

Plant Activity under Snow and Ice, with Particular Reference to Lichens

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ABSTRACT. In polar ecosystems primary producers have to cope with the very limited living conditions of the harsh climate. Vascular plants in the Northern Hemisphere extend to the northern-most edges of the continents, but only two taxa are present as far south as the Antarctic Peninsula region in the Southern Hemisphere. Lower plants, lichens in particular, become more important with increasing latitudes and form the dominant element of the Antarctic vegetation. Based on recent investigations and literature, this paper discusses to what extent lichens are better adapted to snow and ice than vascular plants. Vascular plants in high latitudes have high freezing tolerances but are photosynthetically inactive in winter (e.g., evergreen coniferous species), while lichens in a highly freezing-tolerant stage can be active and productive under winter conditions. Vascular plants can be active under snow but have no photosynthesis if the tissue is frozen. Recent *in situ* measurements indicate that lichens are able to photosynthesize at temperatures below -10°C , apparently in the frozen state. It was also found that photosynthetic CO_2 exchange of dry thalli can be activated by snow during frost. Water uptake during winter was also recorded for coniferous trees at the arctic timberline. This uptake may reduce water stress in conifers but apparently has no relevance for metabolic activity. Water uptake from snow and metabolic activity at -10°C are possible for lichens because they are able to photosynthesize at water potentials lower than -20 MPa. Although lichens are adapted to be active in snow at low temperatures, strong light on clear days may inhibit the photosynthetic apparatus.

Key words: lichens, higher plants, water relations, life strategies, photosynthetic production, ice, snow

RÉSUMÉ. Dans les écosystèmes polaires, les producteurs primaires doivent s'accommoder des conditions de vie précaires dues à la rigueur du climat. L'habitat des plantes vasculaires de l'hémisphère boréal s'étend aux confins nordiques des continents, mais seuls 2 taxons sont présents à l'extrême sud de la région de la péninsule Antarctique de l'hémisphère austral. Plus la latitude augmente, plus les végétaux inférieurs, en particulier les lichens, prennent de l'importance et forment l'élément dominant de la végétation antarctique. S'appuyant sur des recherches et de la documentation récentes, cet article discute du degré auquel les lichens sont mieux adaptés à la neige et à la glace que les plantes vasculaires. Sous de hautes latitudes, ces dernières ont une tolérance élevée au gel mais sont inactives en hiver sur le plan de la photosynthèse (p. ex., les espèces conifériennes à feuilles persistantes), alors que les lichens, dans un état tolérant très bien le gel, peuvent être actifs et productifs en hiver. Les plantes vasculaires peuvent être actives sous la neige, mais elles ne font pas de photosynthèse si le tissu est gelé. Des mesures prises récemment *in situ* révèlent que les lichens peuvent faire la photosynthèse à des températures inférieures à -10°C , apparemment dans un état gelé. On a aussi trouvé que l'échange photosynthétique de CO_2 dans les thalles secs peut être activé par la neige durant le gel. On a aussi enregistré l'absorption d'eau durant l'hiver pour les conifères à la limite forestière arctique. Cette absorption peut réduire le niveau de stress hydrique dans les conifères, mais ne semble pas influencer sur l'activité métabolique. À -10°C , les lichens peuvent absorber l'eau à partir de la neige et avoir une activité métabolique en raison de leur capacité à réaliser la photosynthèse à des potentiels hydriques inférieurs à -20 MPa. Bien que les lichens soient adaptés pour être actifs dans la neige à de basses températures, une lumière excessive les jours dégagés peut empêcher l'appareil photosynthétique de fonctionner.

Mots clés : lichens, végétaux supérieurs, rapports hydriques, stratégies de survie, production photosynthétique, glace, neige

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INTRODUCTION

In regions with extremely cold winters the vegetation may include woody species and even trees (e.g., in northern parts of Canada and Siberia). These vascular plants are highly freezing tolerant in winter, but their existence depends on favourable summer conditions. In regions where summer heat is too low trees disappear and plants become small. For example, in the tundra of the High Arctic and in polar deserts vascular plants are as small as thallophytic (non-vascular) plants. Mosses and lichens are widely dominant in the vegetation of these regions. They also form the entire plant cover beyond a latitude of 68°C in the ice-free oases of the Antarctic continent. This demonstrates that non-vascular plants, particularly lichens, are superior to vascular plants when the summer season is very short and cold.

The absence of roots for water uptake and of epidermis and cuticula as a water-preserving protection characterizes lichens as poikilohydrous plants, which means that their metabolic activity (e.g., photosynthetic and respiratory CO_2 exchange) fully depends on the moisture conditions of the substratum and atmosphere (rain, fog, water vapour). This primitive organization, combined with a high desiccation

tolerance, allows an opportunistic life strategy, with the consequence of very retarded growth. This life strategy is advantageous in environments with limited soil water availability and extreme temperatures (Kappen, 1988).

Vascular plants (seed plants and ferns) that have controlled water relations (homoiohydrous plants) and freezing tolerance in winter suffer in such environments from water stress and heat deficit in summer. In this paper I discuss how recent progress, first, in measuring microclimatic conditions and CO_2 -exchange (the principle process for production and growth) *in situ* and, second, in understanding the limits of photosynthetic activity allows new insights into the ecophysiological performance of plants in cold environments and under winter conditions. Although major emphasis is given to lichens, the capacity of the photosynthetic apparatus in plants in general to operate under the influence of ice and snow will also be discussed.

PHOTOSYNTHETIC ACTIVITY AND FREEZING TOLERANCE

Trees of the boreal forest and of the arctic region are well known for their extremely high freezing tolerance (-40°C and lower), and many conifers, although evergreen, have

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completely inhibited photosynthesis in winter. However freezing tolerance is not necessarily coupled with inactivity of photosynthesis. Winter annuals, geophytes and many winter-green perennial herbs and woody plants are able to photosynthesize throughout the winter or to quickly resume photosynthesis in a warmer winter phase while in a highly tolerant (vital tolerance limit at -25°C and lower) stage (Parker, 1961; Bauer *et al.*, 1975; Levitt, 1980; Larcher and Bauer, 1981; Öquist and Martin, 1986). Rütten and Santarius (1988) discussed to what extent biochemical changes that cause freezing tolerance and influence photosynthetic activity are linked at the cellular and chloroplast level. They found that fatty acid desaturation does not primarily contribute to the increase in cold hardiness, but rather may allow the thylakoid membranes of the chloroplast to remain functional during freezing. On the other hand, it was calculated that the increase of cellular solute concentration during frost hardening is capable of reducing cell volume by osmotic dehydration, and this may inhibit photosynthesis (Kaiser, 1982).

The poikilohydrous cryptogams, such as lichens, that are usually subjected to drastic changes of osmolar concentrations and volume at any time reveal a combination of extremely high freezing tolerance and maintenance of full photosynthetic capacity. This is evident with lichens from polar regions as well as from moderate or subtropical provenances (Table 1) where photosynthesis was tested before and after a freezing experiment. The relatively quick recovery of full photosynthetic capacity was also shown after long-term cold treatments (Lange, 1966; Kallio and Heinonen, 1971) at -15 and -25°C respectively. Nonetheless, reports about natural frost injury to lichens in Europe and North America (Benedict, 1990, and cited literature) indicate that lichens are not entirely resistant to all freezing incidents, such as a rapid drop of temperature to -25°C for meltwater-soaked *Xanthoparmelia* species. Species containing *Trentepohlia* as the algal symbiont (photobiont) were generally more sensitive to freezing (-10 to -30°C) than a symbiosis with other photobionts (Nash *et al.*, 1987). Trentepohlioid lichens

TABLE 1. Freezing tolerance of lichens¹

Species	Region	Month	No injury if frozen	
			Rapidly	Slowly
<i>Caloplaca elegans</i>	Antarctica	Nov.	-196°C	-196°C
<i>Rhizoplaca melanophthalma</i>	Antarctica	Nov.	-196	-196
<i>Xanthoria mawsoni</i>	Antarctica	Nov.	-78	-196
<i>Buellia frigida</i>	Antarctica	Nov.	-78	-196
<i>Umbilicaria decussata</i>	Antarctica	Nov.	-78	-196
<i>Usnea capillacea</i>	New Zealand	Nov.	-78	-196
<i>Lobaria pulmonaria</i>	Central Europe	Sept.	-78	-196
<i>Cladonia rangiferina</i>	Central Europe	Sept.	-78	-196
<i>Ramalina maciformis</i>	Negev desert	Nov.	-78	-196
<i>Umbilicaria vellea</i>	Central Europe	Dec.	-50	-196
<i>Cladonia convoluta</i>	Mediterranean region	Mar.	-50	-50
<i>Sticta marginifera</i>	New Zealand	Nov.	-30	-50
<i>Roccella fucoides</i>	Mediterranean	Apr.	-10	-20
<i>Dendrographa minor</i>	California	Jun.	—	-12

¹Data from Kappen and Lange, 1972; Lange and Kappen, 1972; Nash *et al.*, 1987.

are mainly distributed in tropical and subtropical or mild coastal regions.

Photosynthesis at Temperatures below 0°C

Photosynthetic activity in evergreen woody and herbaceous species from temperate regions and high mountain habitats has been recorded at below-freezing temperatures between -2 and -9°C . As soon as ice formed in the tissues, photosynthesis ceased (Larcher and Bauer, 1981; Tieszen *et al.*, 1981; Kutsch and Kappen, 1990). The low temperature limit for respiratory CO_2 evolution was in many cases even slightly lower than for photosynthesis. Ice, having a diffusion resistance for CO_2 four times higher than water, forms a massive diffusion barrier in higher plant tissues. In lichens, photosynthesis was detectable at much lower temperatures (Table 2), and obviously also when ice was formed in the thallus. Lange (1965) assumed that in the lichen cortex a loose cluster was formed that did not inhibit CO_2 diffusion to the photobiont. Out of 30 lichen species from various climatic regions investigated in the laboratory, those with active photosynthesis at low temperatures were from southern Europe, followed by Antarctic species. The measurements by the infrared gas analysis (IRGA) method were confirmed by ^{14}C fixation analysis at -10.9°C in three species (Lange and Metzner, 1965). Considering the full temperature range of net photosynthesis (Fig. 1), lichens, particularly from polar regions, are well adapted to low temperatures having their optimum temperature within a range between 0 and 10°C (Lange, 1965; Lange and Kappen, 1972; Kappen and Friedmann, 1983). Thus they resemble extremely psychrophilous (cold-adapted) microorganisms.

Field measurements in Europe during winter and in Antarctica confirm that lichens carry out photosynthesis at temperatures between -6 and -17°C under natural light and moisture conditions (Table 2).

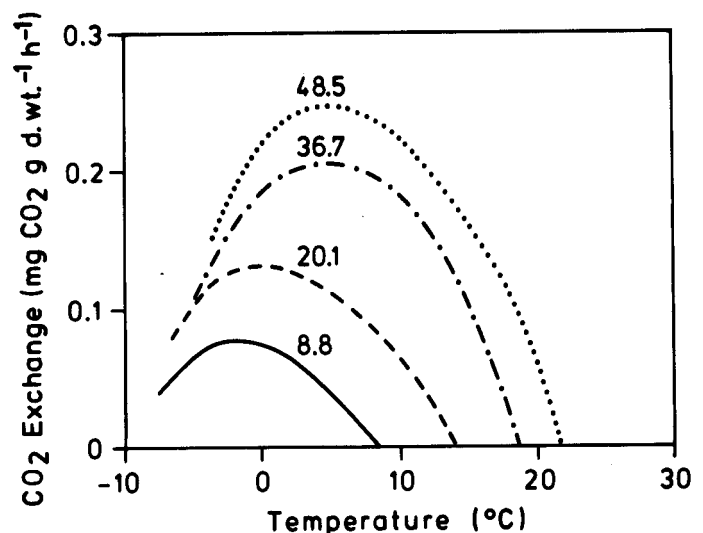


FIG. 1. Net photosynthesis ($\text{mg CO}_2/\text{g dry weight} \times \text{hour}$) of an Antarctic fruticose lichen *Neuropogon acromelanos* (possibly synonymous with *Usnea antarctica*) from near Hallett station, southern Victoria Land. The graph shows the photosynthetic responses to temperature ($^{\circ}\text{C}$) and to irradiance (figures in kLux at the curves). After Lange and Kappen, 1972.

TABLE 2. Lowest recorded temperatures for photosynthetic activity of lichen species measured in the laboratory or in the field

Species	Lowest temperature observed for photosynthetic activity (°C)	Method	Provenance	Authors
A) Laboratory measurements				
<i>Cladonia alpicornis</i>	-24	IRGA closed cycle	Southern Germany	Lange, 1965
<i>Cladonia convoluta</i>	-22	IRGA closed cycle	Southern France	Lange, 1965
<i>Xanthoria parietina</i>	-18	IRGA closed cycle	Southern Finland	Kallio and Heinonen, 1971
<i>Cetraria nivalis</i>	-20	IRGA closed cycle	Kevo, Finland	Kallio and Heinonen, 1971
<i>Neuropogon acromelanos</i> (<i>Usnea antarctica</i>)	-18.5	IRGA closed cycle	Antarctic continent	Lange and Kappen, 1972
<i>Xanthoria mawsoni</i>	-16.5	IRGA closed cycle	Antarctic continent	Lange and Kappen, 1972
<i>Lecanora melanophthalma</i>	-16.5	IRGA closed cycle	Antarctic continent	Lange and Kappen, 1972
B) Field measurements				
<i>Umbilicaria aprina</i>	-17	IRGA, minicuvette	Antarctic continent	Schroeter, 1992 unpubl.
<i>Usnea sphacelata</i>	< -10	IRGA open system	Antarctic continent	Kappen, 1989
<i>Usnea submollis</i>	-10	Ivanov-method CO ₂ absorption and Ba(OH) ₂ titration	Sinaia Mts., Rumania	Atanasiu, 1969
<i>Ramalina farinacea</i>	-9	Ivanov-method	Sinaia Mts., Rumania	Atanasiu, 1974
<i>Letharia vulpina</i>	-9	Ivanov-method	Sinaia Mts., Rumania	Atanasiu, 1974
<i>Hypogymnia physodes</i>	-6	IRGA open system	Solling, Germany	Schulze and Lange, 1968

The Role of Snow and Ice

Higher plants may well exist under snow and carry out photosynthesis if not frozen, for example, during the growing season either in high mountains (*Ranunculus glacialis*: Moser, 1969) or in the tundra where the temperature may drop to -11°C (Tieszen *et al.*, 1981). Conditions under snow may also be suitable for photosynthetic production during winter if there is sufficient light. Winter annuals may be productive under snow in winter, although *in situ* measurements of photosynthesis are difficult under these conditions. Snow reduces temperature extremes, provides a moist environment and allows light transmission that is sufficient for moderate photosynthetic activity (Marchand, 1987; Kappen and Breuer, 1991). Plant activity has been observed mainly in late winter or early spring. Spring "ephemerals" (mostly geophytes) have a remarkable capability to grow, to produce leaves and flowers or even to germinate from seed under a layer of snow up to 50 cm (Salisbury *et al.*, 1973).

We do not know whether and to what extent these developmental processes of plants are accompanied by photosynthetic production. However, Kimball and Salisbury (1974) expect that *Claytonia lanceolata* leaves photosynthesize only when the snow is mostly gone. Chlorophyll content slowly increased when snow depth decreased, and air spaces in the leaves and stomata were formed only when the snow was below 10 cm. In arctic herbaceous plants Tieszen (1974) observed a lack of the full complement of enzymatic activity for photosynthesis before snow melt.

Our knowledge about seasonal changes of photosynthetic activity in lichens from cold regions is limited. Atanasiu (1971) observed photosynthesis of lichens in winter at temperatures below 0°C. However, Gannutz (1970) reports that lichens on the Antarctic Peninsula (65°S) have only respired during winter when subjected to -6°C under a protective snow layer and that photosynthesis was lower in spring than under similar conditions in the Antarctic summer. Do they really rest like higher plants?

On the Antarctic continent the moist and thus, for lichens, photosynthetically relevant period is similar to a winter of cool temperate regions with daily frosts. Thallus temperatures rarely exceed 8°C when moist (Kappen, 1985), and snow is almost the only source of water. In the water vapour-saturated environment under snow lichens are able to gain moderate to high thallus water content (Fig. 2). Yet it still needs to be proved to what extent here an oversaturation of the thallus causes a depression of the photosynthetic rate (see Lange, 1980; Kappen *et al.*, 1988). Covered by a layer of 1-4 cm of snow, lichens are able to photosynthesize (Kappen *et al.*, 1991). Meltwater is likely to be taken up as a consequence of heat absorption by the blackish thalli of the fruticose lichen *Usnea sphacelata* while snow rests on the thallus if the air temperature is near 0°C and irradiance is

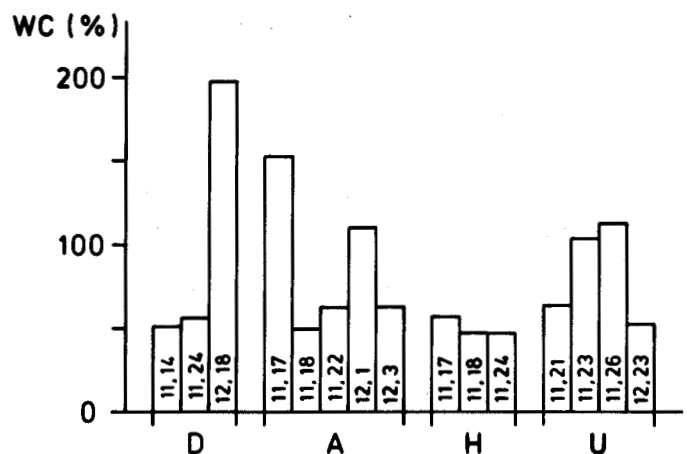


FIG. 2. Thallus water content of the fruticose lichen *Usnea sphacelata* measured near Casey station, Wilkes Land, East Antarctica. The bars are average values of 7-10 different thalli gravimetrically measured in a series of indicated days in November and December. Water contents as a result of snowfall: D = during the snowfall; A = immediately after snowfall has stopped; H = 2-4 hours after snowfall has stopped; U = thalli taken from underneath a snow layer of 10-20 cm. After Kappen and Breuer, 1991.

high. Light intensity under snow layers up to 15 cm depth is high enough to allow nearly light-saturated photosynthetic rates at least during a period of a few hours on sunny days (Kappen and Breuer, 1991). During the peak summer season in Antarctica the snow melts at places where lichens colonize and precipitation is very scarce for 1-2 months. Consequently Antarctic lichens can be productive during winter if light is not a limiting factor and during summer if drought is not a limiting factor.

Water Uptake during Frost

On the Antarctic continent continuous frost periods (below -5°C air temperatures) over several days are not rare in the wet season. Ice formation would block CO_2 exchange in higher plants, but frozen lichens, according to the above findings, should be active while the cellular liquid that is rich in polyols (Hill, 1976) is presumably supercooled. Field experiments in Wilkes Land (Antarctica) during the early season (Kappen, 1989) show that these lichens started photosynthesis when snow became attached to a previously air-dry thallus during a blizzard (Fig. 3). Permanent frost and low irradiance must have prevented melt processes at the thallus surface. Net photosynthesis was still not at its minimum level when the temperature reached -10°C (Fig. 4). Respiration was significant during the night and the light compensation point (threshold light intensity) for net photosynthesis in the early morning was at a low quantum flux density. At this time of day the radiative energy was too low to cause melt processes in the snow on the thallus surface. It has to be assumed, therefore, that water vapour from snow was taken up by the thallus at below 0°C temperatures.

The amount of water necessary to start photosynthesis is low for poikilohydrous lichens, as was earlier demonstrated with desert lichens (Lange, 1969). Aerophilic green algae and lichens (Bertsch, 1966a,b; Lange, 1969; Nash *et al.*, 1990) became photosynthetically active if the thalli were in equilibrium with water potentials of about -35.0 to



FIG. 3. *Usnea sphacelata* near Casey station: the previously air-dry thallus is covered by snow crystals during a snow storm and becomes photosynthetically active.

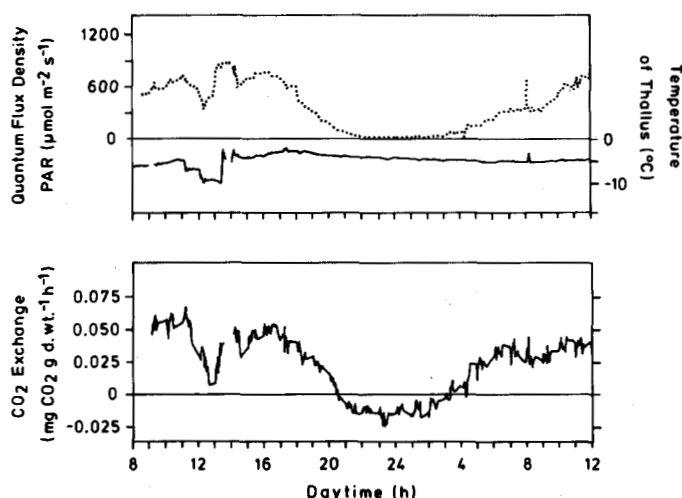


FIG. 4. Diurnal course of net photosynthesis of *Usnea sphacelata* ($\text{mg CO}_2/\text{g dry weight} \times \text{hour}$) near Casey station under the influence of snow and under natural light (PAR) and temperature ($^{\circ}\text{C}$) conditions. Photosynthesis still positive at -10°C . After Kappen, 1989.

-20.0 MPa (about 77-85% r.h.). The enormous capacity of the photosynthetic apparatus to operate under severe cellular water stress is, however, known not only for algae but also for leaves of cormophytic plants (Table 3), such as spinach and *Valerianella* (Bertsch, 1967) and is evident from experiments with isolated chloroplasts (Santarius and Heber, 1967; Cox, 1975).

Water uptake from snow at freezing temperatures may be possible due to a steep water potential gradient between the poorly hydrated lichen and the water-saturated snow system. At -5°C the frozen water may be at a water potential status equivalent to about -5 MPa (Fig. 5). Another precondition for water uptake is that the thallus should be as cold as the snow or colder. Although we could not measure these temperatures, the air turbulence during the measurements (Fig. 4) would have caused heat dissipation from the lichens.

Findings that coniferous trees at the timber line were able to gain water in winter during frost (Marchand, 1987; Scott and Hansell, 1991) may revise the current view that winter-time is only a period of water loss. Marchand and Chabot (1978) demonstrated the supercooling effect of strong wind that reduces water loss of plant tissues. Such effects are insignificant for metabolic activity but may prevent extreme water stress.

TABLE 3. Threshold water potentials allowing 10% and 50% of maximum photosynthetic CO_2 uptake¹

	10% of maximum CO_2 uptake M Pa	50% M Pa
<i>Apatococcus lobatus</i> (coccal algae)	36.0	6.2
<i>Ramalina thrausta</i> (lichen)	23.6	9.8
<i>Evernia prunastri</i> (lichen)	20.3	6.2
Herbaceous plants	2.8 - 4.5	2.0 - 2.5
Woody plants	5.9 - ?	3.8 - 5.0

¹After Bertsch, 1966a,b; Kaiser, 1982.

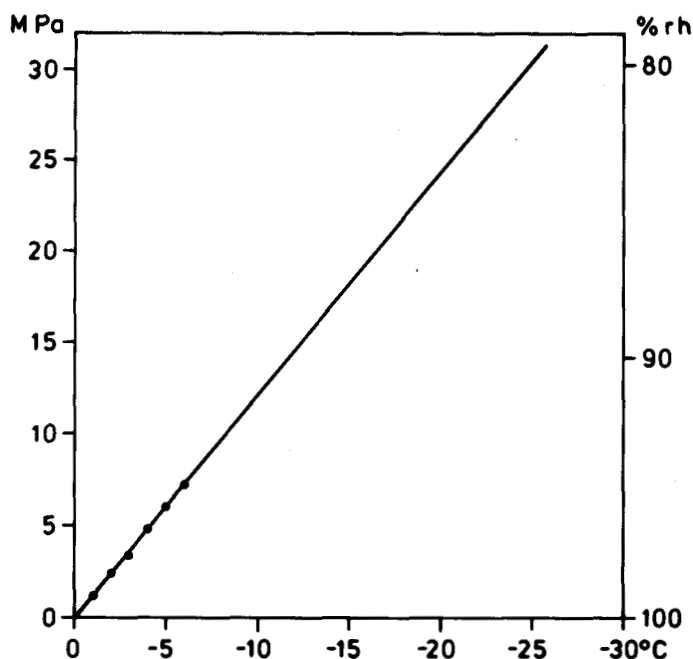


FIG. 5. Relation between freezing-point depression of aqueous solutions and corresponding water potentials (MPa) and relative air humidity (%). Data from Bertsch, 1966a; Walter and Kreeb, 1970.

Energy Use for the Photosynthetic System at Low Temperatures

Reduced photosynthetic production during the cold season is not only a consequence of heat- or light-limited metabolism; it is also caused by an inhibitory effect to the photosynthetic apparatus due to photoinhibition. This has been shown for evergreen conifers (Öquist, 1983; Öquist and Ögren, 1985), as well as for winter-green herbaceous plants (Öquist and Huner, 1991). At low or freezing temperatures light is mostly excessive for the capacity of the photosynthetic apparatus, and this can be so even at $50 \mu\text{mol photons}\cdot\text{m}^{-2}\text{s}^{-1}$ (Öquist and Huner, 1991). In terms of productivity photoinhibition has a negative effect. However, it also has a positive effect because it prevents photodestruction of the thylakoid membranes in the chloroplasts by efficiently dissipating extensive excitation of the photosynthetic apparatus (Demmig-Adams *et al.*, 1990b; Ottander and Öquist, 1991).

Photoinhibition, well known in bryophytes (Valanne, 1984; Kappen *et al.*, 1989), seems also to be common in lichens (Demmig-Adams *et al.*, 1990a), although many species appear to be light-protected by a dark pigmentation of the thallus. Photoinhibition is insignificant during snowfall, when heavy clouds reduce irradiance, or below deep snow layers. On clear, sunny days lichens are usually dry and inactive and thus widely protected against effects of sun radiation. However, photoinhibition affected the photosynthetic rate if the thalli of *U. sphacelata* were freshly covered by a snow layer of 1-3 cm and irradiance rose above $500 \mu\text{mol photons}\cdot\text{m}^{-2}\text{s}^{-1}$ (Kappen *et al.*, 1991). This situation may last for several hours or days at sites of continental Antarctica and perhaps also in the High Arctic. Although photoinhibition is reversible and recovery of full photosynthetic capacity occurs when light is minimal, it forms one mechanism among

others, such as freezing tolerance, that retard production and growth but provide fitness of the lichens in their harsh environment.

CONCLUSIONS

The photosynthetic apparatus, fundamental for primary production in plants, is principally adapted to function within a wide range of low temperatures and low moisture conditions. This potential is less apparent in most vascular plants because their more complicated organization and controlled water relations set a higher threshold of sensitivity to extreme environmental conditions. Adapted to function in a highly balanced water regime, the photosynthetic processes of vascular plants depend on a water supply system that can be blocked by freezing, the function of stomata, hormonal control, osmotic conditions and sensitivity to excessive photonflux density. Dormancy is a very efficient strategy in climates with extreme winter cold. Nevertheless, growth or photosynthetic activity at various stages can be observed in some evergreen species during mild winter periods and particularly in late winter before snow disappears. Photosynthetic activity depends on occasions when no ice is formed in the tissues and on the intactness of the chloroplasts, which may be reversibly injured in many coniferous species or are not mature, as in spring ephemerals, until snow cover is very shallow.

By contrast, lichens, having no roots, water-conducting systems, stomates or water control, are far more capable of challenging the capability of their photosynthetic systems. Fully dependent on external moisture conditions, they should be active during wintertime in regions with dry summers. Their capability to photosynthesize during frost, apparently independent of ice formation, and their immediate recovery after heavy freezing are remarkable. In contrast to vascular plants, they are activated at low water potentials when taking up water vapour, even when frozen. This enables lichens to exist in Antarctic regions, where snow and ice are the sole water sources during the growing season. Photosynthesis can be maintained at temperatures far below -10°C during the austral summer period and happens to be reduced by the effect of photoinhibition. It is not yet established quantitatively how lichens become hydrated by snow or to what extent the photosynthetic apparatus is inactivated during the dark winter period and whether they need a recovery period thereafter.

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