summer green ferns native to Hokkaido, 9 species resisted freezing to $-5°C$, 3 to $-3°C$ and 18 did not survive freezing even at $-3°C$.

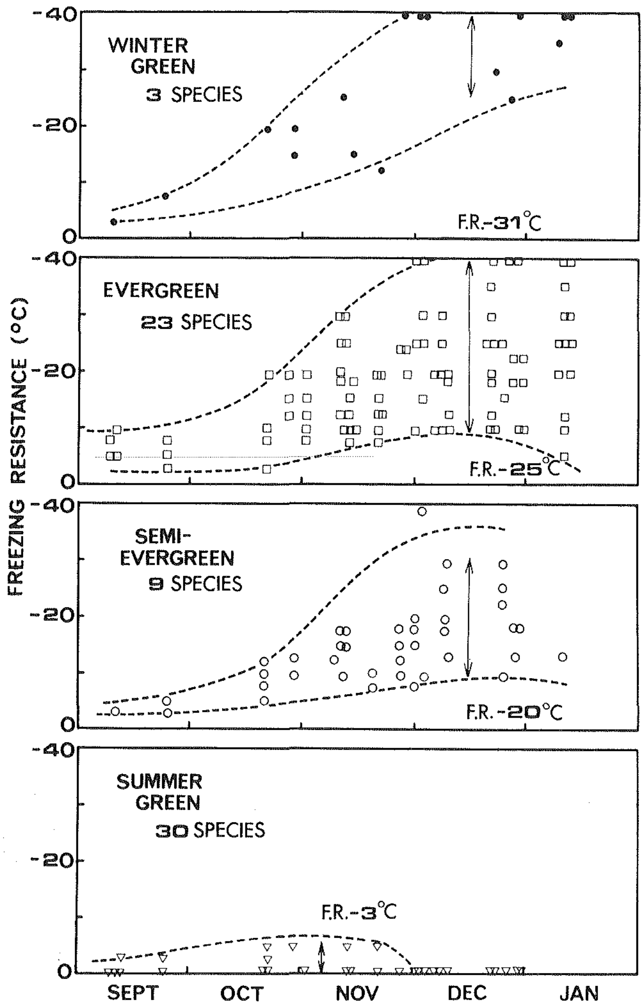

Fig. 4. Seasonal change in freezing resistance of the leaf of 65 species with 4 different life forms. The temperature preceded by F. R., which is defined as average freezing resistance, is the middle value between the upper and lower value of freezing resistance at a specific point of time, mid-December for winter green, evergreen and semi-evergreen and mid-November for summer green ferns.

Seasonal change in freezing resistance of the leaf of 8 species was assessed from September to January in 1978, 1979 and 1980. Some results are shown in Fig. 3. Winter green, evergreen and semi-evergreen ferns increased their freezing resistance of the leaf, more or less, from September to December. However, little or no cold acclimation was observed in summer green ferns; and even in December the leaf still remained least or less resistant to freezing, $-5^{\circ}C$ at most.

A relationship between phenology of the leaf and change in freezing resistance of the leaf of 65 species having the four different life forms is summerized in Fig. 4. Average freezing resistance in mid-December of winter green, evergreen, semi-evergreen and summer green ferns are -31, -25, -20 and $-3^{\circ}C$ respectively. A large variation in freezing resistance of the leaf ranging from -10 to $-40^{\circ}C$ in mid-December was found particularly in evergreen ferns and fern-allies. Species with green leaves in winter resisted freezing below $-10^{\circ}C$. On the other hand, summer green ferns could not resist freezing below $-5^{\circ}C$.

Discussion

Summer green ferns are predominant Pterophytina species in Hokkaido (2). It was also observed that the number of their species decreased with increasing latitudes in Japan, leading to a postulation that they are one of the adaptations to cold climates in this country. As previously reported, the freezing resistance of rhizomes and roots of ferns depends considerably upon the habitats at which they occur (4). This fact suggests that development of freezing resistance of ferns is related to the coldness of their habitats in winter. It was demonstrated in this paper that the freezing resistance of the leaf is related to the phenology of the leaf of Pteridophyta native to Hokkaido. The leaf of summer green ferns did hardly or marginally resist freezing to $-5^{\circ}C$ in early November. The leaf of *Osmunda japonica*, a typical summer green fern, decays before arrival of frost. Leaves of most of summer green ferns in Hokkaido, however, remain green leaves generally before damaged by severe frost from mid-October to mid-November. Thus, it seems likely that the time of decaying of the leaf of summer green ferns in Hokkaido depends upon the time at which severe frost comes. In this country *Coniogramme intermedia* and *Stegnogramma pozoi*, which are summer green species in cool temperate regions, are evergreen in warm temperate regions. Recently we confirmed that the winter leaf of *Coniogramme intermedia* collected at Owase, located on a warm Pacific seacoast, resisted freezing to -3 or $-5^{\circ}C$, which is comparable to the freezing resistance of summer green ferns native to Hokkaido. These facts suggest that one of the main factors limiting the phenology of the leaf of summer green ferns growing in Hokkaido is winter cold, meanwhile, the leaf of most of the evergreen and winter green ferns native to Hokkaido has evolved freezing resistance ranging from -10 to $-40°C$, similarly to the rhizome of summer green ferns (4). The senior author recently elucidated that evergreen ferns sampled in warm temperate regions resisted freezing to between -3 and $-7°C$. Thus winter cold appears to be the principal factor limiting the northward migration of the natural ranges of evergreen ferns in warm temperate climates which are less resistant to freezing.

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