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Cold and heat resistance of five species of *Sphagnum*

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Differences in the resistance of the chlorophyll-containing cells of the branch leaves of five species of the genus *Sphagnum* L. were revealed by direct freezing and heating. *Sphagnum baltícum* (Russ.) C. Jens., *S. subsecundum* Nees and *S. teres* (Schimp.) Ångstr. were shown to be more frost-resistant than *S. magellanicum* Brid. and *S. fuscum* (Schimp.) Klinggr. Differences in heat resistance between the mosses studied were smaller than those in cold resistance. However, there was correlation between the two responses. The thermo-resistance of *Sphagnum* mosses was shown to be strongly affected by environmental conditions.

Key words: cold resistance, heat resistance, *Sphagnum* mosses

INTRODUCTION

In Carelia, mires cover an area of 3.6 million hectares. About 2.5 million hectares are occupied by raised and transitional bogs with a continuous cover of *Sphagnum* L. (peat mosses, family Sphagnaceae), and about 1 mln ha by aapa mires in the central parts of which only hillocks and ridges are overgrown with peat mosses. However, the margins of the aapa mires are fully covered by mosses. There are 36 *Sphagnum* species in the mire flora of Carelia (Volkova & Maksimov 1993). In most Carelian mire ecosystems they are responsible for organic matter production and peat formation. Their distribution pattern is closely related to their high flexibility. *Sphagnum* mosses are moisture-loving and light-demanding plants, ecologically defined as hydro- and hygrophytes (Savich-Lyubitskaya 1952). Hydrophytes can endure intensive and prolonged moisture stress conditions, inevitable when they grow on more or less considerable microrelief elevations where an abruptly changing humidity regime is established. Hygrophytes can survive only a short and not very intensive desiccation (Botch & Smagin 1993).

Being poikilohydric plants, many mosses (class *Musci*) can withstand appreciable desiccation, accompanied by a rise in low and high temperature resistance, without losing their viability (Irmscher 1912, Lange 1955, Biebl 1962). However, the thermal resistance of mosses is seldom studied, and the available data are conflicting. There is evidence for substantial interspecific differences in the heat and cold resistance of mosses (Irmscher 1912, Lange 1955), but there appears generally an absence of such differences within a single species, even in plants growing under entirely different climatic conditions (Lange 1955, Biebl 1967, Larcher 1976). Conversely, Lange (1955) found the heat resistance of *Hypnum cupressiforme* Hedw. to depend on its habitat.

When studying the heat and cold resistances of leaf cells in four mosses, Antropova (1974, 1975) found that they were not affected by variation in air temperature from 3 to 22°C *in vivo* or by temperatures of 10 and 20°C maintained for 3 days *in vitro*.

The above evidence and the scarcity of relevant data on *Sphagnum* mosses, which behave as major peat-formers and play an important role in the circulation of organic matter and ash elements in mire biogeocoenoses, provided the basis for the present study. The main goal was to compare selected *Sphagnum* species growing in different environments in terms of the low and high temperature resistance of their cells.

MATERIAL AND METHODS

Five *Sphagnum* species, viz. *S. fuscum* (Schimp.) Klinggr., *S. magellanicum* Brid., *S. balticum* (Russ.) C. Jens., *S. subsecundum* Nees and *S. teres* (Schimp.) Ongstr. were studied (Savich- Lyubitskaya & Smirnova 1968). According to the data of Lopatin (1973) the first two species belong to the hummock-ridge hydrophilous-psychrophilous group and can endure intensive and prolonged desiccation throughout the growing period. The other three species belong to the hollow hyperhydrophilous group and can not endure prolonged moisture stress conditions.

Three sites were used for sampling in the Nenazvannoe mire located in the mid-taiga subzone, South Carelia. The mosses studied are plant cover dominants, but they grow under conditions differing slightly in mineral nutrition and water regimes.

Mire site 1 is an ombrotrophic ridge-hollow complex. Samples of *Sphagnum fuscum* were collected in ridge top microcoenoses, those of *S. magellanicum* were taken in low flat microcoenoses and those of *S. balticum* were collected in hollow microcoenoses.

Mire site 2 is a mesotrophic herb - *Sphagnum-Hypnum* hummock-flark complex. *Sphagnum subsecundum* was sampled in depression microcoenoses.

Mire site 3 is a mesoeutrophic herb-moss hummock-flark complex with scattered Scots pine (*Pinus sylvestris* L.). Samples of *Sphagnum fuscum* were taken in near-trunk hummock microcoenoses and those of *S. teres* were collected in the flark.

Moss samples 15–17 cm in height were placed in containers 30 × 40 cm × 20 cm high. Disturbance to the natural colony structure was reduced to a minimum. In the course of the experiment the plants were kept in the open air in a shady place unaffected by direct sunlight. Their cold and heat resistances were determined after one-week preadaptation under the above conditions. 3 cm of the moss shoot apices were removed and the small branches taken from its middle portion were subjected to 5 min freezing and heating to determine the lethal temperature (LT_{50}) of 50% of the chlorophyll-containing cells of the branch leaves (Drozdov *et al*. 1976). They were heated in Hepler thermostats and frozen in TZhR-02-20 thermostats. The required temperature was maintained with an accuracy of ± 0.1°C. The plasmolytic capacity of the cell cytoplasm provided the criterion of their viability. A sucrose solution (1 M) was used as a plasmolytic medium. After freezing and heating the small branches were placed into the solution and examined under the microscope for 5–10 min. An MBI-15 microscope with an APO 40× water-immersion lens and 10× eye piece was used.

The above method for the evaluation of thermo-resistance agrees, in principle, with the technique proposed by Streusand and Ikuma (1986) to estimate the degree of damage to moss caused by dehydration. Due to short testing action and quick noting of the damage result the method allows determination of protoplasm components resistance to direct temperature action when the consequences of destructive and homeostatic processes have not yet managed to fully display themselves. It is termed primary resistance not to be mistaken for the general resistance determined in a prolonged experience where the result depends on compound interaction of destructive, adaptive and repair processes in a cell (Alexandrov 1975). Primary cell resistance indices have a high coefficient of correlation with plant general resistance indices (Drozdov *et al*. 1980).

Two series of experiments were conducted, one in June and the other in July. In each series three independent experiments were replicated and in each experiment resistance was determined for six separate plants.

RESULTS AND DISCUSSION

This study shows that the *Sphagnum* species analysed differ in the cold and heat resistances of their leaf cells. In the first series of experiments performed in June (Fig. 1A) the highest frost resistance was displayed by *S. subsecundum*, *S. balticum* and *S. teres* which, in turn, differed in the lethal temperature of cells: – 21.8°C, – 21.0°C and – 19.6°C, respectively. The leaf cells of *S. magellanicum*, whose LT_{50} was – 16.6°C, proved to be least resistant to freezing. The cold tolerance of *S. fuscum* taken from a raised bog was slightly lower than that of *S. fuscum* sampled from a fen.

Differences in the heat resistance of the mosses studied were smaller than those in cold tolerance (Fig. 1A). However, the lethal temperature of cells was higher in *S. subsecundum* (60.3°) and lower in *S. magellanicum* (58.7°) than in the other species.

In the second series of experiments conducted in July the cold and heat resistance level of almost all the moss species studied was lower than that observed in June, but specific differences in resistance persisted (Fig. 1B). *Sphagnum subsecundum* and *S. balticum* whose LT_{50} were – 21.2 and – 19.7°C respectively, were most resistant to freezing, whereas *S. magellanicum* and *S. fuscum*, collected from a raised bog, had the same lethal temperature of cells (– 16.1°C) and were the least resistant. By then, specific differences in the heat resistance of the leaf cells had increased (Fig. 1B). The highest value was observed in *S. subsecundum* (59.1°C) and *S. teres* (58.6°C), and the lowest value was recorded in *S. magellanicum* (57.4°C) and *S. fuscum* taken from a fen (56.1°C).

If we compare the temperature showing cell resistance to freezing in the examined mosses (from – 16.1 to – 21.8°C) with that of some agricultural plants (from – 5°C to – 14°C), which had been determined by us earlier using the described method (Drozdov *et al.* 1984), considerable differences are found. The high frost resistance of mosses is most probably due to their capacity to resist dehydration (Scheibmair 1938, Biebl 1962, Larcher 1976, Wagner & Titus 1984) because dehydration is one of the main reasons for damage caused by extracellular ice formation in plant tissue (Samygin 1974, Levitt 1978). The ability of peat mosses to tolerate high degrees of desiccation is conditioned by their hydrolabile type of water exchange, which results in the cell protoplasm being more adaptable to rapid and considerable fluctuations in water supply and high cell sap concentration (Lang 1955, Larcher 1978).

The *Sphagnum* species tested were more resistant to low temperatures than cultivated plants and showed substantial interspecific differences in heat resistance. *Sphagnum subsecundum*, *S. balticum* and *S. teres* are more resistant to low temperatures, whereas *S. magellanicum* and *S. fuscum* are less tolerant.

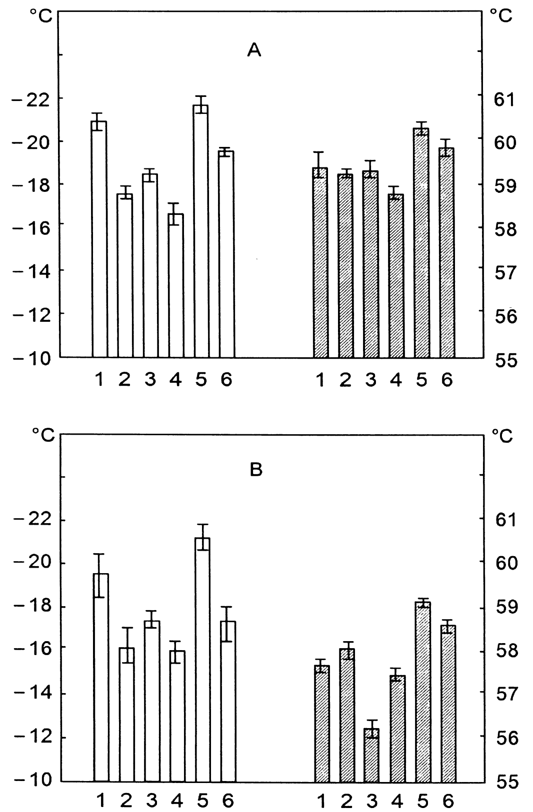

Fig. 1. Lethal temperature (LT_{50}) for chlorophyll-containing cells of branch leaves of five species of *Sphagnum* induced by freezing (left hand ordinate, white columns) and heating (right hand ordinate, dark columns). A determined in June, B determined in July. The data indicate mean values obtained from 18 replicates. The bars indicate 95% confidence interval. — 1: *S. balticum* (Russ.) C. Jens. — 2: *S. fuscum* (Schimp.) Klinggr. (raised bog). — 3: *S. fuscum* (fen). — 4: *S. magellanicum* Brid. — 5: *S. subsecundum* Nees. — 6: *S. teres* (Schimp.) Ångstr.

Differences in the cold tolerance of peat mosses are probably due to their provenance and environmental conditions. For example, the least tolerant species *Sphagnum magellanicum* originated from southern provinces where the climate is less severe than in the geographic origins of the cold-resistant *S. subsecundum* (Shlyakov 1961). The difference remained irrespective of the fact that the species characterised by high frost resistance grew in hollows, whereas *S. magellanicum* grew on hummocks. The microclimate of hollows is generally milder than that of hummocks. In hollows minimum spring temperatures are also higher, there are no night frosts, their snow cover is thicker and snow thawing begins later. On hummocks the snow starts to thaw earlier, but it proceeds more slowly. In autumn, maximum temperatures are higher and minimum temperatures are lower on hummocks than in hollows. Hummocks become frozen earlier than hollows (Eurola 1968). It seems likely that the adaptive effect which, undoubtedly, must have appeared when *S. magellanicum* grew on hummocks does not exceed genotype differences in resistance with more frost- resistant species growing in less severe microclimatic conditions.

The species generally differed in both cold and heat resistance. The positive correlation observed between their heat and cold resistances suggests the existence of common links that provide both low and high temperature resistance. Contrastingly, when the resistances of *Sphagnum fuscum* collected from a fen are compared with those of *S. fuscum* sampled from a raised bog in July, their cold tolerance and heat resistance are observed to be inversely related, whereas in June such a negative correlation was not revealed. The inverse relation is presumably due to the species-specific effect exerted on heat resistance by a combination of climatic factors characteristic of the period preceding the two sampling dates. Our experiments show that the cold and heat resistance of almost all the moss species studied was lower in July than in June, except for *S. fuscum* taken from a fen whose heat resistance remained constant. Consequently, variation in heat resistance observed in summer seems to be induced by variable environmental conditions, in particular temperature and water regime.

The influence of environmental conditions on the formation of intraspecific differences in heat resistance is traceable in *Sphagnum fuscum* growing in different ecological niches. Thus, plants collected from an eutrophic mire were more resistant to low temperatures than those growing on an ombrotrophic mire.

These experiments have led the authors to conclude that the leaf cells of *Sphagnum* mosses are highly resistant to freezing. Interspecific differences in the cold tolerance of the mosses studied were more substantial than those in heat resistance. In species markedly differing in cold resistance, such tolerance is positively correlated with heat resistance. Environmental conditions were shown to affect the thermo-resistance of peat mosses.

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