Overwintering ecology of northern field layer plants – snow and photosynthesis in *Vaccinium vitis-idaea* L.

Robin Lundell

Department of Biosciences
Faculty of Biological and Environmental Sciences
University of Helsinki
Finland

Academic dissertation

To be presented for public examination with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki in Auditorium XV of the University main building, Unioninkatu 34, fourth floor, on 16 September 2011 at 12 noon.

Cover photo: *Vaccinium vitis-idaea* and *V. myrtillus* exposed by melting snow in spring. Evo, Finland, March 2005. Robin Lundell.

List of original articles

This thesis is based on the following research articles, which are referred to in the text by their roman numerals:

I   Lundell, R., Saarinen, T., Åström, H., & Hänninen, H. 2008: The boreal dwarf shrub *Vaccinium vitis-idaea* retains its capacity for photosynthesis through the winter. Botany 86: 491–500. (© 2008 NRC Canada or its licensors. Reproduced with permission).

II Saarinen, T., Lundell, R. & Hänninen, H. 2011: Recovery of photosynthetic capacity in *Vaccinium vitis-idaea* during mild spells in winter. Plant Ecology 212: 1429–1440.

III Lundell, R., Saarinen, T. & Hänninen, H. 2010: Effects of snowmelt on the springtime photosynthesis of the evergreen dwarf shrub *Vaccinium vitis-idaea*. Plant Ecology & Diversity 3: 121–130.

IV Saarinen, T. & Lundell, R. 2010: Overwintering of *Vaccinium vitis-idaea* in two Sub-Arctic microhabitats: a reciprocal transplantation experiment. Polar Research 29: 38–45.

V   Rasmus, S., Lundell, R. & Saarinen, T. 2011: Interactions between snow, canopy and vegetation in a boreal coniferous forest. Plant Ecology & Diversity 4: 55–65.

The articles are reprinted with the kind permission of NRC Research Press (I), Springer Science + Business Media (II), Taylor & Francis (III and V), and John Wiley & Sons (IV).

Contributions:

	I	II	III	IV	V
Study design	RL, TS, HH	RL, TS	RL, TS	TS, RL	SR, RL, TS
Experiment setup	RL, TS	RL, TS	RL, TS, HH	TS	SR, RL, TS
Field and laboratory measurements	TS, RL, HÅ	RL, TS	RL, TS	RL, TS	SR, RL, TS
Modelling, programming	RL				RL
Data calculations and statistical analyses	RL, TS	TS, RL	RL	TS, RL	RL, TS
Manuscript	RL, TS, HH, HÅ	TS, RL, HH	RL, TS, HH	TS, RL	SR, RL, TS

Abbreviations: RL Robin Lundell, TS Timo Saarinen, HH Heikki Hänninen, HÅ Helena Åström, SR Sirpa Rasmus.

Contents

Overwintering ecology of northern field layer plants – snow and photosynthesis in *Vaccinium vitis-idaea* L.

Abstract

Winter is a significant period for the seasonality of northern plants, but is often overlooked when studying the interactions of plants and their environment. This study focuses on the effects of overwintering conditions, including warm winter periods, snow, and snowmelt on boreal and sub-Arctic field layer plants. Wintertime photosynthesis and related physiological factors of evergreen dwarf shrubs, particularly of *Vaccinium vitis-idaea*, are emphasised. The work combines experiments both in the field and in growth chambers with measurements in natural field conditions. Evergreen dwarf shrubs are predominantly covered by snow in the winter. The protective snow cover provides favourable conditions for photosynthesis, especially during the spring before snowmelt. The results of this study indicate that photosynthesis occurs under the snow in *V. vitis-idaea*. The light response of photosynthesis determined in field conditions during the period of snow cover shows that positive net CO_2 exchange is possible under the snow in the prevailing light and temperature. Photosynthetic capacity increases readily during warm periods in winter and the plants are thus able to replenish carbohydrate reserves lost through respiration. Exposure to low temperatures in combination with high light following early snowmelt can set back photosynthesis as sustained photoprotective measures are activated and photodamage begins to build up. Freezing may further decrease the photosynthetic capacity. The small-scale distribution of many field layer plants, including *V. vitis-idaea* and other dwarf shrubs, correlates with the snow distribution in a forest. The results of this study indicate that there are species-specific differences in the snow depth affinity of the field and ground layer species. Events and processes taking place in winter can have a profound effect on the overall performance of plants and on the interactions between plants and their environment. Understanding the processes involved in the overwintering of plants is increasingly important as the wintertime climate in the north is predicted to change in the future.

Abbreviations

ATP = Adenosine triphosphate

CO_2 = Carbon dioxide

D1 protein = "Diffuse-1" protein

ELIP = Early light induced protein

F_v/F_m = Variable fluorescence / maximum fluorescence

HLIP = High light induced protein

IRGA = Infrared gas analyser

NADPH = Reduced nicotinamide adenine dinucleotide phosphate

PAR = Photosynthetically active radiation

P_{max} = Theoretical maximum light-saturated rate of photosynthesis

PsbS = Photosystem II protein S

RuBisCO = Ribulose bisphosphate carboxylase-oxygenase

UV = Ultraviolet (radiation)

UV-A = Ultraviolet radiation with wavelengths between 315 and 400 nm

UV-B = Ultraviolet radiation with wavelengts between 280 and 315 nm

Introduction

Northern plants and winter

Northern plants are adapted to large variation across seasons, with cold winters and warm summers. Different plant growth forms possess different ways of surviving the adverse times of the year (Raunkiaer 1934). Plants are able to acclimate themselves to the conditions of the oncoming season by cues in the environment, mainly changes in temperature and photoperiod (Li et al. 2003, Welling & Palva 2006, Olsen 2010). Before the onset of winter, perennial northern plants already begin increasing their cold hardiness, a process that can take several weeks or even months (Wisniewski et al 2003, Kalberer et al. 2006). Many species, especially trees and other woody plants, and deciduous perennial herbs, also cease growth and enter a state of dormancy (Vegis 1964, Arora et al. 2003, Rohde & Bhalerao 2007). The process of cold acclimation is initiated by a combination of cues, both internal, such as developmental stage and circadian rhythms, and environmental, such as photoperiod and changes in temperature (Lüttge & Hertel 2009, Resco et al. 2009, Olsen 2010), and controlled by a complex network of signalling pathways and gene expression (Thomashow 1999, Xin & Browse 2000, Nakashima & Yamaguchi-Shinozaki 2006, Chinnusamy et al. 2007, Ruelland et al. 2009). Deacclimation occurs mainly in response to warm temperatures and proceeds much faster than cold acclimation (Kalberer et al. 2006). Premature deacclimation during a warm period in winter can thus have severe effects on northern plants (Strimbeck et al. 1995, Zhu et al. 2002, Bokhorst et al. 2010). Accordingly, Bokhorst and co-workers (2009) reported extensive damage to the dwarf shrub *Empetrum hermaphroditum* in the Swedish sub-Arctic during the growing season following a warm period in the preceding winter, and they confirmed the effects in a field warming experiment. Ögren (1996) also reported lethal injuries in *Vaccinium myrtillus* during a warmer-than-average winter in northern Sweden. Taulavuori and co-workers (1997) showed that a small elevation of 2-3 °C in air temperature is sufficient to cause dehardening in *V. myrtillus* in winter.

Cold and freezing temperatures have numerous effects on the plants. Low temperatures rigidify the membranes in the cells and may cause disturbances in membrane functions (Steponkus 1984, Uemura et al. 2006, Ruelland et al. 2009). Protein structures may be altered, protein complexes may be destabilised, and enzyme activity is lowered. Many reactions in the cells slow down, including enzymatic scavenging of reactive oxygen species, which may have adverse effects on membranes, enzymes, and other compounds in the cells (Ruelland et al. 2006). Freezing temperatures cause ice formation in the apoplast leading to

extracellular freezing of the plant (Pearce 2001). Water is drawn from inside the cells by the difference in the water potential created by the extracellular freezing, leading to dehydration of the cells (Xin & Browse 2000). Severe dehydration, especially if followed by a thaw, may cause disruption of cell membranes severe enough to kill the cell (Guy 2003). Ice formation within the cells also kills the cells by deteriorating their internal structure (Ruelland et al. 2009). In association with cold acclimation, changes also occur in the membrane lipid composition; this increases the amount of desaturated lipids, making the membranes more fluid and less prone to detrimental phase changes and lesions (Steponkus 1984, Thomashow 1999, Uemura et al. 2006). Changes in the cell wall structure and cytoskeleton microtubule constituents have also been reported (Ruelland et al. 2009). Also associated with acclimation is the accumulation in the cell of proteins related to cold hardiness, such as various dehydrins (Welling et al. 2004, Ruelland et al. 2009), and other substances. These substances may have membrane-stabilising properties, act as cryoprotectants or antifreeze compounds in the cytosol (Hoshino et al. 1999, Kasuga et al. 2008), or improve the action of other enzymes in the dehydrated cells (Ruelland et al. 2009). Plants are able to control the formation of extracellular ice by synthesizing proteins that bind to the ice crystals and alter their growth (Griffith & Yaish 2004, Moffatt et al. 2006). The amount of soluble sugars, especially sucrose, in the cells also increases with cold acclimation. Soluble sugars have been proposed to act as osmolytes in the cells, reducing the extent of cellular dehydration at subzero temperatures (Steponkus 1984, Guy et al. 1992). Other roles of soluble sugars and other soluble compounds include depression of the ice nucleation temperature of the cell sap (Kasuga et al. 2008) and stabilisation of the plasma membrane by maintaining the hydrophilic environment in the immediate vicinity of the membrane (Ruelland et al. 2009). The slowdown of essential enzymatic reactions in the cells at low temperatures is also countered by increased synthesising of enzymes catalysing these reactions in connection with cold acclimation (Ensminger et al. 2006, Goulas et al. 2006). Winter is not, however, a period of metabolic inactivity. Many studies have shown that respiration (Bannister 1980, Björkman et al. 2010, Morgner et al. 2010), the uptake and transport of water (Sevanto et al. 2006), the uptake of nutrients (Andresen & Michelsen 2005, Onipchenko et al. 2009), and even photosynthesis (Zeller 1951, Oberbauer & Starr 2002, Starr & Oberbauer 2003, Sevanto et al. 2006) continue during winter.

Northern evergreen plants and strategies for wintertime photosynthesis

Many northern plants have leaves that stay green over the winter (Givnish 2002). Evergreen plants retain their green leaves over several growing seasons, having a leaf life span of more than one year, whereas wintergreen herbaceous plants form leaves that stay green during the winter but are replaced by new leaves at the

beginning of the growing season (Chabot & Hicks 1982). In the north, evergreen plants are found both among trees and in the field layer. Evergreen leaves require higher investments per unit leaf area than short-lived deciduous leaves, but they may provide some advantages, especially in nutrient-poor environments when the growing season is short (Chabot & Hicks 1982, Karlsson 1985, Aerts 1995, Kudo et al. 1999, Givnish 2002, Warren & Adams 2004). Plants that have wintergreen leaves may be able to start photosynthesizing immediately in spring, taking advantage of the early season (Kikuzawa 1984, Karlsson 1989, Repo et al. 2006), and may also continue photosynthesis well into the autumn (Landhäusser et al. 1997) and even in winter if the conditions permit (Schaberg et al. 1995, Schaberg 2000, Lehner & Lütz 2003, Starr & Oberbauer 2003).

Photosynthesis is thought to be regulated by the balance between the utilisation and availability of photosynthetates in a process known as photostasis (Huner et al. 1998, Öquist & Huner 2003, Ensminger et al. 2006). Two main strategies for wintertime photosynthetic activity have been recognised (Regehr & Bazzaz 1976, Verhoeven et al 1999, Adams et al. 2004). Many plants, especially evergreens such as northern conifer trees, cease their growth during autumn and enter a dormant state (Arora et al. 2003, Rohde & Bhalerao 2007, Tanino et al. 2010), reducing their need for photosynthetates, i.e., their sink strength, with a concomitant reduction in photosynthetic capacity (Vogg et al. 1998b, Öquist & Huner 2003, Ensminger et al. 2006). Some wintergreen herbaceous plants, such as winter wheat (*Triticum aestivum*), on the other hand, continue their growth, and may even experience an upregulation of photosynthesis during winter (Huner et al. 1998, Savitch et al. 2002, Adams et al. 2004). The biennial herb *Malva neglecta* is an extreme example of this strategy, with a photosynthetic capacity at saturating levels of CO_2 almost twice as high in winter as in summer (Verhoeven et al. 1999, Adams et al. 2004). These two strategies of wintertime photosynthesis represent two ends of a continuum, and the winter strategies of most plants with green leaves are somewhere between these two extremes (Adams et al. 2004). The downregulation of photosynthesis during winter in evergreen northern trees is not always complete and also depends on the overwintering environment, especially on the temperature and the light conditions (Pisek & Winkler 1958, Schaberg et al. 1995, Šiffel & Šantruček 2005, Koh et al. 2009). Studies on Scots pine and other conifers report extensive degradation of the photosynthetic apparatus during winter and especially during early spring in response to low temperatures in combination with high light levels (Ensminger et al. 2004, Zarter et al. 2006c). In branches less exposed to light, photosynthesis has been found to be less downregulated and photoprotective measures less extensive than in the most exposed branches (Sveshnikov et al. 2006, Verhoeven et al. 2009).

If there is a temporary change, such as a warm spell, in the environmental conditions of overwintering plants, even small photosynthetic activity can reduce the respiratory losses of the plants over the winter, provided that the photo-

synthetic apparatus is able to respond to the change in the conditions. Positive net photosynthesis has been shown to occur in wintergreen herbaceous plants during winter (Zeller 1951, Bauer et al. 1994, Adams et al. 2001). Photosynthetic activity during winter has also been reported at temperatures close to, or even slightly below, 0 °C in northern conifers (Zeller 1951, Parker 1953, Schaberg et al. 1995, Šiffel & Šantruček 2005, Sevanto et al. 2006), contributing to the replenishment of carbohydrates lost through respiration (Parker 1961, Schulze et al. 1967, Schaberg et al. 2000). During colder periods the rates of photosynthesis nevertheless reach zero before respiration ceases (Pisek & Winkler 1958, Ungerson & Sherdin 1965). Longer periods of freezing temperatures, however, cause a sustained depression of photosynthesis in northern conifers (Pisek & Winkler 1958, Ensminger et al. 2004, 2008), possibly associated with changes in the structure of the photosynthetic apparatus (Ottander et al. 1995, Gilmore & Ball 2000). Photosynthetic activity has also been found in evergreen dwarf shrub species before snowmelt during early spring in the Alaskan Arctic (Oberbauer & Starr 2002, Starr & Oberbauer 2003). Larsen and co-workers (2007) estimated that photosynthesis occurring during spring and late autumn may account for up to 19 % of the annual gross CO_2 uptake in a subarctic heath. Considerable photosynthetic activity has also been found in *Lolium perenne* at close to 0 °C (Höglind et al. 2010).

The mechanisms of photosynthesis, photoinhibition and photoprotection

In plants, most of the reactions associated with photosynthesis take place within the chloroplasts and can be roughly divided into light-driven and carbon-fixing reactions. The light-driven reactions of photosynthesis are associated with protein complexes located in the thylakoid membranes, which form a continuous three-dimensional network in the aqueous space inside the chloroplasts (Nelson & Yocum 2006). Light is captured by chlorophyll bound to antenna protein complexes that transfer the energy to the reaction centres of either of the two photosystem protein complexes, exciting them. Upon excitation of photosystem II, an electron is transferred from the reaction centre to a series of compounds in the electron transport chain, and protons are released in the process. The oxidized reaction centre of photosystem II is subsequently reduced back to its original state by receiving an electron through the splitting of water by the oxygen-evolving complex attached to photosystem II, releasing oxygen and protons (Nelson & Yocum 2006). When excited by light, the reaction centre of photosystem I transfers an electron through a similar electron transport chain, eventually generating NADPH, and is subsequently reduced by accepting an electron from the electron transport chain of photosystem II (Nelson & Yocum 2006). The proton gradient that is created across the thylakoid membrane by the released protons is dissipated by a transmembrane ATP-ase that forms ATP. The NADPH and ATP formed are used by the Calvin-Benson cycle, in which carbon

dioxide is captured by the RuBisCO enzyme and a three-carbon sugar phosphate is formed through a cyclic series of enzymatically catalysed steps (Raines 2003). The fraction of this three-carbon sugar that is not needed to run the Calvin-Benson cycle is then exported from the chloroplast and used to form glucose, sucrose, or other carbohydrates depending on the needs of the plant (Ensminger et al. 2006).

Low temperatures affect various aspects of the photosynthetic process. While light-trapping and charge-separation in photosystems I and II are independent of temperature, the increased viscosity of the thylakoid membranes can slow the electron transport and the diffusion of electron carriers, creating an energy imbalance in the thylakoids (Vogg et al. 1998a, Ruelland et al. 2009). The activity of the enzymes of the Calvin-Benson cycle is slowed by low temperature, reducing the utilisation of ATP and NADPH and adding to the energy imbalance. Sucrose synthesis in the cytosol is also slowed, which leads to an accumulation of phosphorylated intermediates and further depletion of the inorganic phosphate in the cell, which may impede ATP synthesis (Stitt & Hurry 2002). The formation of extracellular ice may impede the diffusion of CO_2 in the leaf and may also affect the function of both the thylakoid membranes and the plasma membrane through freeze dehydration (Neuner & Pramsohler 2006). During the cold acclimation of plants, particularly of herbs that do not experience a downregulation of photosynthesis, the amounts and the activity of the Calvin-Benson cycle enzymes, including RuBisCO, are increased (Goulas et al. 2006), sucrose biosynthesis is improved (Stitt & Hurry 2002), and the content of inorganic phosphate is increased (Strand et al. 1999). The fluidity of the thylakoid membranes is also increased (Vogg et al. 1998a). Evergreen conifers and other plants that downregulate photosynthesis in winter undergo a reorganization of the photosynthetic apparatus, including a loss of chlorophyll, a reduction in the number of functional reaction centres of photosystem II, and an aggregation of the thylakoid protein complexes (Ottander et al. 1995, Gilmore & Ball 2000, Savitch et al. 2002, Ensminger et al. 2006).

While light is essential for driving photosynthesis, light absorbed by the photosynthetic apparatus but not used in photochemical reactions can lead to a sustained decline in the photosynthetic activity of plants. This decline in photosynthetic activity after exposure to high levels of light is often referred to as photoinhibition (Long et al. 1994, Keren & Krieger-Liszkay 2011). In the literature, the use of the term is somewhat ambiguous, since it is sometimes, especially in the ecological literature, used to describe any light-induced reductions in photosynthetic capacity regardless of whether they are caused by photodamage or by readily reversible photoprotective processes, and sometimes used strictly to denote only those reductions in photosynthetic capacity that are caused by the breakdown of the reaction centre of photosystem II due to light (Cavender-Bares & Bazzaz 2004). In this study, the term is mainly used in its broader sense, except where it is explicitly specified. At low temperatures, the

suppression of temperature-dependent enzymatic functions and alterations in membrane function increase the risk of the excess absorption of light leading to the formation of reactive oxygen species and inhibition of photosynthesis (Huner et al. 1998, Ensminger et al. 2006).

Photoinactivation of photosystem II occurs when the D1 protein of the reaction centre is degraded and the reaction centre is disassembled. This is sometimes also referred to as photodamage or photoinhibition of photosystem II and is a process that readily occurs in all plants exposed to light (Edelman & Mattoo 2008, Tyystjärvi 2008). In association with the conditions enabling photo-inactivation of photosystem II, reactive oxygen species are formed (Long et al. 1994, Krieger-Liszkay et al. 2008, Oguchi et al. 2011). A number of molecular mechanisms for the photoinactivation of photosystem II have been suggested, with differences in both the sequence of events and the primary site of damage (Keren & Krieger-Liszkay 2011, Oguchi et al. 2011, Vass 2011). These mechanisms need not be mutually exclusive – even though some of them cannot occur simultaneously in the same photosystem, they probably all occur in nature, even in the same leaves (Oguchi et al. 2011, Vass 2011). Depending on the mechanism involved, photoinactivation of photosystem II occurs in visible light in rough proportion to the irradiance, with an action spectrum resembling that of chlorophyll (Oguchi et al. 2011, Vass 2011), or on exposure to mainly ultraviolet (UV) radiation, in proportion to the amount of incident photons (Tyystjärvi 2008, Takahashi & Badger 2011, Takahashi et al. 2010, Keren & Krieger-Liszkay 2011). After the degradation of the reaction centre, specific repair mechanisms resynthesize the D1 protein and reassemble the reaction centre (Baena-Gonzáles & Aro 2002, Rokka et al. 2005, Mohanty et al. 2007, Yoshioka & Yamamoto 2011). As long as the rate of repair matches the rate of damage, no net loss of photosynthetic activity is observed (Greer et al. 1991, Murata et al. 2007, Edelman & Mattoo 2008). The repair process is easily suppressed by stress factors such as low temperatures, and by the buildup of reactive oxygen species in the chloroplasts, leading to a buildup of non-functional photosystem II complexes (Nishiyama et al. 2006, Murata et al. 2007, Takahashi & Murata 2008). The reactive oxygen species may damage the photosynthetic proteins, the membranes, and other structures in the cells directly (Keren & Krieger-Liszkay 2011), but they have also been shown to be part of a complex signalling network adjusting plant responses to abiotic stress (Suzuki & Mittler 2006, Jaspers & Kangasjärvi 2010).

In natural conditions, photoinhibition seems to occur more frequently in photosystem II in cold acclimated plants, but photosystem I is also easily photoinhibited (Ivanov et al. 2001, Scheller & Haldrup 2005, Sonoike 2011). Photoinhibition occurs in photosystem I when oxygen is reduced in the electron transport chain of photosystem I and reactive oxygen species are formed that immediately destroy certain parts of the photosystem (Sonoike 2011). Recovery from the photoinhibition of photosystem I requires total degradation and

rebuilding of the reaction centre, which is a slow process that could take days or even weeks (Scheller & Haldrup 2005, Sonoike 2011). Since the photoinhibition of photosystem I requires electrons from photosystem II, the photoinactivation of photosystem II is sometimes also seen as a way of restricting damage, as photosystem II is much more readily repaired than photosystem I (Scheller & Haldrup 2005, Krieger-Liszkay et al. 2008, Sonoike 2011).

Plants have evolved a number of photoprotective mechanisms both to avoid and to cope with the detrimental effects of absorbed light not used in photosynthesis. Some plants, such as certain species of *Rhododendron*, are able to turn their leaves away from direct sunlight in conditions more adverse for photosynthesis, such as cold periods (Adams et al. 2004, Wang et al. 2008). Movement of chloroplasts within the cells, thought to be a photoprotective measure, have also been observed in some species in response to high light (Park et al. 1996, Wada et al. 2003) and low temperature (Tanaka 2007). Waxy cuticular layers and protective pigments can also be used to shield the photosynthetic apparatus from excess light (Adams et al. 2004). The concentrations of anthocyanins and red carotenoid pigments have been shown to increase in wintergreen plants exposed to high light levels at low temperatures (Oberbauer & Starr 2002, Hughes et al. 2005, Hughes 2011). Anthocyanins act as shields from excessive radiation both in the PAR and the UV range (Hoch et al. 2001) and in some cases may also act as scavengers of reactive oxygen species through their antioxidant capabilities (Gould et al. 2002, Hughes 2011). Other phenolic compounds have also been assumed to participate in photoprotection by acting as antioxidants (Close & McArthur 2002). Various carotenoids may also have a role as antioxidants besides their other roles in photoprotection (Demmig-Adams & Adams 2002). Other major scavengers of reactive oxygen species in plants are glutathione and ascorbate, either separately through various reactions or together through the glutathione-ascorbate cycle (Wildi & Lütz 1996, Noctor & Foyer 1998, Rouhier et al. 2008).

Photoprotective mechanisms also occur within the thylakoid membranes of the chloroplasts. Most plants employ a variety of mechanisms for the dissipation of excess energy as heat, termed nonphotochemical quenching (Müller et al. 2001, Adams et al. 2004, Demmig-Adams et al. 2008). There is a short-term, rapidly reversible form of thermal dissipation of excess energy, located in the light-harvesting antennae of photoystem II, which is associated with the buildup of a pH gradient across the thylakoid membranes in the chloroplasts due to light being absorbed in excess of the utilisation of ATP produced (Demmig-Adams et al. 1995, Müller et al. 2001, Adams et al. 2004, Demmig-Adams & Adams 2006). This pH gradient then facilitates the enzymatic conversion of the carotenoid violaxanthin through antheraxanthin to zeaxanthin in what is termed the xanthophyll cycle, activating the dissipation of excess energy as heat through the interaction of zeaxanthin with the chlorophyll molecules in the antennae (Demmig-Adams et al. 1995, Müller et al. 2001). This dissipation mechanism

(Holt et al 2005), present in all plants, involves the PsbS protein as well as zeaxanthin (Li et al. 2000) and is employed in situations of moderate transient stress in conditions that would otherwise be favourable, such as high light or temperature during part of the day (usually mid-day) or transient sunflecks of high light in an otherwise shaded environment (Demmig-Adams et al. 2006). The thermal dissipation of energy is immediately relaxed when the leaves are darkened and the pH gradient is released. In concert with the rapidly reversible form of thermal dissipation, the phosphorylation and dephosphorylation of the light-harvesting complexes of photosystem II serve to balance the excitation between photosystem II and photosystem I in a process referred to as state transitions (Tikkanen et al. 2006, Rochaix 2010, Tikkanen et al. 2010, 2011). Additional complementary quenching of excess energy as heat also occurs in the reaction centre through charge recombinations, regardless of the level of zeaxanthin present (Ivanov et al. 2008). Cyclic electron flow around photosystem I (Manuel et al. 1999, Ivanov et al, 2001) and the formation and quenching of hydrogen peroxide through the water-water cycle (Asada 1999) may also contribute to photoprotection. Photorespiration has also been proposed to have a photoprotective role (Niyogi 1999, Ort & Baker 2002) thought to be particularly important in some alpine plants (Streb et al. 1998, Lütz 2010).

In addition to the rapidly reversible form, there are several forms of sustained thermal dissipation that also involve zeaxanthin. Some plants are able to maintain a pH gradient across the thylakoid membrane in darkness at a low temperature and thus to sustain the thermal dissipation of energy for a prolonged period. This state is quickly reversed, however, when the temperature rises (Verhoeven et al. 1998, Adams et al. 2008). Under lasting conditions of stress many plants, especially evergreens in winter, replace the flexible thermal dissipation mechanism depending on the presence of a pH gradient by a less flexible sustained thermal dissipation mechanism that is not dependent on a pH gradient. Zeaxanthin levels are retained, maintaining the capacity for thermal dissipation as the xanthophyll cycle is essentially arrested, and no conversion of zeaxanthin back to violaxanthin occurs (Verhoeven et al. 1998, Demmig-Adams et al. 2008). This state is accompanied by an upregulation of ELIP and HLIP proteins related to PsbS (Zarter et al. 2006a, b) and a phosphorylation of the D1 protein of the photosystem II core (Demmig-Adams et al. 2006, Demmig-Adams et al. 2008). The phosphorylation of the D1 protein may be related to the degradation and the repair cycle of photosystem II (Baena-Gonzales & Aro 2002, Ivanov et al. 2008). Degraded photosystem II cores are also thought to be able to dissipate excess excitation energy as heat, thus protecting not only the reaction centres themselves but also neighbouring active reaction centres against further damage (Greer et al. 1991, Demmig-Adams et al. 2008, Ivanov et al. 2008). Some studies, however, indicate that this neighbour-protective effect is negligible or non-existent, at least in plants that are not cold-acclimated (Sarvikas et al. 2010). As the sustained form of photoprotection also seems to involve a breakdown of the reaction centre of photosystem II in addition to photoprotective measures, it

14

is difficult to distinguish photoprotective measures from damage. The degradation of photosystem II can thus also be regarded as a measure for preventing further damage to other parts of the photosynthetic apparatus and to the rest of the leaf (Öquist et al 1992, Krieger-Liszkay et al. 2008), and for adjusting the photosynthetic capacity to the prevailing conditions (Adams et al. 2008).

The effects of snow on northern plants

Snow is an essential factor in the overwintering of northern plants (Havas 1966, 1985, Jones 1999). Snow is a complex mixture of ice crystals, water vapour, liquid water, and air (Pomeroy & Brun 2001). The snow cover has a stratified structure, formed by successive snowfalls and thermodynamically driven transformations, including snow settling and metamorphoses of snow crystals (Pomeroy & Brun 2001). The snow cover acts as an effective thermal insulator (Sturm et al. 1997, Simons et al. 2010) and provides a stable environment with high air humidity for field layer plants during winter. The snow cover also affects the depth of soil frost in winter and thus influences the overwintering of both plant roots (Cooper 2004) and soil microbes and the hydrological conditions of the soil after snowmelt (Groffman et al. 2001, Hardy et al. 2001, Venäläinen et al. 2001, Mellander et al. 2005). Under the snow cover, temperatures remain fairly close to $0 - $-5 °C, due to heat transfer from the soil, even when the air temperature above the snow is considerably lower, and rapid fluctuations in the air temperature are greatly reduced (Pomeroy & Brun 2001, Oberbauer & Starr 2002). In the course of the winter, the snow undergoes metamorphic changes through water vapour flow driven by temperature gradients present in the snow, leading to changes in the grain sizes, bonding, and structure of the snow (Sturm & Benson 1997, Rasmus et al. 2007). A porous depth-hoar layer consisting of large loosely bound grains is formed near the base of the snow cover (Sturm & Benson 1997), surrounding plants such as dwarf shrubs overwintering within the snow. Sometimes air spaces can form around and under the stems and leaves of these plants as the snow accumulates and undergoes metamorphosis (Pomeroy & Brun 2001, Solantie & Drebs 2006). Intermittent warm periods and winter rain may lead to the formation of icy layers within the snow, restricting or preventing both the percolation of water and the transport of gasses through the snowpack (Colbeck 1997, Albert & Perron 2000). This may further alter the conditions under the snow cover and affect the development of the snow structure itself. As the snow melts in spring, the amount of liquid water in the snow increases and large rounded melt grains are formed (Pomeroy & Brun 2001). Upon snowmelt, the structure of the snow cover usually becomes more uniform and more permeable to water and gas flow, provided that the ice crusts in the snow are disintegrating (Albert & Perron 2000).

Under the snow, the concentration of carbon dioxide can be significantly higher than the ambient atmospheric level (Fahnestock et al. 1998, Musselman et al. 2005), especially in the presence of extensive icy layers in the snow (Albert & Perron 2000). In combination with the high moisture level and light penetrating the snow, this provides an environment under the snow that is favourable for photosynthesis, especially in late winter (Oberbauer & Starr 2002, Starr & Oberbauer 2003). The light level below the snow cover depends not only on the thickness of the snow but also on the structure of the snowpack (Curl et al. 1972). Visible light and ultraviolet (UV) radiation may penetrate deep into the snowpack as they are highly scattered by snow crystals, while infrared wavelengths are more effectively absorbed (King & Simpson 2001). As the winter progresses and the snow grains grow in size (Sturm & Benson 1997), especially after the onset of snowmelt, light penetrates further down into the snow (Curl et al. 1972, Gerland et al. 1999, Oberbauer & Starr 2002). Depending on the structure of the snowpack, one per cent of the photosynthetically active radiation (PAR) incident on the surface of the snow has been shown to penetrate the snowpack down to a depth of 30-110 cm in late winter and spring (Curl et al. 1972, Gerland et al. 1999, 2000, Gorton & Vogelmann 2003). This is more than enough for positive net photosynthesis to occur under the snow, especially in shade-adapted plants on sunny days in spring, when the PAR level, measured as the photon flux density, incident on the snow surface can reach 1000-1500 µmol photons m^{-2} s^{-1} and above, also in the boreal zone (Kappen et al. 1995). The amount of PAR penetrating a moderate snow cover is only slightly dependent on the wavelength. The spectral properties of snow vary somewhat with snow structure, but they are much more affected by particles and other impurities in the snow than by the snow structure itself (Curl et al. 1972, Gerland et al. 2000). However, under a very thick snow cover (one to two metres), the PAR spectrum is shifted towards blue light (Richardson & Salisbury 1977). With increasing depth, UV radiation is extinguished more readily than PAR, with longer-wavelength UV-A radiation penetrating deeper than shorter-wavelength UV-B radiation (King & Simpson 2001, Gorton & Vogelmann 2003). The snow cover therefore also protects evergreen field layer plants by attenuating high levels of both PAR and UV radiation, which could otherwise cause photodamage and necessitate the induction of sustained photoprotective measures, as the air temperatures in late winter and spring can still limit photosynthesis and impair the repair processes in photosystem II (Adams et al. 2004, Ensminger et al. 2004).

In arctic and alpine areas, local variations in snow cover can be large, as the wind readily removes snow from exposed sites in the open landscape and deposits it in protected places (Billings & Bliss 1959). Plants growing in exposed areas are adapted to overwintering in cold and windy conditions without much protection from the snow, whereas snowbed plants are sheltered below a thick snow cover and face much milder conditions (Björk & Molau 2007). In the boreal forest the variations in snow cover are much smaller, and the snow distribution is affected by the canopy structure as well as variation in topography (Hedstrom & Pomeroy

1998, Pomeroy et al. 2002, López-Moreno & Latron 2008). The tree canopy affects the thickness and structure of the snow cover by intercepting snow and by altering the radiation balance of the snow beneath the canopy both by shading from short-wave radiation and by altering the sub-canopy thermal regime leading to variations in long-wave radiation at the snow surface (Pomeroy & Dion 1996, Hedstrom & Pomeroy 1998, Essery et al. 2008, Veatch et al. 2009). Ground vegetation, such as dwarf shrubs, may also affect the local distribution of snow by trapping (Sturm et al. 2001).

The spatial distribution of snow can also have profound effects on the vegetation. Studies of arctic and alpine plants show that the distribution of many plant species coincides with fairly narrow ranges of snow depth (Walker et al. 1993). Changes in snow cover and snowmelt patterns have been shown to result in changes in the vegetation composition, indicating a connection between snow and the success of various plant species (Wipf & Rixen 2010). In boreal forests, where the spatial differences in snow depth are less extreme than in the Arctic, the occurrence of *Vaccinium myrtillus* is dependent on a sufficient snow cover during the winter, while *V. vitis-idaea* can also be found where the snow cover is thin (Havas 1966). Local variations in snow cover can thus be expected to contribute to the spatial variations in vegetation in boreal forests, too.

Climate change and the overwintering of northern field layer plants

The climate in the north is predicted to change in the future (Christensen et al. 2007, Jylhä et al. 2009). Mean temperatures will generally rise, and the warming is predicted to be particularly pronounced in winter (Jylhä et al. 2009). Intermittent warm periods during the winter will be more frequent, leading to changes in the structure, thickness, and extent of the snow cover, and an increased occurrence of freeze-thaw events (Mellander et al. 2007) and rain-on-snow events (Rasmus 2005, Jylhä et al. 2008). A significant reduction in the number of days with a minimum temperature below 0 °C is predicted to occur in northern Europe in the coming decades, particularly in autumn and spring (Jylhä et al. 2008). Though wintertime precipitation levels are predicted to increase in northern Europe, the number of days with a snow cover is predicted to decrease in spring and autumn (Mellander et al. 2007, Jylhä et al. 2008, Räisänen 2008). Changes in air temperature and snow cover will also affect the depth and extent of soil frost. A thinner snow cover in combination with occasional low temperatures may lead to increases in soil frost depth, whereas warmer temperatures will have the opposite effect, especially in combination with snow (Venäläinen et al. 2001, Mellander et al. 2007).

The success of northern plants depends not only on their performance during the season favourable for growth. Wintertime processes and activity also play a great role in the ecology of northern plants. Winter is not a period of rest with no

activity, for many biological processes can and do take place at low temperatures, affecting the plants significantly (Bannister 1980, Starr & Oberbauer 2003, Campbell et al. 2005, Sevanto et al. 2006). Many of the events and processes taking place during winter can have effects that are seen during the following growing season or even later (Kreyling 2010). Understanding wintertime activity is therefore crucial for understanding the ecology of northern plants, and it is becoming even more important with the ongoing climate change (Campbell et al. 2005). Knowledge of the effects of changes occurring over longer periods, such as the increase in mean air temperatures that has been projected, is necessary for understanding the ecology of northern plants and the changes they face, but a complete understanding cannot be achieved without also knowing the effects of extreme events, such as intermittent warm spells during winter, which have also been projected to become more common in the future (Jentsch et al. 2007). The wintertime ecology and processes of plants have been underrepresented in research, despite their importance for the ecology of northern plants, especially outside the arctic and alpine regions (Campbell et al. 2005). The effects of climate change on the overwintering of boreal trees have been the focus of some research (Ögren 2001, Saxe et al. 2001, Slaney et al. 2007, Hänninen et al. 2006, 2007), but field layer plants have been given very little attention despite their importance for both the forest ecosystem and the carbon exchange of boreal forests (Widén 2002, Kolari et al. 2006, Kulmala et al. 2011).

The aim of the thesis

The aim of this PhD thesis study is to examine the overwintering of boreal evergreen dwarf shrubs, especially the role of wintertime photosynthetic activity, with an emphasis on *Vaccinium vitis-idaea*. The study explicitly addresses the roles of snow and snowmelt and the effects of changes in wintertime environmental conditions, particularly the warm spells occurring in winter.

The specific aims of the study are the following:

- to observe the seasonal variations in photosynthestic capacity of *V. vitis-idaea* in the field and clarify the importance of wintertime photosynthetic activity for the species (I).
- to study the role of air temperature, in relation to other factors such as physiological restraints, in driving the changes in photosynthetic capacity in the course of the year (I, II).
- to examine the role and importance of the snow cover and other overwintering conditions on the photosynthesis of *V. vitis-idaea* (III, IV).

- to study the changes in the photosynthesis of *V. vitis-idaea* that take place at snowmelt in spring (III).
- to test whether adaptation or acclimation to local wintertime microclimate affects the performance of plants under changing overwintering conditions (IV).
- to examine the effect of persistent long-term spatial variations in the snow cover on the field layer vegetation, including *V. vitis-idaea*, in a boreal forest (V).

Materials and methods

An outline of the parts of the study

In (I) the photosynthetic capacity of *V. vitis-idaea* was followed during one year by means of approximately weekly measurements of the light response of photosynthesis, chlorophyll fluorescence, electrolyte leakage, and carbohydrate content. A first-order temperature-driven dynamic model describing the time course of photosynthetic capacity as a function of temperature was used to determine the influence of temperature on the photosynthetic capacity of *V. vitis-idaea* by comparing the measured data with the model predictions.

In (II) the effect of various environmental factors, such as temperature, photoperiod, and preceding frosts, on the recovery of photosynthesis in *V. vitis-idaea* was studied during three winters. Pot-grown plants overwintering outdoors were transferred to growth chambers at various times of winter, and the recovery of photosynthesis was followed for eight days by measuring the light response of photosynthesis. An experiment involving a series of consecutive freezing and non-freezing temperatures was also carried out.

In (III) the photosynthetic capacity of *V. vitis-idaea* was studied during snowmelt in spring both in a natural setting and, in more detail, by artificially thinning the snow cover. The effect of snowmelt on the photosynthetic capacity was studied by means of measuring the light response of photosynthesis and chlorophyll fluorescence of the leaves.

In (IV), *V. vitis-idaea* plants originating from two sites in Kilpisjärvi, northern Finland, one on a treeless deflation site above the treeline and the other in a mountain birch forest, were potted and reciprocally transferred between the two sites in order to study the effects of winter conditions on photosynthesis. The potted plants were allowed to overwinter. In the spring, all plants were transferred to identical conditions in a cold store, where they were allowed to recover. The light response of photosynthesis and chlorophyll fluorescence were

measured upon the transfer and eight days after. Electrolyte leakage and carbohydrate content were also determined immediately after the transfer.

In (V) the long-term effects of snow cover distribution on ground layer vegetation were studied in a boreal pine forest by mapping the vegetation and measuring the snow depth on a 1×1-metre grid on several occasions during two winters. The effect of the tree canopy on the distribution of snow was also quantified by using several indices of tree and canopy influence.

The study sites and plants

Vaccinium vitis-idaea L. (Ericaceae) was chosen for the focus of most work in this study because it is a common evergreen field layer species representative of the boreal zone. It is an evergreen dwarf shrub with subterranean rhizomes and forms large, sometimes intermingled clones (Ritchie 1955, Persson & Gustavsson 2001). It has erect woody aerial stems, about 10-30 cm high, carrying sturdy leaves with a thick glossy upper surface and inrolled leaf margins (Ritchie 1955). *V. vitis-idaea* has a circumpolar distribution and is common in a range of habitats (Gustavsson 2001, Garkava-Gustavsson et al. 2005). In many boreal coniferous forests it is one of the most common species in the field layer, but it can also be found on heaths in arctic and alpine regions, e.g., in the mountain birch zone and above the treeline in northern Fennoscandia. *V. vitis-idaea* shows a fairly low genetic diversity on the regional scale in comparison with the diversity within populations (Gustavsson 2001, Persson & Gustavsson 2001, Debnath 2007).

The field work was carried out at three locations. The photosynthesis and overwintering of *V. vitis-idaea* was studied at Kallahdenniemi, Helsinki, southern Finland (60° 11′N, 25° 08′E; I, III) and in Kilpisjärvi, northern Finland (69°03′N, 20°50′E; III, IV). The effect of snow distribution on field layer plants was studied in a Scots pine (*Pinus sylvestris*) forest in Evo, Hämeenlinna, southern Finland (61°11′N, 25°05′E; V). The site at Kallahdenniemi is located on a glaciofluvial ridge extending into the sea. The dominant tree species was Scots pine, and the species in the field layer included *Vaccinium myrtillus*, *Calluna vulgaris*, and *Arctostaphylos uva-ursi*. The Evo site was located on a large flat glaciofluvial sand deposit covered with Scots pine-dominated even forest. The site is described in detail in (V). In Kilpisjärvi, the snow manipulation experiments (III) were carried out in a mountain birch forest in the vicinity of Lake Kilpisjärvi. The sheltered and exposed overwintering sites of the transplant experiment (IV) were located close to the snow manipulation site in the same mountain birch forest and on the slope of Mount Jehkats above the tree line, respectively.

To minimise the effects of genetic variation in the plant material, the experimental work on the activation of photosynthesis of *V. vitis-idaea* was carried out using a commercially available cultivar, 'Sanna', growing in pots (II).

This work was carried out in growth chambers (Sanyo MLR-350 and a walk-in phytotron for the freezing treatments) at the Viikki campus of the University of Helsinki. The plants were kept outdoors in the experimental garden on the campus before the experiments and transferred to the growth chambers only for the experimental treatments. The 'Sanna' cultivar originates from the province of Småland, Sweden and was developed by the Department of Horticultural Plant Breeding at Balsgård, Kristianstad, which is part of the Swedish University of Agricultural Sciences (Gustavsson 1993, Gustavsson & Stanys 2000).

Methods

The photosynthetic performance of leaves of *Vaccinium vitis-idaea* was determined by measuring leaf net CO_2 gas exchange at different levels of light, using a Li-Cor LI-6400 portable photosynthesis system with a blue-red light source (LI-6400-02B, Li-Cor inc. Lincoln, Nebraska, USA, I-IV). In most cases, nine different light intensities (0, 20, 50, 100, 200, 300, 500, 1000 and 1500 µmol photons m^{-2} s^{-1}) were used to determine the light response curve of the photosynthetic gas exchange of the leaves. The measurements were carried out using the built-in automatic light response measuring programme of the system. In (II), three light intensities (0, 50 and 500 µmol photons m^{-2} s^{-1}) were used for the measurements in the longer-term natural snowmelt experiment instead of full light-response curves because of time constraints in the performance of the measurements. The airflow through the chamber was kept at a low rate, usually 80 µmol s^{-1}. The block temperature of the measuring device was set to approximate that of the ambient air, and the atmospheric CO_2 concentration of the incoming air was set at 380 ppm and regulated by using the CO_2 regulation module of the system (LI-9964-026). Leaves were detached from the plants immediately before the measuring by means of a scalpel and inserted into the measuring chamber of the photosynthesis system on a thin nylon mesh support in order to keep them positioned correctly with respect to the light unit and light and temperature sensors in the chamber. The leaves to be obtained from under snow were carefully dug up and excised immediately before the measuring in order to preserve their natural conditions as long as possible and to minimise their exposure during the transfer to the measuring chamber. The snow was immediately replaced to minimise the disturbance to the plants remaining on the plots.

The light response of photosynthesis was analysed by means of a nonrectangular hyperbolic function (Marshall & Biscoe 1980, Thornley 1998) that was fitted to the measured light responses by means of the nonlinear regression procedure of SPSS (SPSS Inc., Chicago, Illinois, USA). The formulation of the function is given and the parameters described in (I). In the fitting of the light response curves, the average measure for the release of CO_2 in darkness was used as the value for the leaf respiration term for each set of replicates. The horizontal asymptote

parameter (P_{max}) of the fitted curve, indicating the theoretical maximum light-saturated rate of photosynthesis, was used as an indicator of photosynthetic capacity.

In (I), a temperature-driven dynamic model was applied in order to examine the long-term relationship between air temperature and photosynthetic capacity. The model was first fitted to the data on photosynthetic capacity measured during the autumn months of the first year, when the temperature was thought to be the limiting factor, then run for the whole data set on photosynthetic capacity. The model assumes that photosynthetic capacity depends on temperature alone, so that the ability of the model to predict the measured photosynthetic capacity at a certain point of time can be used as a qualitative indicator of the relative role of temperature and other factors in determining the photosynthetic capacity at that particular time. More details on the model can be found in (I).

The maximum quantum efficiency of photosystem II photochemistry was assessed by measuring the F_v/F_m ratio of chlorophyll fluorescence induction of dark-adapted leaves (I-IV). The F_v/F_m parameter is often used in ecological research to assess the level of stress experienced by plants (Maxwell & Johnson 2000, Baker & Rosenqvist 2004, Cavender-Bares & Bazzaz 2004). It can be used as a good indicator of photoinhibitory damage caused by the absorption of excess light (Bolhàr-Noredenkampf et al. 1989). However, a decline in F_v/F_m can be caused by either photodamage to the reaction centres of photosystem II or an increase in photoprotective non-photochemical quenching of excess energy, or a combination of both (Bolhàr-Nordenkampf et al. 1989, Demmig-Adams et al. 1995, Maxwell & Johnson 2000, Adams et al. 2008). The measurements were made with a PSM Mark-II fluorometer (Biomonitor, Umeå, Sweden; for a description of an older version of the instrument, see Öquist & Wass 1988, Bolhàr-Nordenkampf et al. 1989) by using a combined excitation and actinic light with an irradiance of 400 µmol photons m^{-2} s^{-1}. The leaves were dark-adapted in leaf clips for 30 minutes prior to the measurements.

Leaf damage suffered by the overwintering plants was assessed by measuring the relative electrolyte leakage from the leaves (I, IV). The electrolyte leakage method is often used to assess damage in determining the freezing tolerance of plants (Sutinen et al. 1992, Deans et al. 1995, Lim et al. 1998, Luoranen et al. 2004), but it can also be readily used to assess winter damage to membranes directly, in examining the temporal variation in the damage (I) or comparing the damage across different treatments (IV). Five leaves were detached, immediately cut in six pieces each, rinsed with deionized water, and incubated in 10 ml of deionized water in sealable plastic test tubes for 22 hours. The electric conductivity of the solute was then measured, after which the samples were killed by placing the tubes in a water bath at 100 °C for 60 minutes. After the samples had been allowed to cool, the conductivity was measured again. Leaf damage was expressed

as the percentual ratio of the conductivities measured before and after killing the samples by heating the tubes.

The content of nonstructural carbohydrates was determined from freeze-dried leaf samples (I, IV). The samples were ground in 80-% (v/v) ethanol, and the soluble sugar content was determined from the supernatant after centrifuging the homogenized samples by means of the p-hydroxybenzoic acid hydrazide method of Blakeney and Mutton (1980) For a standard, glucose was used. The content of storage carbohydrates, mainly in the form of starch, were determined from the pellets formed in centrifuging the samples by resuspending and incubating the pellets in 30-% (v/v) perchloric acid at 80 °C. After centrifuging, the amount of storage carbohydrates in the samples was determined with the anthrone method of Quarmby and Allen (1989), using glucose as a standard. A more detailed description of the extraction procedure is given in (I).

In (V), the trees, ground vegetation, and snow depth were mapped in a 10 × 40-metre study area, positioned in the north-south direction in an even forest dominated by Scots pine. Permanent marker poles were driven into the ground at the corners of the study area, and indicator lines marking every metre were suspended across the area, taking care to thread only along the edges of the grid cells. The positions of all trees taller than 0.5 metres were mapped in the study area and 5 metres outside the area on all sides, with the help of the indicator lines and measuring tapes, to the nearest 10 cm. The ground vegetation cover was assessed by using a 1 × 1-metre frame positioned with the help of the indicator lines. Snow depth was measured with an avalanche probe along the indicator lines, taking care to disturb the snow in the grid cells as little as possible. The indicator lines were removed when the measurements were finished and suspended again for each measurement occasion so as to cause as little disturbance to the site as possible. Nevertheless, the positioning errors were on the scale of a few centimetres, as shown by comparisons with small marker poles permanently positioned in the study area. The horizontal canopy dimensions of the tallest trees (Scots pines taller than 20 metres) were mapped by using a self-made version of a sighting device known as the Cajanus tube (Rautiainen et al. 2005), which consists of a tube, a mirror, and a spirit level and allows the user to look vertically upwards to determine if the point below the instrument is covered by the canopy or not.

Four indices, calculated from the tree or canopy position data, were used to assess the influence of trees on the snow cover and ground vegetation (V). The indices used were the distance to the nearest tree taller than 20 metres, the tree influence index of Kuuluvainen and Pukkala (1989), the canopy projection (i.e., whether the point of interest was under the canopy of a tall tree or faced a free sky above), and an index of canopy cover developed for this study. More details on the indices are given in (V).

Statistical analyses of the results were carried out, where applicable, by means of SPSS 15 (SPSS Inc., Chicago, Illinois, USA) except where otherwise indicated. Different variations of the Analysis of Variance (ANOVA) procedure of SPSS, which is based on general linear models, and appropriate post-hoc tests were used to analyse the results of experiments with two or more treatments (II, III, IV; more details are given in the respective publications). The spatial correlations among the snow cover, the indices of tree influence, and the ground vegetation in (V) were analysed by means of Pearson's product-moment correlation coefficients and tested by means of a t-test modified to account for effects of possible autocorrelations in the variables (Dutilleul 1993). The relations among the snow, tree influence, and individual species were analysed by means of Pearson's contingency coefficients calculated from four-by-four contingency tables and tested with Pearson's X^2-test.

Results and discussion

Photosynthetic capacity and air temperature

In the study of the annual cycle of photosynthesis of *Vaccinium vitis-idaea* (I), the photosynthetic capacity, as indicated by the theoretical maximum rate of light-saturated photosynthesis calculated from the light response curves measured in the field, was highest in September, with values of above 8 µmol CO_2 m^{-2} s^{-1}, and approached zero during cold periods in winter (Fig 1). Similar or slightly lower annual maximum rates in the field are reported for *V. vitis-idaea* in the literature, e.g., for the Alaskan Arctic areas (Oberbauer & Oechel 1989) and the Swedish sub-Arctic (Karlsson 1985). The photosynthetic capacity followed the air temperature with a delay of a few days through most of the year (Fig 1). After snowmelt in spring, the photosynthetic capacity increased at a slower rate than predicted by the temperature-driven dynamic model applied here. In the summer months the photosynthetic capacity declined, with the July values being less than half of the maximum values observed in September. In the growth chamber experiments, the photosynthetic capacity increased readily upon transfer of the plants from outdoors to the favourable conditions in the chambers at all times of the year, with a delay similar to that observed in the field (Table 1, II). Thus the induction of growth arrest and dormancy and the concomitant cold-acclimation at the end of the growing season does not seem to cause a drop in the photosynthetic capacity, and the ability for the recovery of photosynthesis during warm spells is more dependent on environmental factors before and during the warm spell, contrary to what has been reported for some tree species in the literature (Ottander et al. 1995, Vogg et al. 1998b, Savitch et al. 2002, Zarter et al. 2006b, Busch et al. 2007). The results from this study suggest that the
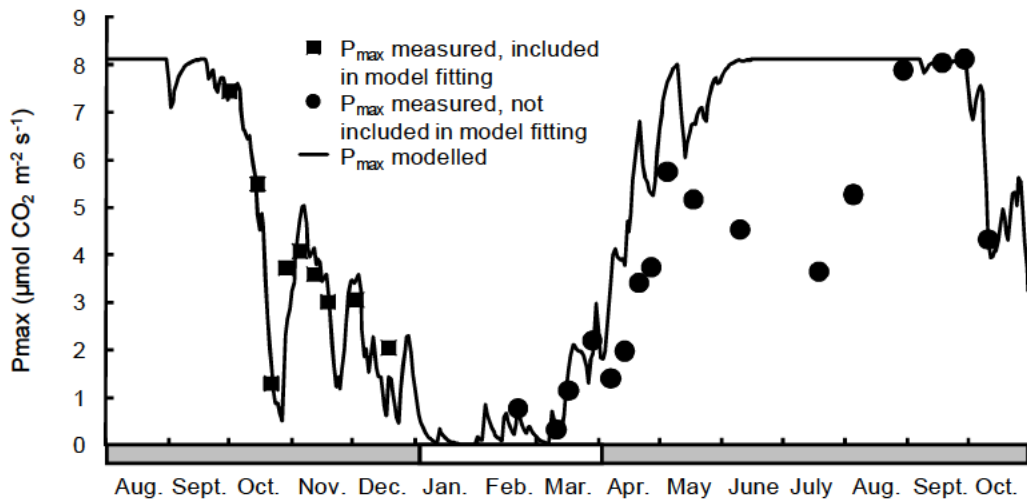
Figure 1. Measured and modelled maximum photosynthetic capacities (P_{max}) of *Vaccinium vitis-idaea* in the field during one year (I). The open part of the bar at the bottom shows the duration of persistent snow cover. The parameters of the temperature-driven model were estimated by means of measurement data obtained before snow cover formation in the first autumn. For further details, see the text and (I). Redrawn from (I). © 2008 NRC Canada or its licensors. Reproduced with permission.

photosynthetic capacity of *V. vitis-idaea* may even be slightly upregulated during the autumn (I), a feature more typical for wintergreen herbs (Huner et al. 1998, Adams et al. 2001, Savitch et al. 2002, Hacker & Neuner 2006). In Kulmala et al. (2011), relatively high light-saturated photosynthetic rates until mid-October are reported for *V. vitis-idaea* in a 45-year-old Scots pine forest in southern Finland. A similar but smaller transient upregulation in the response to decreasing temperatures in the autumn has, however, also been reported for several conifers in the Rocky Mountains (Koh et al. 2009). This upregulation was followed by strong but not complete downregulation when the trees were exposed to winter temperatures.

A delayed dynamic relation between air temperature and photosynthetic capacity similar to the one found in this study (I) has been reported for forest trees, especially in the boreal zone, during the growing season in modelling studies (Pelkonen & Hari 1980, Mäkelä et al. 2004, Kolari et al. 2007, Gea-Izguierdo et al. 2010). The activation of photosynthesis in spring and the rates of photosynthesis during the growing season have also been shown to be closely related to temperature in boreal trees (Bergh et al. 1998, Suni et al. 2003).

When the conditions are favourable and the air temperature is sufficiently high, the recovery of photosynthetic capacity is relatively quick, as demonstrated by the results (II and IV, Table 1) and by results in the literature (Lundmark et al. 1988,

Table 1. The recovery of photosynthetic capacity, measured as the theoretical maximum light saturated rate of photosynthesis (P_{max}) by fitting a non-rectangular hyperbolic function to measured light response curves, of leaves of *Vaccinium vitis-idaea* in various controlled environments following a) and b) transfer from outdoor overwintering conditions, or c) in a series of controlled environments, each lasting one week. P_{max} values ± 95 % confidence intervals for the fitted values are shown for the first day, and for the eighth day after transfer, except for c), where the first and seventh days are shown. More details on the experimental setups are given in the text and in the respective original articles (Ref) on which the study is based. Note that the measurements in a) and b) represent separate treatments, while c) shows results from a series of consecutive temperature treatments on the same plants.

Conditions prior to transfer	Recovery conditions (day / night)	time of year	P_{max} day 1 ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)	P_{max} day 8 ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)	Ref
a)					
Outdoors	10 °C / 2 °C, ambient day	Dec	2,75 ± 0,42	2,34 ± 0,38	II
Outdoors	10 °C / 2 °C, ambient day	Jan	0,07 ± 0,04	2,31 ± 0,46	II
Outdoors	10 °C / 2 °C, ambient day	Mar	0,56 ± 0,10	1,63 ± 0,33	II
Outdoors	15 °C / 2 °C, ambient day	Mar	0,42 ± 0,17	1,61 ± 0,24	II
Outdoors	5 °C / 2 °C, ambient day	Mar	0,32 ± 0,06	0,72 ± 0,14	II
Outdoors	7 °C, short day (-1 h)	Dec	1,56 ± 0,49	3,22 ± 1,04	II
Outdoors	7 °C, ambient day	Dec	2,11 ± 0,52	3,31 ± 0,81	II
Outdoors	7 °C, long day (+1 h)	Dec	2,53 ± 0,59	3,38 ± 0,89	II
Outdoors	7 °C, short day (-1 h)	Jan	2,89 ± 0,59	4,36 ± 0,46	II
Outdoors	7 °C, ambient day	Jan	3,13 ± 0,33	4,66 ± 0,81	II
Outdoors	7 °C, long day (+1 h)	Jan	2,67 ± 0,49	3,71 ± 1,14	II
Outdoors	7 °C, short day (-1 h)	Feb	1,71 ± 0,63	3,80 ± 0,99	II
Outdoors	7 °C, ambient day	Feb	2,48 ± 0,71	4,42 ± 0,37	II
Outdoors	7 °C, long day (+1 h)	Feb	2,10 ± 0,42	3,77 ± 0,54	II
b)					
sheltered site (sheltered origin)	5 °C, 16 h / 8 h	Apr	0,82 ± 0,10	0,66 ± 0,47	IV
sheltered site (exposed origin)	5 °C, 16 h / 8 h	Apr	1,38 ± 0,54	1,82 ± 0,89	IV
exposed site (sheltered origin)	5 °C, 16 h / 8 h	Apr	n.d.	0,29 ± 0,69	IV
exposed site (exposed origin)	5 °C, 16 h / 8 h	Apr	n.d.	1,07 ± 0,32	IV
c)					
-5 °C, 8 h day	3 °C, 8 h / 16 h	Jan-Feb	0,24 ± 0,11	2,92 ± 0,29 [1]	II
3 °C, 8 h day	9 °C, 8 h / 16 h	Jan-Feb	2,94 ± 0,17	3,02 ± 0,24 [1]	II
9 °C, 8 h day	0.6 °C, 8 h / 16 h	Jan-Feb	3,60 ± 0,56	2,48 ± 0,73 [1]	II
-14 °C, 8 h day	3 °C, 8 h / 16 h	Jan-Feb	0,72 ± 0,15	1,25 ± 0,16 [1]	II

[1] day 7.

n.d., not detectable

26

Harris et al. 2006). In natural settings, however, where the conditions often fluctuate, e.g., with low night temperatures, the recovery is slower (I, III), as the repair of the photosynthetic apparatus is slowed and sustained photoprotective measures continue to depress the photosynthetic capacity. Karlsson (1985) found that one-year-old leaves of *V. vitis-idaea* attain their summertime photosynthetic capacity in about two weeks after snowmelt, with little variation during the summer.

The effect of photoperiod on the photosynthetic capacity

The photoperiod experiment in (II) indicates that the effects of the prevailing photoperiod on the photosynthetic capacity are small and that photosynthesis is activated by a rise in temperature in a similar way throughout the winter (Table 1). The highest light-saturated photosynthetic rates were measured under the ambient photoperiod, whereas slightly lower rates were found under both shortened and lengthened photoperiods. In the literature, greater decreases in photosynthetic rates, combined with lower chlorophyll content and other changes in the photosynthetic apparatus, have been reported for Scots pine and other conifer trees under short-day conditions than under long-day conditions (Vogg et al. 1998b, Busch et al. 2007). Vogg and co-workers (1998b) also report that the chlorophyll content increased when the plants were transferred from short-day to long-day conditions.

The results of this study do not, however, rule out an effect of photoperiod on photosynthetic capacity, since other factors could have been involved. Longer day lengths could have lead to an increase in the carbon gain of the plants in comparison with shorter day lengths in otherwise similar conditions. The resulting possible buildup of carbohydrates in the leaves could have caused a downregulation of photosynthesis if the carbohydrates were not transported to other parts of the plant or otherwise utilised (Paul & Foyer 2001). Such sink-limitation of photosynthesis may possibly occur during shorter warm periods in winter, when growth onset has not yet taken place, the shoot meristems are dormant, and the utilisation of carbohydrates is low.

Photosynthesis under snow

The results of this study indicate that photosynthesis occurs under snow in *Vaccinum vitis-idaea*. The light response of photosynthesis determined in field conditions during the period of snow cover (I, III, IV) showed that the compensation point of photosynthesis occurred at very low light levels under the snow, thus indicating that positive net CO_2 exchange is possible under snow in the prevailing light and temperature. However, the direct uptake of CO_2 in leaves under snow was not measured in this study because of technical limitations

pertaining to the equipment available. The increase in the nonstructural carbohydrate content of the leaves before snowmelt observed in (I) suggests the presence of photosynthetic activity under snow during spring. Bannister (1980) suggests possible wintertime photosynthesis in *V. vitis-idaea* and other evergreen shrubs on the basis of measurements of carbohydrate levels at different times of the year. Lütz and co-workers (2005) report a capability of photosynthesis in leaves of the alpine evergreens *Rhododendron ferrugineum* and *Loiseleuria procumbens* and the herb *Homogyne alpina* before snowmelt and conclude that photosynthesis also occurs under snow as soon as the amount of irradiation is sufficient.

Few if any studies in the literature have measured the photosynthesis of individual leaves or plants under an intact snow cover. Working on the Alaskan Arctic tundra and using a leaf chamber attached around a leaf by digging a hole in the snow and then covering the hole with a cloth, Starr & Oberbauer (2003) measured a small positive net CO_2 exchange, increasing with decreasing snow depth, in *V. vitis-idaea* in ambient light under a melting snow pack. They also report clearly positive light-saturated photosynthesis values measured by using an external light source, indicating retained photosynthetic capacity under the snow. Chamber measurements of net ecosystem CO_2 flux over undisturbed snow in the same study indicated photosynthetic activity under snow large enough to compensate for the CO_2 efflux from respiration, measured by darkening the surface of the snow (Starr & Oberbauer 2003). Grogan and Jonasson (2006) and Larsen and co-workers (2007) also report possible photosynthesis of ground vegetation under snow in experiments involving chamber measurements of ecosystem CO_2 exchange in the Swedish sub-Arctic. Photosynthetic activity during winter has also been shown in lichens (Kappen et al. 1996), mosses (Larsen et al. 2007), and some aquatic plants (Marchand 1985). Tieszen (1974), however, concludes on the basis of measurements of gas exchange and chlorophyll content of intact leaves excavated from under snow that the photosynthetic activity of grasses and sedges on the Alaskan tundra before snowmelt is negligible because of low photosynthetic capacity in combination with low temperatures. Similar results have been reported for *Eriophorum* on an alpine bog by Lütz (1996), who nevertheless acknowledges the ability of the plants to green and begin photosythesizing immediately after snowmelt and considers the incompleteness of the photosynthetic apparatus under snow in these plants to be an adaptation to winter conditions.

The significance of wintertime photosynthesis

Photosynthesis during winter periods with more favourable conditions may help to replenish the carbohydrates lost through respiration, maintaining the carbon balance of the plant as respiration rates also increase during warmer periods (Stewart & Bannister 1973, Crawford 2000). In (I), the total amount of nonstructural carbohydrates in the leaves of *V. vitis-idaea* was highest in summer

and decreased towards autumn, then increased again in late autumn. The amount of soluble sugars in the leaves was markedly higher from October until well after snowmelt than during the summer, resulting from a buildup of reducing sugars during autumn and elevated levels of both reducing sugars and sucrose in the leaves during winter and spring, in comparison with the summertime levels (I). High concentrations of soluble sugars, especially sucrose, are associated with cold-tolerance in many species (Guy et al. 1992, Ögren 1997, Pagter et al. 2010). There was a slight drop in the total amount of nonstructural carbohydrates from December to early March, when the amount of storage carbohydrates in particular began increasing again, while the amount of soluble sugars remained constant. This suggests that soluble sugars are converted to storage carbohydrates while at the same time new soluble sugars are produced through net photosynthesis. In *Picea rubens*, an increase in soluble sugars without a simultaneous reduction in starch content has been reported for a period of mild weather in late winter (Schaberg et al. 2000).

In the transplant experiment (IV), the plants that overwintered at the sheltered site under a thick snow cover had significantly lower amounts of storage carbohydrates in their leaves at the end of winter than the plants from the exposed site. No difference was found in the amounts of soluble sugars. The difference was probably caused by increased respiration at temperatures close to or above freezing at the sheltered site. Because of the polar night, little or no photosynthesis is possible at high latitudes through most of the winter. In the spring, the plants at the exposed site experienced high light levels, which in combination with the low fluctuating temperatures caused the inhibition of photosynthesis, preventing the replenishment of carbohydrates, while the low level of light under the snow prevented photosynthesis in the otherwise functional plants at the sheltered site (IV).

On a sub-arctic heath in northern Sweden, photosynthetic activity outside the growing season has been found to account for up to 19 % of the gross annual photosynthesis, indicating that photosynthesis during the cold season is an important part of the annual carbon budget of this ecosystem (Larsen et al. 2007). In *Tsuga canadensis*, wintertime photosynthesis has also been suggested to provide up to 10 % of the total annual carbon fixed (Hadley 2000). The results of this study, together with the literature (Hadley 2000, Starr & Oberbauer 2003, Larsen et al. 2007), suggest that wintertime photosynthetic activity in *V. vitis-idaea*, and possibly also in other evergreen and wintergreen field layer plants, may significantly affect the annual carbon budget of both the individual plants and the ecosystem. This means that possible wintertime activity must also be accounted for when the total carbon uptake and release of boreal ecosystems are estimated. The field layer has been shown to contribute significantly to the overall carbon budget in boreal forests (Widén 2002, Kolari et al. 2006, Kulmala et al. 2011).

Photosynthesis at snowmelt

The snow cover plays a major role in the overwintering of *V. vitis-idaea*. A thick snow cover provides a stable environment for overwintering plants, with a fairly steady temperature close to 0 °C, a slightly elevated concentration of CO_2, and relatively high humidity but low light intensities (Woolgrove & Woodin 1996). At snowmelt, the environment of the plants changes drastically. Rapid fluctuations in temperature, high light levels, and the wind expose the plants to stressful conditions. The change in conditions affects the photosynthetic performance of the plants significantly, depending on the weather conditions following their emergence from the snow (III).

When the snow melts, the photosynthetic capacity of *V. vitis-idaea* slowly declines as photoprotective measures are activated and photodamage begins to build up, as indicated by the measurements of photosynthetic capacity and the maximum photochemical quantum efficiency of photosystem II (F_v/F_m, III). Photoinhibition already begins before the snow has melted completely and the leaves are fully exposed, as indicated by the steady decrease in the F_v/F_m ratio (III) as the snow got thinner on the snowmelt line. Increasing levels of photosynthetically active radiation under the melting snow, in combination with a fairly low temperature, can lead to the inhibition of photosynthesis by damage to the photosynthetic apparatus and to an increase in nonphotochemical quenching of excess energy. As the snow cover gets thinner, the extent of photodamage to photosystem II may be further increased by the action of ultraviolet light penetrating the snow (King & Simpson 2001, Gorton & Vogelmann 2003). After snowmelt, the observed decline in F_v/F_m became more rapid, but the photosynthetic capacity of the leaves did not decrease at the same rate during the first few days (III). This suggests an increase in the thermal dissipation of energy in relation to photochemistry (Demmig-Adams & Adams 2006). This is further supported by the lower initial slope of the light response curves measured immediately after snowmelt in comparison with the one measured before the leaves were exposed from the snow while the maximum light-saturated rate of photosynthesis remained fairly constant (III). The photoinhibition of photosystem II and nonphotochemical quenching of excess energy as heat affect the light-limited part of the photosynthetic light response curve to a greater extent than the high-light part when the rate of photosynthesis is limited mainly by enzymatic reactions, particularly RuBisCO activity (Leverenz & Öquist 1987, Ögren 1993, Hikosaka et al. 2004). At low temperatures capable of inducing photoinhibition, there is a surplus of photosystem II capacity in relation to the capacity of the Calvin-Benson cycle, especially in plants that have been acclimated to low light conditions (Öquist & Malmberg 1989, Behrenfeld et al. 1998). Sustained exposure to unfavourable conditions after snowmelt leads to a reduction in the number of active photosystem II reaction centres as the resynthesis of the D1 protein and the repair mechanisms of the reaction centre decrease, leading to an imbalance between the breakdown and the renewal of the

photosystem II complexes (Greer et al. 1991, Nishiyama et al. 2006, Murata et al 2007, Edelman & Mattoo 2008). Low temperatures have been shown to inhibit several steps in the repair process of the reaction centre (Mohanty et al. 2007), leading to a more sustained inhibition of photosystem II. Prolonged exposure to photoinhibitive conditions have also been shown to lead to an irreversible inhibition of photosystem II (Hideg & Murata 1997, Allakhverdiev et al. 2005).

In the natural snowmelt experiment in (III), a decrease in the photosynthetic capacity was observed in addition to a decrease in Fv/Fm after several days or weeks of exposure, in comparison with the plants that were still covered by snow. This indicates that prolonged photoinhibition also decreases photosynthesis at high light levels, leading to an overall decrease in photosynthetic capacity. In conditions of severe photoinhibition, the overall electron transport through photosystem II becomes the limiting factor for photosynthesis at high light levels, too (Öquist & Malmberg 1989, Kaňa et al. 2002, Hikosaka et al. 2004). In accordance with the results of this study (III), Lehner & Lütz (2003) observed lower values of F_v/F_m in twigs of *Pinus mugo* from above snow than in those under snow and a concomitant lower net photosynthesis at saturating light on the alpine timberline. Neuner et al. (1999) also report lower F_v/F_m ratios in leaves of *Rhododendron ferrugineum* that were not protected by snow during a winter period than in ones covered by snow.

After snowmelt, the fluctuating air temperatures, which can rise considerably above zero during the day and drop well below freezing during the night, may have a considerable effect on the photosynthetic recovery of the plants. Warm temperatures during the day allow for higher metabolic rates, including photosynthesis and repair, but low temperatures may set back the recovery or even cause damage, preventing the full utilisation of the daytime temperatures (Ensminger et al. 2004, 2008). The frequent low night temperatures in combination with the high light levels induce sustained forms of thermal dissipation of energy with concomitant changes in the structure of the photosynthetic apparatus and other metabolic changes (Germino & Smith 2000, Demmig-Adams et al. 2006, 2008), ultimately leading to the observed decrease in photosynthetic capacity (III). The difference between the slow activation of photosynthesis in the field after snowmelt in the spring (I, III) and the relatively rapid activation in the controlled favourable conditions in the laboratory (II, IV) can be explained by this fluctuation between favourable and unfavourable conditions experienced by the plants in the field. A similar difference was observed in seedlings of three conifer trees by Lundmark and co-workers (1988), who observed that the recovery of photosynthesis took several months in the field but only a few days in controlled optimal conditions in the laboratory. Lütz (1996) reports chloroplast damage and yellowing of green leaves in *Eriophorum* subjected to adverse conditions after snowmelt on an alpine bog.

Zarter et al. (2006a) report differences in the downregulation of photosynthesis in *Arctostaphylos uva-ursi* between a montane and a subalpine site. Photosynthesis was almost completely downregulated at the alpine site, and especially the plants not shaded from direct sunlight showed a large increase in sustained photoprotective dissipation of energy, whereas the plants at the montane site at a lower altitude retained their photosynthetic capacity. Variations in the degree of photoinhibition and the downregulation of photosynthesis in relation to environmental factors, particularly light and temperature, have also been reported for overwintering evergreen trees (Zarter et al. 2006b, Koh et al. 2009). Photoinhibition has been found to be less severe and photosynthesis less downregulated on the shaded side of trees than on the side facing the sun in winter (Ottander & Öquist 1991, Sveshnikov et al. 2006, Verhoeven et al. 2009). The results from this study show that *V. vitis-idaea* does not face photoinhibition and the downregulation of photosynthesis until the plants are exposed to high light levels and low temperature conditions during and after snowmelt (I, III). The relations of the degree of photoinhibition and the downregulation of photosynthesis to the temperature and light conditions that the plants face in winter, observed for both field layer dwarf shrubs and trees (Ottander & Öquist 1991, Zarter et al. 2006a, b, Koh et al. 2009, Verhoeven et al. 2009), indicate that the decrease in photosynthetic capacity experienced by the plants is mainly an acclimational response to the environmental conditions and only to a lesser degree a result of direct damage.

The effect of freezing on photosynthesis

Freezing can have a negative effect on photosynthetic capacity, especially when following a period of relative warmth, as shown by the results of the temperature series experiment in (II), where the plants recovered rapidly at 3 °C after a week at -5 °C, but after a week at -14 °C, recovery at 3 °C was limited (Table 1). The low photosynthetic capacity measured in the plants that overwintered at the exposed site on the first day in the transplant experiment (IV) may also have been accentuated by freezing effects. Damage to plasma membranes, especially the thylakoid membranes, and other parts of the plant can prolong the time needed for photosynthesis to recover (Vogg et al. 1998a, Ruelland et al. 2009). Photo-damage to photosystem II in combination with the inhibition of repair mechanisms and sustained forms of photoprotection also lower the photo-synthetic capacity after exposure to light in combination with low temperatures (Murata et al. 2007, Demmig-Adams et al. 2008). DeLucia (1987) reports a small drop in the daytime photosynthesis of *Picea engelmannii* seedlings after a light night freeze during the growing season, with full recovery after a few days in favourable conditions. In the same study, however, a hard night freeze, especially when repeated over several nights, caused a substantial and irreversible depression of photosynthesis. Decreased membrane fluidity has been suggested

to affect the processing of the D1 protein during the repair cycle of photosystem II, resulting in sustained irreversible photoinhibition (Allakhverdiev et al. 2005). Desiccation of the cells in connection with extracellular freezing may also disrupt membranes within the cell and damage enzymes essential for the photosynthetic activity, extending the time required for the recovery of photosynthesis (Bauer & Kofler 1987, Ruelland et al. 2009).

Persistent effects of snow distribution on field layer plants

In the southern boreal Scots pine-dominated forest studied in (V), the spatial snow distribution pattern persisted through the winter and also over the years, despite variation in snowfall across the years. The snow distribution correlated weakly but significantly with the indices of tree and canopy influence calculated in the study, which was expected on the basis of results reported in the literature (Havas 1985, Sturm 1992, Hardy & Albert 1995). The tree canopy influences the distribution of snow in northern forests through interception of snow by tree branches (Pomeroy et al. 2002) and by altering the pattern of short- and long-wave radiation incident on the snow surface (Pomeroy & Dion 1996, Essery et al. 2008). The spatial distribution of dwarf shrubs correlated significantly with the spatial distribution of snow but did not correlate with the tree or canopy influence, nor with summertime rainfall (V). The distribution of the moss cover, however, correlated with the indices of tree and canopy influence but not with the snow distribution. The frequency distribution of the plant cover on plots classified according to snow depth indicates that there are differences in the snow depth affinity of the species. *Vaccinium myrtillus* was most abundant on the plots that had the thickest snow cover, and *Empetrum nigrum* and *V. vitis-idaea* also preferred thicker snow, whereas *Linnaea borealis* preferred plots with less snow and was absent from the plots with the thickest snow cover. However, the study does not imply any causal relationship between snow and the distribution of the species. The observed correlation may be the result of either of these factors affecting the other and maybe even interacting with some third environmental factor that was not measured. The more erect dwarf shrub species with sturdy overwintering stems can have a trapping effect on snow redistributed by the wind and may also affect the metamorphic processes and settling of the snow, leading to a thicker snow cover (Sturm et al. 2001). A thicker snow cover gives a better thermal insulation and protection from drought in winter and can thus affect the survival of overwintering plants. In accordance with our results, the distribution of *V. myrtillus* has previously been shown to be sensitive to snow depth and is usually not found in places where the snow cover is thin, whereas *V. vitis-idaea* is less sensitive and can also be found in locations with a thin snow cover (IV, V, Havas 1966, Odland & Munkejord 2008).

In arctic and alpine areas, where variations in snow depth are larger than in the boreal forest, studies of the relation between snow depth and the occurrence of

plant species have shown that many species occur in relatively narrow ranges of snow depth (Walker et al. 1993) and that the effects of changes in the snow cover on plants are species-specific and also differ across functional groups (Uemura 1989, Wipf & Rixen 2010). In arctic and alpine regions, the timing of snowmelt varies greatly across locations and is highly dependent on the maximum snow depth (Odland & Munkejord 2008). Thus many of the effects of snow depth on plants in these regions are probably the result of the timing and pattern of snowmelt rather than the thickness of the snow as such (Odland & Munkejord 2008), even though both factors are important (Wipf et al. 2009). In the boreal forest the snow cover is generally thinner and the amplitude of the spatial variation smaller, resulting in less local variation in the timing of snowmelt (Rasmus 2005). However, the thin snow cover also means that a relatively modest spatial variation in snow depth can cause significant variations in the overwintering conditions of the plants under the snow, which may lead to spatial differences in species composition in the long run (V). Local differences in the timing of snowmelt can also have an effect on the plants, depending on the weather conditions that the plants face after they are exposed from the snow. As the results of this study show (III), photosynthetic performance can be severely reduced for a long period of time if the plants face conditions that induce sustained photoinhibition and damage to the photosynthetic apparatus. Freezing damage and desiccation can also occur, causing both further setbacks in photosynthetic activity (II, IV) and structural damage to cell membranes and organs in the plants (Pearce 2001, Taulavuori et al. 2011). Changes in species composition related to changes in the snow cover have been observed on ski pistes both without (Banaš et al. 2010) and with added artificial snow (Rixen et al. 2003). Similar results have also been obtained in snow manipulation studies on the arctic tundra (Wahren et al. 2005, Wipf et al. 2005, 2006, 2009, Cooper et al. 2011)

The overwintering of field layer plants in a changing climate

The predicted climate change will have a profound effect on wintertime conditions in the north in particular (Jylhä et al. 2009). The overwintering conditions of field layer plants will be altered significantly as warm periods become more frequent, the snow cover becomes more ephemereal and intermittent, and the structure and depth of the snow is changed (Rasmus 2005, Christensen et al. 2007, Jylhä et al. 2008). The results of this study indicate that *V. vitis-idaea* retains its capacity for photosynthesis during the winter (I) and may be able to utilise warm periods in winter for photosynthesis, provided there is enough light available (II). This means that the period of active photosynthesis outside the actual growing season will be extended in warmer winters. However, if the warm periods in winter are followed by freezing temperatures, the plants of the field layer will be exposed to harsh winter conditions without the full

protection of a snow cover. As the results of this study show, exposure to high light levels in combination with low temperatures following snowmelt will reduce the photosynthetic capacity, as sustained photoprotective mechanisms are activated and photoinhibition sets in (III). If temperatures remain low, the recovery of photosynthesis is limited, and the photoinhibited state can last for a long period of time (III). If the photoinhibition is not complete, the higher light levels may compensate for some of the loss of photosynthetic capacity and allow at least partial replenishment of lost carbohydrates. It is, however, possible that photosynthetic capacity cannot be fully recovered even if a new snow cover is formed over the plants. If the plants are covered by new snow, the lost photosynthetic capacity will no longer be compensated for by higher light levels, and thus the replenishment of carbohydrates under the snow is prevented. This may have long-lasting effects on the plants. Respiration rates also affect the carbohydrate levels of the plants, and thus plants that are able to adjust their respiration rates according to the environmental conditions are less likely to suffer adverse effects (Cooper 2004). With the more fluctuating winter temperatures that have been predicted, snowmelt events followed by the formation of a new snow cover are likely to become more frequent in the future (Jylhä et al. 2008).

In addition to the loss of the protection provided by the snow, warm periods in winter may also cause dehardening in the plants, which may lead to frost damage if the warm period is followed by freezing temperatures (Ögren 1996, Bokhorst et al. 2010). Freezing affects not only the survival of the shoots but also further affects the ability of the plants to recover their photosynthetic capacity, as shown by the results of this study (III). Taulavuori and co-workers (2011) showed that *V. vitis-idaea* suffered from both long-lasting inhibition of photosynthesis and damage caused by desiccation when the formation of a snow cover to protect the plants was artificially prevented. In an experiment simulating an extreme winter warming event by using infrared heaters and soil-warming cables, significantly lower rates of flowering and berry production were found in *V. vitis-idaea* and *V. myrtillus*, whereas no significant effects were found for *Empetrum hermaphroditum* (Bokhorst et al. 2008). Bud burst was delayed by winter warming in *V. myrtillus* and *E. hermaphroditum*. The authors also suggested a possible decrease in the rates of photosynthesis in second-year leaves of *V. vitis-idaea* at the beginning of the next growth season, but the results were not significant. The effects of warm periods in winter may also include long-term ones affecting the plants indirectly, e.g., through changes in soil microbe activity (Groffman et al. 2001, Grogan et al. 2004). Kreyling and co-workers (2010) found that an increased frequency of soil freeze-thaw cycles during winter increased the above-ground biomass production on experimental grassland plots in the next growing season but decreased the production on heath plots in the second growing season following the treatment, with no changes observed during the first growing season.

Many northern plants adapted to adverse conditions are fairly resilient to change (Crawford 2008), possibly because of the high phenotypic plasticity of many of the species (Valladares et al. 2007). The results of the transplant experiment in this study (IV) show that *V. vitis-idaea* possesses a high plasticity in its overwintering traits. Phenotypic plasticity is also characteristic of other traits of *V. vitis-idaea*, such as leaf size and shoot morphology (Ritchie 1955). Even if the plants are able to withstand the physiological consequences of changes in overwintering conditions, species-specific responses to these changes (Crawford 2000, Aerts et al. 2006, Kreyling et al. 2011) may manifest themselves through changes in the competitive success of the plants. The present study shows that even small spatial differences in the snow cover during the winter relate to differences in vegetation (V). Increased patchiness of the snow cover in the future may increase the differences in overwintering conditions across neighbouring plants, which may further increase the effects on both the physiology of individual plants and the species composition of the field layer. The results of this study, backed by results reported in the literature, show that wintertime conditions and events can have profound effects on both the success of individual plants and the whole ecosystem and can be important drivers of changes in ecosystem functions and the species composition of the vegetation (Campbell et al. 2005, Aerts et al. 2006, Kreyling et al. 2008, 2010, Bokhorst et al. 2009). The mechanisms through which climate change affects the plant communities are complex, and many factors interact on many time scales, from minutes or hours to years. Changes in the wintertime climate and wintertime events also affect the responses to changes in environmental conditions during the growing season, which calls for research that takes the whole annual cycle of the plants into consideration.

Considerations on the setup and methods of the study

The purpose of the field measurements was to address the photosynthetic capacity and related factors of *Vaccinum vitis-idaea* in natural conditions and to assess the effects of the snow cover on the plants. The field sites were chosen so as to represent typical sites where *V. vitis-idaea* can be found, so that the results would be as generalisable as possible. It can be argued, of course, that field measurements restricted to one site and one specific winter may not necessarily give a full picture of the processes and events of overwintering. Comparison of the results of the different parts of this study with results reported in the literature does indicate, however, that the conclusions from the study can be generalised. The snow distribution study (V) also concerned one forest site only, which must be taken into account in the interpretation of the significance of the results. While the effects of the canopy on the distribution of snow and the relative effects of snow and the canopy on plant distribution are certainly specific for the site and

only generalisable to similar sites, the conclusion that different plant species show different snow affinities is more generally valid.

The use of a commercially available cultivar in (II) instead of plant material collected in the wild ensured that the genetic variation of the plants used was as small as possible. The 'Sanna' cultivar has been selected from wild populations and has a relatively short breeding history, so that the results can be generalised to wild populations of *V. vitis-idaea*. Potted plants in controlled growth chamber experiments do not necessarily react in exactly the same way as plants in natural conditions, nor do they face changes in the environment in exactly the same way. However, the possibility of exactly controlling the conditions that the plants face by moving potted plants into controlled growth chambers makes it easier to elucidate the effects of the environmental factor of interest. Potted plants were also used in the transplant experiment (IV), where the pots may have altered the particular conditions that the roots and rhizomes faced during the winter.

Studies in natural field conditions and manipulative experimental setups carried out in the field are always at the mercy of the natural variation in a number of environmental factors that cannot be controlled. While it can be argued that results from natural conditions provide the best basis for generalisation to wild plants, the multitude of factors affecting the study or experiment, many of which are impossible to control or measure adequately, may easily confound the results and make the interpretation of causal relationships difficult. Experimental manipulation of environmental factors, such as the snow cover (III), in field conditions is often less precise than it is in laboratory settings. Field studies are also subject to day-to-day variations in weather conditions, which can be eliminated in growth chambers and other laboratory experiments.

The light response of photosynthesis was measured at approximately the temperature to which the plants were exposed at the time of the measurement. In winter, the measurements were made at temperatures very close to 0 °C in field conditions. The gas exchange rates measured were low, and as the surface area of the leaves measured was small in relation to the chamber used, the difference in CO_2 content between the chamber air and control air were close to the noise level of the photosynthesis measurement system even when using a low rate of airflow through the chamber. The use of the CO_2 regulation module instead of free air helped to reduce the noise level in the measurements. The leakage of CO_2 across the gasket of the chamber (Flexas et al. 2007) was minimised by the design of the wire mesh used to support the leaf and by keeping the CO_2 gradient across the gasket as small as possible. The CO_2 gradient was kept small by doing much of the measurements outdoors and by enclosing the chamber in an external container, as proposed by Long & Bernacchi (2003), filled with air drawn from outdoors, when doing measurements in laboratory conditions, where the air CO_2 content was high due to the air exhaled by the researchers. The low measuring temperature was also prone to cause fogging in the IRGAs, which could easily

have rendered the readings useless if the state of the system had not been monitored at all times and any suspicious readings discarded and remeasured if necessary. The measuring of the complete light response curves of the leaves and the fitting of a response function to the measurements also helped to reduce the uncertainty introduced by single measurement errors. The attempted further reduction of measurement error by increasing the number of replicate samples for a given condition proved impractical due to the time required to make the individual light response curve measurements.

The light response of photosynthesis was measured by using leaves detached from the plants. In some species, the detaching of leaves causes immediate closure of the stomata and consequently also the cessation of gas exchange (Buckley 2005). Tests prior to the study, however, clearly indicated that detaching leaves of *V. vitis-idaea* had no immediate effect on the stomatal conductance or photosynthesis in the leaves for up to one hour (data not shown), which is significantly longer than the time required to measure the light response curve of photosynthesis, thus validating the use of detached leaves for these measurements. The measurements would otherwise have been very difficult or impossible to carry out in field conditions with the present equipment. A possible explanation is that the structure of the leaves of *V. vitis-idaea* is highly xeromorphic, and the leaves are thus able to, and readily do, keep their stomata open even in conditions of water stress.

The electrolyte leakage method can sometimes be sensitive to the method used to kill the samples and to the length of the time the samples are incubated (Deans et al. 1995). Too weak a methods of killing or too short an exposure may lead to failure to release all diffusable electrolytes, even after a prolonged incubation. The method of measuring damage by electrolyte leakage in leaves of *V. vitis-idaea* was therefore experimentally optimised prior to the study (data not shown) in order to obtain a reliable method yielding results that were comparable from one experiment to another. However, when comparing the results of electrolyte leakage tests in this study to those reported in the literature, and especially when comparing leakage percentages, one must keep in mind that the method used can and does affect the leakage percentages significantly.

Chlorophyll fluorescence induction was measured from leaves that had been dark-adapted in closed leaf clips for 30 minutes prior to the measuring. Care was taken to prevent any light from accidentally entering the leaf clip by wrapping a thick piece of cloth around the clip when the fiber optic probe of the fluorescence meter was attached. It has been suggested that in some situations even a minute amount of light may activate and close photosystem II reaction centres in the leaf and possibly alter the readings (Baker 2008, Bokhorst et al. 2010). The buildup of moisture on the fiber optic probe when fluorescence induction is measured in cold surroundings has been reported to cause inflated fluorescence readings in some cases (Huner et al. 1992). The effect is accentuated by a longer exposure to

actinic light and the use of temperature-controlled cuvettes, neither of which was done in this study. It is unlikely that this effect had any influence on the results of this study, since the leaves were wiped dry before they were inserted in the leaf clips and since care was taken to keep the end of the probe dry and free of fog. The data sets were also screened for possible outliers.

Conclusions

The photosynthetic capacity of *V. vitis-idaea* followed the air temperature with a delay of a few days through most of the year. During the spring following snowmelt, the photosynthetic capacity increased at a slower rate than was predicted by the temperature-driven dynamic model applied, indicating that the recovery of photosynthetic capacity was depressed by sustained photoinhibition. During the summer months the photosynthetic capacity declined, the July values being less than half of the maximum values observed in September. In the growth chamber experiments, photosynthetic capacity increased readily, with a delay similar to that observed in the field, upon the transfer of the plants from outdoors to the favourable conditions in the chambers at all times of the year. Thus, in contrast to what has been reported for evergreen trees, the induction of growth arrest and dormancy and the concomitant cold-acclimation at the end of the growing season does not cause a drop in photosynthetic capacity in *V. vitis-idaea*.

The results of this study indicate that photosynthesis occurs under the snow in *Vaccinum vitis-idaea*. The light response of photosynthesis determined in field conditions during the period of snow cover shows that positive net CO_2 exchange is possible under the snow in the prevailing light and temperature. Wintertime photosynthesis under a protective snow cover may help to replenish the carbohydrate reserves lost through respiration, especially during spring, when abundant light reaches the leaves through the snow. This notion is supported by the increasing carbohydrate levels before snowmelt observed in this study.

When the snow melts, the photosynthetic capacity of *V. vitis-idaea* slowly declines as photoprotective measures are activated and photodamage begins to build up. Photoinhibition already begins before the snow has melted completely and the leaves are fully exposed.

Freezing can have a negative effect on photosynthetic capacity, especially when it follows a period of relative warmth. Damage to membranes, especially the thylakoid membranes, and other parts of the plant can prolong the time needed for photosynthesis to recover. The decrease in photosynthetic capacity after exposure to light in combination with low temperatures can also possibly be explained by the breakdown of photosystem II in combination with the inhibition of repair mechanisms and sustained forms of photoprotection.

The spatial distribution of snow in a boreal forest is fairly stable through the winter and across winters. The distribution of many field layer plants, including *V. vitis-idaea* and other dwarf shrubs, correlates with the snow distribution. The results of this study indicate that there are species-specific differences in the snow depth affinity of the field and ground layer species, corroborating the results obtained from studies on arctic and alpine plants. The plants, especially erect dwarf shrubs, may possibly also modify the snow cover by trapping drifting snow and by changing the structure of the snow pack.

In the north, winters are predicted to become warmer, and snow conditions are predicted to change. The results of this study show that *V. vitis-idaea* retains its photosynthetic capacity during the winter and can thus utilise warm periods for photosynthesis, extending the period of active photosynthesis beyond the growing season. The protection from cold and drought, however, is lost with the loss of the snow cover, and thus the photosynthetic capacity will be lowered by freezing temperatures in combination with high light during colder periods, especially in spring. If a new snow cover is formed, the depression of photosynthesis may be even more prolonged. Winter warming may thus lead to a loss of carbohydrates in the plant as the photoinhibition of photosynthesis is sustained and the carbon lost in respiration cannot be replenished. The results of this study also show that *V. vitis-idaea* is plastic in its response to changes in overwintering conditions, which may facilitate its survival in the face of climatic change. Wintertime CO_2 exchange and the effects of changes in wintertime environmental conditions need to be taken into account in any predictions of the future success of evergreen field layer plants and also in any calculations of annual carbon budgets for the field layer.

The results of this study, in combination with many reports in the literature, show that winter is not a period of complete rest that can be ignored in ecological studies. Events and processes taking place in winter can have a profound and possibly long-term effect on the overall performance of plants and on the interactions between plants and their environment. Although the carbon balance of the plants was not explicitly measured in this study, the results suggest that wintertime photosynthesis and respiration, in combination with possible sustained photoinhibition if early snowmelt occurs, may have a considerable effect on the annual carbon balance of the plants and possibly on the whole ecosystem. Accordingly, failure to account for wintertime processes and events may hinder or even prevent a full understanding of plant performance during the growing season.

Prospects for future research

The effects of changes in the overwintering conditions of plants are complex and, as the results of this study show, the possible beneficial effects of warming may

easily be overturned by small variations in the conditions of the plants. Further elucidation of the mechanisms involved in the overwintering of plants and their effects and interactions is needed in order to gain an overall understanding of the overwintering of plants in the present climate and in the changing climate of the future. The effects of repeated freezes and thaws, only briefly touched upon in this study, are a theme that has only recently gained attention in the literature, although they are predicted to become more frequent in the future. Long-term effects of wintertime conditions, especially of more extreme, event-like conditions such as warm spells, on the survival and success of different species also need to be addressed. Studies need to be conducted both in the laboratory and in field conditions in order to address and understand the specific mechanisms behind the responses of the plants, both at the level of individual plants and at the community and ecosystem level. Mechanistic dynamic models can be useful research tools in this context, especially when the effects of multiple environmental factors on plants are studied, provided that the models are properly formulated and parameterized by adequate experimental data and field observations.

So far, very few studies have measured the wintertime CO_2 exchange of field layer plants under snow directly. Neither has the wintertime allocation and utilisation of carbon within the plants been studied. The effects of changes in the snow cover structure on the overwintering and possible wintertime photosynthesis of field layer plants also need attention. Possible differences across species in this respect also have to be addressed. Changes in wintertime conditions may have profound effects on the carbon budget of the field layer, and wintertime events must thus be included in any assessment of the carbon balance and sequestration of northern ecosystems.

Acknowledgements

I thank my supervisors, professor Heikki Hänninen and Dr Timo Saarinen for the opportunity to join the then newly formed Plant Ecophysiology and Climate Change (PECC) research group as a full member and start my Ph.D. work. The PECC group has provided a very encouraging and supporting environment for doing research that sometimes has strayed well beyond (and out of) the scope of this thesis. I want to thank Heikki for introducing me to the world of plant ecophysiology and dynamic modelling, for having faith in my work at all times despite all the strange detours and setbacks that have occurred on the way, and for always encouraging me to carry on, participate in meetings and congresses, and do teaching and other tasks besides the thesis work, but also for firmly requiring me to finish my thesis. Timo has been a great partner and mentor during the work in the field and the laboratory, always ready to take even the craziest ideas one step further and come up with several more in long undulating

References

Adams, W.W.III, Demmig-Adams, B., Rosenstiel, T.N. & Ebbert, V. 2001. Dependence of photosynthesis and energy dissipation activity upon growth form and light environment during the winter. Photosynthesis Research 67: 51–62.

Adams, W.W.III, Zarter, C.R., Ebbert, V., Demmig-Adams, B. 2004. Photoprotective strategies of overwintering evergreens. BioScience 54: 41–49.

Adams, W.W.III, Zarter, C.R., Mueh, K.E., Amiard, V. & Demmig-Adams, B. 2008. Energy dissipation and photoinhibition: a continuum of photoprotection. In: Demmig-Adams, B., Adams, W.W.III & Mattoo, A.K. (eds) Photoprotection, photoinhibition, gene regulation, and environment. Advances in Photosynthesis and Respiration 21: 49–64.

Aerts, R. 1995. The advantages of being evergreen. Trends in Ecology and Evolution 10: 402–407.

Aerts, R., Cornelissen, J.H.C. & Dorrepal, E. 2006. Plant performance in a warmer world: general responses of plants from cold, northern biomes and the importance of winter and spring events. Plant Ecology 182: 65–77.

Albert, M.R. & Perron, F.E.Jr. 2000. Ice layer and surface crust permeability in a seasonal snow pack. Hydrological processes 14: 3207–3214.

Allakhverdiev, S.I., Tsvetkova, N., Mohanty, P., Szalontai, B., Moon, B.Y., Debreczeny, M. & Murata, N. 2005. Irreversible photoinhibition of photosystem II is caused by exposure of *Synechocystis* cells to strong light for a prolonged period. Biochimica et Biophysica Acta 1708: 342–351.

Andresen, L.C. & Michelsen, A. 2005. Off-season uptake of nitrogen in temperate heath vegetation. Oecologia 144: 585–597.

Arora, R., Rowland, L.J. & Tanino, K. 2003. Induction and release of bud dormancy in woody perennials: a science comes of age. HortScience 38: 911–921.

Asada, K. 1999. The water-water cycle in chloroplasts: Scavenging of active oxygens and dissipation of excess photons. Annual Review of Plant Physiology and Plant Molecular Biology 50: 601–639.

Baena-Gonzalez, E. & Aro, E.-M. 2002. Biogenesis, assembly and turnover of photosystem II units. Philosophical Transactions of the Royal Society B - Biological Sciences 357: 1451–1460.

Baker, N.R. 2008. Chlorophyll fluorescence: a probe of photosynthesis in vivo. Annual Review of Plant Biology 59: 89–113.

Baker, N.R. & Rosenqvist, E. 2004. Application of chlorophyll fluorescence can improve crop production strategies: an examination of future possibilities. Journal of Experimental Botany 55: 1607–1621.

Banaš, M., Zeidler, M., Duchoslav, M. & Hosek, J. 2010. Growth of Alpine lady-fern (*Athyrium distentifolium*) and plant species composition on a ski piste in the Hrubý Jeseník Mts., Czech Republic. Annales Botanici Fennici 47: 280–292.

Bannister, P. 1980. The non-structural carbohydrate contents of ericaceous shrubs from Scotland and Austria. Acta Œcologia 1: 275–292.

Bauer, H. & Kofler, R. 1987. Photosynthesis in frost-hardened and frost-stressed leaves of *Hedera helix* L. Plant, Cell and Environment 10: 339–346.

Bauer, H., Nagele, M., Comploj, M., Galler, V., Mair, M. & Unterpertinger, E. 1994. Photosynthesis in cold acclimated leaves of plants with various degrees of freezing tolerance. Physiologia Plantarum 91: 403–412.

Behrenfeld, M.J., Prasil, O., Kolber, Z.S., Babin, M. & Falkowski, P.G. 1998. Compensatory changes in Photosystem II electron turnover rates protect photosynthesis from photoinhibition. Photosynthesis Research 58: 259–268.

Bergh, J., McMurtrie, R.E. & Linder, S. 1998. Climatic factors controlling the productivity of Norway spruce: a model-based analysis. Forest Ecology and Management 110: 127–139.

Billings, W.D. & Bliss, L.C. 1959. An alpine snowbank environment and its effects on vegetation, plant development, and productivity. Ecology 40: 388–397.

Björk, R.G. & Molau, U. 2007. Ecology of alpine snowbeds and the impact of global change. Arctic, Antarctic and Alpine Research 39: 34–43.

Björkman, M.P., Morgner, E., Björk, R.G., Cooper, E.J., Elberling, B. & Klemedtsson, L. 2010. A comparison of annual and seasonal carbon dioxide effluxes between sub-Arctic Sweden and High-Arctic Svalbard. Polar Research 29: 75–84.

Blakeney, A.B. & Mutton, L.L. 1980. A simple colorimetric method for the determination of sugars in fruit and vegetables. Journal of the Science of Food and Agriculture 31: 889–897.

Bokhorst, S., Bjerke, J.W., Bowles, F.W., Melillo, J., Callaghan, T.V. & Phoenix, G.K. 2008. Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland. Global Change Biology 14: 2603–2612.

Bokhorst, S., Bjerke, J.W., Davey, M.P., Taulavuori, K., Taulavuori, E., Laine, K., Callaghan, T. & Phoenix, G. 2010. Impacts of extreme winter warming events on plant physiology in a sub-Arctic heath community. Physiologia Plantarum 140: 128–140.

Bokhorst, S.F., Bjerke, J.W., Tømmervik, H., Callaghan, T.V. & Phoenix, G.K. 2009. Winter warming events damage sub-Arctic vegetation: consistent evidence from an experimental manipulation and a natural event. Journal of Ecology 97: 1408–1415.

Bolhàr-Nordenkampf, H.R., Long, S.P., Baker, N.R., Öquist, G., Schreiber, U. & Lechner, E.G. 1989. Chlorophyll fluorescence as a probe of the photosynthetic competence of leaves in the field: A review of current instrumentation. Functional Ecology 3: 497–514.

Buckley, T.N. 2005. The control of stomata by water balance. New Phytologist 168: 275–292.

Busch, F., Hüner, N.P.A. & Ensminger, I. 2007. Increased air temperature during simulated autumn conditions does not increase photosynthetic carbon gain but affects the dissipation of excess energy in seedlings of the evergreen conifer jack pine. Plant Physiology 143: 1242–1251.

Campbell, J.L., Mitchell, M.J., Groffman, P.M., Christenson, L.M. & Hardy, J.P. 2005. Winter in northeastern North America: a critical period for ecological processes. Frontiers in Ecology and the Environment 3: 314–322.

Cavender-Bares, J. & Bazzaz, F.A. 2004. From leaves to ecosystems: assessing photosynthesis and plant function in ecological studies. In: George C. Papageorgiou and Govindjee (eds.): Chlorophyll fluorescence: a signature of photosynthesis. pp. 737–755.

Chabot, B.F. & Hicks, D.J. 1982. The ecology of leaf life spans. Annual Review of Ecology and Systematics 13: 229–259.

Chinnusamy, V., Zhu, J. & Zhu, J.-K. 2007. Cold stress regulation of gene expression in plants. Trends in Plant Science 12: 444–451.

Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.-T., Laprise, R., Magaña Rueda, V., Mearns, L., Menéndez, C.G., Räisänen, J., Rinke, A., Sarr, A. & Whetton, P. 2007. Regional climate projections. In: Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.)]. Cambridge UniversityPress, Cambridge, United Kingdom and New York, NY, USA. pp. 847–940.

Close, D.C. & McArthur, C. 2002. Rethinking the role of many plant phenolics - protection from photodamage not herbivores. Oikos 99: 166–172.

Colbeck, S.C. 1997. Model of wind pumping for layered snow. Journal of Glaciology 43: 60–65.

Cooper, E.J. 2004. Out of Sight, Out of Mind: Thermal Acclimation of Root Respiration in Arctic *Ranunculus*. Arctic, Antarctic and Alpine Research 36: 308–313.

Cooper, E.J., Dullinger, S. & Semenchuk, P. 2011. Late snowmelt delays plant development and results in lower reproductive success in the High Arctic. Plant Science 180: 157–167.

Crawford, R.M.M. 2000. Ecological hazards of oceanic environments. New Phytologist 147: 257–281.

Crawford, R.M.M. 2008. Cold climate plants in a warmer world. Plant Ecology & Diversity 1: 285–297.

Curl, H.Jr, Hardy, J.T. & Ellermeier, R. 1972. Spectral absorption of solar radiation in alpine snowfields. Ecology 53: 1189–1194.

Deans, J.D., Billington, H.L. & Harvey, F.J. 1995. Assessment of frost damage to leafless stem tissues of *Quercus petraea*: A reappraisal of the method of relative conductivity. Forestry 68: 25–34.

Debnath, S.C. 2007. Inter simple sequence repeat (ISSR) to assess genetic diversity within a collection of wild lingonberry (*Vaccinium vitis-idaea* L.) clones. Canadian Journal of Plant Science 87: 337–344.

DeLucia, E.H. 1987. The effect of freezing nights on photosynthesis, stomatal conductance, and internal CO_2 concentration in seedlings of Engelmann spruce (*Picea engelmannii* Parry). Plant, Cell and Environment 10: 333–338.

Demmig-Adams, B., Adams, W.W. III, Logan, B.A. & Verhoeven, A.S. 1995. Xanthophyll cycle-dependent energy dissipation and flexible photosystem II efficiency in plants acclimated to light stress. Australian Journal of Plant Physiology 22: 249–260.

Demmig-Adams, B. & Adams, W.W. III. 2002. Antioxidants in photosynthesis and human nutrition. Science 298: 2149–2153.

Demmig-Adams, B. & Adams W.W.III. 2006. Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. New Phytologist 172: 11–21.

Demmig-Adams, B., Ebbert, V., Mellman, D.L., Mueh, K.E., Schaffer, L., Funk, C., Zarter, C.R., Adamska, I., Jansson, S. & Adams, W.W.III. 2006. Modulation of PsbS and flexible vs sustained energy dissipation by light environment in different species. Physiologia Plantarum 127: 670–680.

Demmig-Adams, B., Ebbert, V., Zarter, C.R. & Adams, W.W.III. 2008. Characteristics and species-dependent employment of flexible versus sustained thermal dissipation and photoinhibition. In: Demmig-Adams, B., Adams, W.W.III & Mattoo, A.K. (eds) Photoprotection, photoinhibition, gene regulation, and environment. Advances in Photosynthesis and Respiration 21: 39–48.

Dutilleul, P. 1993. Modifying the t test for assessing the correlation between two spatial processes. Biometrics 49: 305–314.

Edelman, M. & Mattoo, A.K. 2008. D1-protein dynamics in photosystem II: the lingering enigma. Photosynthesis Research 98: 609–620.

Ensminger, I., Busch, F. & Huner, N.P.A. 2006. Photostasis and cold acclimation: sensing low temperature through photosynthesis. Physiologia Plantarum 126: 28–44.

Ensminger, I., Schmidt, L. & Lloyd, J. 2008. Soil temperature and intermittent frost modulate the rate of recovery of photosynthesis in Scots pine under simulated spring conditions. New Phytologist 177: 428–442.

Ensminger, I., Sveshnikov, D., Campbell, D.A., Funk, C., Jansson, S., Lloyd, J., Shibistova, O. & Öquist, G. 2004. Intermittent low temperatures constrain spring recovery of photosynthesis in boreal Scots pine forests. Global Change Biology 10: 995–1008.

Essery, R., Pomeroy, J., Ellis, C. & Link, T. 2008. Modelling longwave radiation to snow beneath forest canopies using hemispherical photography or linear regression. Hydrological Processes 22: 2788–2800.

Fahnestock, J.T., Jones, M.H., Brooks, P.D., Walker, D.A. & Welker, J.M. 1998. Winter and early spring CO_2 efflux from tundra communities of northern Alaska. Journal of Geophysical Research 103: 29023–29027.

Flexas, J., Díaz-Espejo, A., Berry, J.A., Cifre, J., Galmés, J., Kaldenhoff, R., Medrano, H. & Ribas-Carbó, M. 2007. Analysis of leakage in IRGA's leaf chambers of open gas exchange systems: quantification and its effects in photosynthesis parameterization. Journal of Experimental Botany 58: 1533–1543.

Garkava-Gustavsson, L., Persson, H.A., Nybom, H., Rumpunen, K., Gustavsson, B.A. & Bartish, I.V. 2005. RAPD-based analysis of genetic diversity and selection of lingonberry (*Vaccinium vitis-idaea* L.) material for ex situ conservation. Genetic Resources and Crop Evolution 52: 723–735.

Gea-Izquierdo, G., Mäkelä, A., Margolis, H., Bergeron, Y., Black, T.A., Dunn, A., Hadley, J., Paw, U.K.T., Falk, M., Wharton, S., Monson, R., Hollinger, D.Y., Laurila, T., Aurela, M., McCaughley, H., Bourque, C., Vesala, T. & Berninger, F. 2010. Modeling acclimation of photosynthesis to temperature in evergreen conifer forests. New Phytologist 188: 175–186.

Gerland, S., Liston, G.E., Winther, J.-G., Ørbæk, J.B., Ivanov, B.V. 2000. Attenuation of solar radiation in Arctic snow - field observations and modelling. Annals of Glaciology 31: 364–368.

Gerland, S., Winther, J.-G., Ørbæk, J.B., Liston, G.E., Øritsland, N.A., Blanco, A. & Ivanov, B. 1999. Physical and optical properties of snow covering Arctic tundra on Svalbard. Hydrological Processes 13: 2331–2343.

Germino, M.J. & Smith, W.K. 2000. Differences in microsite, plant form, and low-temperature photoinhibition in alpine plants. Arctic, Antarctic and Alpine Research 32: 388–396.

Gilmore, A.M. & Ball, M.C. 2000. Protection and storage of chlorophyll in overwintering evergreens. Proceedings of the National Academy of Science 97: 11098–11101.

Givnish, T.J. 2002. Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. Silva Fennica 36: 703–743.

Gorton, H.L. & Vogelmann, T.C. 2003. Ultraviolet radiation and the snow alga *Chlamydomonas nivalis* (Bauer) Wille. Photochemistry and Photobiology 77: 608–615.

Goulas, E., Schubert, M., Kieselbach, T., Kleczkowski, L.A., Gardeström, P., Schröder, W. & Hurry, V. 2006. The chloroplast lumen and stromal proteomes of *Arabidopsis thaliana* show differential sensitivity to short- and long-term exposure to low temperature. The Plant Journal 47: 720–734.

Gould, K.S., Neill, S.O. & Vogelmann, T.C. 2002. A unified explanation for anthocyanins in leaves? Advances in Botanical Research 37: 167–192.

Greer, D.H., Ottander, C. & Öquist, G. 1991. Photoinhibition and recovery of photosynthesis in intact barley leaves at 5 and 20°C. Physiologia Plantarum 81: 203–210.

Griffith, M. & Yaish, M.W.F. 2004. Antifreeze proteins in overwintering plants - a tale of two activities. Trends in Plant Science 9: 399–405.

Groffman, P.M., Driscoll, C.T., Fahey, T.J., Hardy, J.P., Fitzhugh, R.D. & Tierney, G.L. 2001. Colder soils in a warmer world - A snow manipultion study in a northern hardwood forest ecosystem. Biogeochemistry 56: 135–150.

Grogan, P., Jonasson, S. 2006. Ecosystem CO_2 production during winter in a Swedish subarctic region: the relative importance of climate and vegetation type. Global Change Biology 12: 1479–1495.

Grogan, P., Michelsen, A., Ambus, P. & Jonasson, S. 2004. Freeze-thaw regime effects on carbon and nitrogen dynamics in sub-arctic heath tundra mesocosms. Soil Biology & Biochemistry 36: 641–654.

Gustavsson, B.A. 1993. Lingonberry breeding and cultivation (*Vaccinium vitis-idaea* L.). Acta horticulturae 346: 311–313.

Gustavsson, B.A. 2001. Genetic variation in horticulturally important traits of fifteen wild lingonberry *Vaccinium vitis-idaea* L. populations. Euphytica 120: 173–182.

Gustavsson, B.A. & Stanys, V. 2000. Field performance of 'Sanna' lingonberry derived by micropropagation vs. stem cuttings. HortScience 35: 742–744.

Guy, C.L. 2003. Freezing tolerance of plants: current understanding and selected emerging concepts. Canadian Journal of Botany 81: 1216–1223.

Guy, C.L., Huber, J.L.A. & Huber, S.C. 1992. Sucrose phosphate synthase and sucrose accumulation at low temperature. Plant Physiology 100: 502–508.

Hacker, J. & Neuner, G. 2006. Photosynthetic capacity and PSII efficiency of the evergreen alpine cushion plant *Saxifraga paniculata* during winter at different altitudes. Arctic, Antarctic and Alpine Research 38: 198–205.

Hadley, J.L. 2000. Effect of daily minimum temperature on photosynthesis in eastern hemlock (*Tsuga canadensis* L.) in autumn and winter. Arctic, Antarctic and Alpine Research 32: 368–374.

Hänninen, H., Kolari, P. & Hari, P. 2006. Seasonal development of Scots pine under climatic warming: effects on photosynthetic production. Canadian Journal of Forest Research 35: 2092–2099.

Hänninen, H., Slaney, M. & Linder, S. 2007. Dormancy release of Norway spruce under climate warming: testing ecophysiological models of bud burst with a whole-tree chamber experiment. Tree physiology 27: 291–300.

Hardy, J.P. & Albert, M.R. 1995. Snow-induced thermal variations around a single conifer tree. Hydrological Processes 9: 923–933.

Hardy, J.P., Groffman, P.M., Fitzhugh, R.D., Henry, K.S., Welman, A.T., Demers, J.D., Fahey, T.J., Driscoll, C.T., Tierney, G.L. & Nolan, S. 2001. Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest. Biogeochemistry 56: 151–174.

Harris, G.C., Antoine, V., Chan, M., Nevidomskyte, D. & Königer, M. 2006. Seasonal changes in photosynthesis, protein composition and mineral content in *Rhododendron* leaves. Plant science 170: 314–325.

Havas, P. 1966. Pflanzenökologische Untersuchungen im Winter. I. Zur Bedeutung der Schneedecke für das Überwintern von Heidel- und Preisselbeere. Aquilo Ser. Botanica 4: 1–36.

Havas, P. 1985. Winter and the boreal forest. Aquilo Ser. Botanica 23: 9–16.

Hedstrom, N.R. & Pomeroy, J.W. 1998. Measurements and modelling of snow interception in the boreal forest. Hydrological processes 12: 1611–1625.

Hideg, E. & Murata, N. 1997. The irreversible photoinhibition of the photosystem II complex in leaves of *Vicia faba* under strong light. Plant Science 130: 151–158.

Hikosaka, K., Kato, M.C. & Hirose, T. 2004. Photosynthetic rates and partitioning of absorbed light energy in photoinhibited leaves. Physiologia Plantarum 121: 699–708.

Hoch, W.A., Zeldin, E.L. & McCown, B.H. 2001. Physiological significance of antocyanins during autumnal leaf senescence. Tree physiology 21: 1–8.

Höglind, M., Hanslin, H.M. & Mortensen, L.M. 2010. Photosynthesis of *Lolium perenne* L. at low temperatures under low irradiances. Environmental and Experimental Botany 70: 297–304.

Holt, N.E., Zigmantas, D., Valkunas, L., Li, X.-P., Niyogi, K.K. & Fleming, G.R. 2005. Carotenoid cation formation and the regulation of photosynthetic light harvesting. Science 307: 433–435.

Hoshino, T., Odaira, M., Yoshida, M. & Tsuda, S. 1999. Physiological and biochemical significance of antifreeze substances in plants. Journal of Plant Research 112: 255–261.

Hughes, N.M. 2011. Winter leaf reddening in 'evergreen' species. New Phytologist 190: 573–581.

Hughes, N.M., Neufeld, H.S. & Burkey, K.O. 2005. Functional role of anthocyanins in high-light winter leaves of the evergreen herb *Galax urceolata*. New Phytologist 168: 575–588.

Huner, N.P.A., Öquist, G. & Sarhan, F. 1998. Energy balance and acclimation to light and cold. Trends in Plant Science 3: 224–230.

Huner, N.P.A., Öquist, G. & Sundblad, L.-G. 1992. Low measuring temperature induced artifactual increase in chlorophyll a fluorescence. Plant Physiology 98: 749–752.

Ivanov, A.G., Hurry, V., Sane, P.V., Öquist, G. & Huner, N.P.A. 2008. Reaction centre quenching of excess light energy and photoprotection of photosystem II. Journal of Plant Biology 51: 85–96.

Ivanov, A.G., Sane, P.V., Zeinalov, Y., Malmberg, G., Gardeström, P., Huner, N.P.A. & Öquist, G. 2001. Photosynthetic electron transport adjustments in overwintering Scots pine (*Pinus sylvestris* L.). Planta 213: 575–585.

Jaspers, P. & Kangasjärvi, J. 2010. Reactive oxygen species in abiotic stress signaling. Physiologia Plantarum 138: 405–413.

Jentsch, A., Kreyling, J. & Beierkuhnlein, C. 2007. A new generation of climate change experiments: events, not trends. Frontiers in Ecology and the Environment 5: 365–374.

Jones, H.G. 1999. The ecology of snow-covered systems: a brief overview of nutrient cycling and life in the cold. Hydrological processes 13: 2135–2147.

Jylhä, K., Fronzek, S., Tuomenvirta, H., Carter, T.R. & Ruosteenoja, K. 2008. Changes in frost, snow and Baltic sea ice by the end of the twenty-first century based on climate model projections for Europe. Climatic Change 86: 441–462.

Jylhä, K., Ruosteenoja, K., Räisänen, J., Venäläinen, A., Tuomenvirta, H., Ruokolainen, L., Saku, S. ja Seitola, T. 2009. Arvioita Suomen muuttuvasta ilmastosta sopeutumistutkimuksia varten. ACCLIM-hankkeen raportti 2009. (The changing climate in Finland: estimates for adaptation studies. ACCLIM project report 2009.) Ilmatieteen laitos, Raportteja 2009: 1–102. [In Finnish, with english abstract, extended abstract and captions].

Kalberer, S.R., Wisniewski, M. & Arora, R. 2006. Deacclimation and reacclimation of cold-hardy plants: Current understanding and emerging concepts. Plant Science 171: 3–16.

Kaňa, R., Lazár, D., Prášil, O. & Nauš, J. 2002. Experimental and theoretical studies on the excess capacity of Photosystem II. Photosynthesis Research 72: 271–284.

Kappen, L., Schroeter, B., Hestmark, G., Winkler, J.B. 1996. Field measurements of photosynthesis of umbilicarious lichens in winter. Botanica Acta 109: 292–298.

Kappen, L., Sommerkorn, M. & Schroeter, B. 1995. Carbon acquisition and water relations of lichens in polar regions - potentials and limitations. Lichenologist 27: 531–545

Karlsson, P.S. 1985. Photosynthetic characteristics and leaf carbon economy of a deciduous and an evergreen dwarf shrub - *Vaccinium uliginosum* L. and *V. vitis-idaea* L. Holarctic Ecology 8: 9–17.

Karlsson, P.S. 1989. In situ photosynthetic performance of four coexisting dwarf shrubs in relation to light in a subarctic woodland. Functional Ecology 3: 481–487.

Kasuga, J., Hashidoko, Y., Nishioka, A., Yoshiba, M., Arakawa, K. & Fujikawa, S. 2008. Deep supercooling xylem parenchyma cells of katsura tree (*Cercidiphyllum japonicum*)

contain flavonol glycosides exhibiting high anti-ice nucleation activity. Plant, Cell and Environment 31: 1335–1343.

Keren, N. & Krieger-Liszkay, A. 2011. Photoinhibition: molecular mechanisms and physiological significance. Physiologia Plantarum 142: 1–5.

Kikuzawa, K. 1984. Leaf survival of woody plants in deciduous broad-leaved forests. 2. Small trees and shrubs. Canadian Journal of Botany 62: 2551–2556.

King, M.D. & Simpson, W.R. 2001. Extinction of UV radiation in Arctic snow at Alert, Canada (82°N). Journal of Geophysical Research 106: 12499–12507.

Koh, S.C., Demmig-Adams, B. & Adams, W.W.III. 2009. Novel Patterns of Seasonal Photosynthetic Acclimation, Including Interspecific Differences, in Conifers over an Altitudinal Gradient. Arctic, Antarctic and Alpine Research 41: 317–322.

Kolari, P., Lappalainen, H.K., Hänninen, H. & Hari, P. 2007. Relationship between temperature and the seasonal course of photosynthesis in Scots pine at northern timberline and in southern boreal zone. Tellus 59B: 542–552.

Kolari, P., Pumpanen, J., Kulmala, L., Ilvesniemi, H., Nikinmaa, E., Grönholm, T. & Hari, P. 2006. Forest floor vegetation plays an important role in photosynthetic production of boreal forests. Forest Ecology and Management 221: 241–248.

Kreyling, J. 2010. Winter climate change: a critical factor for temperate vegetation performance. Ecology 91: 1939–1948.

Kreyling, J., Beierkuhnlein, C. & Jentsch, A. 2010. Effects of soil freeze-thaw cycles differ between experimental plant communities. Basic and Applied Ecology 11: 65–75.

Kreyling, J., Beierkuhnlein, C., Pritsch, K., Schloter, M. & Jentsch, A. 2008. Recurrent soil freeze-thaw cycles enhance grassland productivity. New Phytologist 177: 938–945.

Kreyling, J., Jurasinski, G., Grant, K., Retzer, V., Jentsch, A. & Beierkuhnlein, C. 2011. Winter warming pulses affect the development of planted temperate grassland and dwarf-shrub heath communities. Plant Ecology & Diversity: [in press].

Krieger-Liszkay, A., Fufezan, C. & Trebst, A. 2008. Singlet oxygen production in photosystem II and related protection mechanism. Photosynthesis Research 98: 551–564.

Kudo, G., Nordenhäll, U. & Molau, U. 1999. Effects of snowmelt timing on leaf traits, leaf production, and shoot growth of alpine plants: Comparisons along a snowmelt gradient in northern Sweden. Écoscience 6: 439–450.

Kulmala, L., Pumpanen, J., Hari, P. & Vesala, T. 2011. Photosynthesis of ground vegetation in different aged pine forests: Effect of environmental factors predicted with a process-based model. Journal of Vegetation Science 22: 96–110.

Kuuluvainen, T. & Pukkala, T. 1989. Effect of Scots pine seed trees on the density of ground vegetation and tree seedlings. Silva Fennica 23: 159–167.

Landhäusser, S.M., Stadt, K.J. & Lieffers, V.J. 1997. Photosynthetic strategies of summergreen and evergreen understory herbs of the boreal mixedwood forest. Oecologia 112: 173–178.

Larsen, K.S., Ibrom, A., Jonasson, S., Michelsen, A. & Beier C. 2007. Significance of cold-season respiration and photosynthesis in a subarctic heath ecosystem in Northern Sweden. Global Change Biology 13: 1498–1508.

Lehner, G. & Lütz, C. 2003. Photosynthetic functions of cembran pines and dwarf pines during winter at timberline as regulated by different temperatures, snowcover and light. Journal of Plant Physiology 160: 153–166.

Leverenz, J.W. & Öquist, G. 1987. Quantum yields of photosynthesis at temperatures between -2 °C and 35 °C in a cold-tolerant C3 plant (*Pinus sylvestris*) during the course of one year. Plant, Cell and Environment 10: 287–295.

Li, C., Junttila, O., Ernstsen, A., Heino, P. & Palva, E.T. 2003. Photoperiodic control of growth, cold acclimation and dormancy development in silver birch (*Betula pendula*) ecotypes. Physiologia Plantarum 117: 206–212.

Li, X.-P., Björkman, O., Shih, C., Grossman, A.R., Rosenquist, M., Jansson, S. & Niyogi, K.K. 2000. A pigment-binding protein essential for regulation of photosynthetic light harvesting. Nature 403: 391–395.

Lim, C.C., Arora, R. & Townsend, E.C. 1998. Comparing Gompertz and Richards functions to estimate freezing injury in *Rhododendron* using electrolyte leakage. Journal of the American Society for Horticultural Science 123: 246–252.

Long, S.P. & Bernacchi, C.J. 2003. Gas exchange measurments, what can they tell us about the underlying limitations to photosynthesis? Procedures and sources of error. Journal of Experimental Botany 54: 2393–2401.

Long, S.P., Humphries, S. & Falkowski, P.G. 1994. Photoinhibition of photosynthesis in nature. Annual Review of Plant Physiology and Plant Molecular Biology 45: 633–662.

López-Moreno, J.I. & Latron, J. 2008. Influence of canopy density on snow distribution in a temperate mountain range. Hydrological processes 22: 117–126.

Lundmark, T., Hällgren, J.-E. & Hedén, J. 1988. Recovery from winter depression of photosynthesis in pine and spruce. Trees 2: 110–114.

Luoranen, J., Repo, T. & Lappi, J. 2004. Assessment of the frost hardiness of shoots of silver birch (*Betula pendula*) seedlings with and without controlled exposure to freezing. Canadian Journal of Forest Research 34: 1108–1118.

Lüttge, U & Hertel, B. 2009. Diurnal and annual rhythms in trees. Trees 23: 683–700.

Lütz, C. 1996. Avoidance of photoinhibition and examples of photodestruction in high alpine *Eriophorum*. Journal of Plant Physiology 148: 120–128.

Lütz, C. 2010. Cell physiology of plants growing in cold environments. Protoplasma 244: 53–73.

Lütz, C., Schönauer, E. & Neuner, G. 2005. Physiological adaptation before and after snow melt in green overwintering leaves of some alpine plants. Phyton 45: 139–156.

Mäkelä, A., Hari, P., Berninger, F., Hänninen, H. & Nikinmaa, E. 2004. Acclimation of photosynthetic capacity in Scots pine to the annual cycle of temperature. Tree Physiology 24: 369–376.

Manuel, N., Cornic, G., Aubert, S., Choler, P., Bligny, R. & Heber, U. 1999. Protection against photoinhibition in the alpine plant *Geum montanum*. Oecologia 119: 149–158.

Marchand, P.J. 1985. Oxygen evolution by *Elodea canadensis* under snow and ice cover: a case for winter photosynthesis in subnivean vascular plants. Aquilo Ser. Botanica 23: 57–61.

Marshall, B. & Biscoe, P.V. 1980. A model for C3 leaves describing the dependence of net photosynthesis on irradiance. Journal of Experimental Botany 31: 29–39.

Maxwell, K. & Johnson, G.N. 2000. Chlorophyll fluorescence - a practical guide. Journal of Experimental Botany 51: 659–668.

Mellander, P.-E., Laudon, H. & Bishop, K. 2005. Modelling variability of snow depths and soil temperatures in Scots pine stands. Agricultural and Forest Meteorology 133: 109–118.

Mellander, P.-E., Ottoson Löfvenius, M. & Laudon, H. 2007. Climate change impact on snow and soil temperature in boreal Scots pine stands. Climatic Change 85: 179–193.

Moffatt, B., Ewart, V. & Eastman, A. 2006. Cold comfort: plant antifreeze proteins. Physiologia Plantarum 126: 5–16.

Mohanty, P., Allakhverdiev, S.I. & Murata, N. 2007. Application of low temperatures during photoinhibition allows characterization of individual steps in photodamage and the repair of photosystem II. Photosynthesis Research 94: 217–224.

Morgner, E., Elberling, B., Strebel, D. & Cooper, E. 2010. The importance of winter in annual ecosystem respiration in the High Arctic: effects of snow depth in two vegetation types. Polar Research 29: 58–74.

Müller, P., Li, X.-P. & Niyogi, K.K. 2001. Non-photochemical quenching. a response to excess light energy. Plant Physiology 125: 1558–1566.

Murata, N., Takahashi, S., Nishiyama, Y. & Allakhverdiev, S.I. 2007. Photoinhibition of photosystem II under environmental stress. Biochimica et Biophysica Acta 1767: 414–421.

Musselman, R.C., Massman, W.J., Frank, J.M. & Korfmacher, J.L. 2005. The temporal dynamics of carbon dioxide under snow in a high elevation rocky mountain subalpine forest and meadow. Arctic, Antarctic and Alpine Research 37: 527–538.

Nakashima, K. & Yamaguchi-Shinozaki, K. 2006. Regulons involved in osmotic stress-responsive and cold stress-responsive gene expression in plants. Physiologia Plantarum 126: 62–71.

Nelson, N. & Yocum, C.F. 2006. Structure and Function of Photosystems I and II. Annual Review of Plant Biology 57: 521–565.

Neuner, G., Ambach, D. & Aichner, K. 1999. Impact of snow cover on photoinhibition and winter desiccation in evergreen *Rhododendron ferrugineum* leaves during subalpine winter. Tree Physiology 19: 725–732.

Neuner, G. & Pramsohler, M. 2006. Freezing and high temperature thresholds of photosystem 2 compared to ice nucleation, frost and heat damage in evergreen subalpine plants. Physiologia Plantarum 126: 196–204.

Nishiyama, Y., Allakhverdiev, S.I. & Murata, N. 2006. A new paradigm for the action of reactive oxygen species in the photoinhibition of photosystem II. Biochimica et Biophysica Acta 1757: 742–749.

Niyogi, K.K. 1999. Photoprotection Revisited: Genetic and Molecular Approaches. Annual Review of Plant Physiology and Plant Molecular Biology 50: 333–359.

Noctor, G. & Foyer, C.H. 1998. Ascorbate and glutathione: Keeping active oxygen under control. Annual Review of Plant Physiology and Plant Molecular Biology 49: 249–279.

Oberbauer, S.F. & Oechel, W.C. 1989. Maximum CO_2-assimilation rates of vascular plants on an Alaskan arctic tundra slope. Holarctic Ecology 12: 312–316.

Oberbauer, S.F & Starr, G. 2002. The role of anthocyanins for photosynthesis of Alaskan arctic evergreens during snowmelt. Advances in Botanical Research 37: 129–145.

Odland, A. & Munkejord, H.C. 2008. Plants as indicators of snow layer duration in southern Norwegian mountains. Ecological Indicators 8: 57–68.

Ögren, E. 1993. Convexity of the photosynthetic light-response curve in relation to intensity and direction of light during growth. Plant Physiology 101: 1013–1019.

Ögren, E. 1996. Premature dehardening in *Vaccinium myrtillus* during a mild winter - a cause for winter dieback. Functional Ecology 10: 724–732.

Ögren, E. 1997. Relationship between temperature, respiratory loss of sugar and premature dehardening in dormant Scots pine seedlings. Tree Physiology 17: 47–51.

Ögren, E. 2001. Effects of climatic warming on cold hardiness of some northern woody plants assessed from simulation experiments. Physiologia Plantarum. 112: 71–77.

Oguchi, R., Terashima, I., Kou, J. & Chow, W.S. 2011. Operation of dual mechanisms that both lead to photoinactivation of Photosystem II in leaves by visible light. Physiologia Plantarum 142: 47–55.

Olsen, J.E. 2010. Light and temperature sensing and signaling in induction of bud dormancy in woody plants. Plant Molecular Biology 73: 37–47.

Onipchenko, V.G., Makarov, M.I., van Logtestijn, R.S.P., Ivanov, V.B., Akhmetzhanova, A.A., Tekeev, D.K., Ermak, A.A., Salpagarova, F.S., Kozhevnikova, A.D. & Cornelissen, J.H.C. 2009. New strategy for nitrogen uptake: specialized snow roots. Ecology Letters 12: 758–764.

Öquist, G., Chow, W.S. & Anderson, J.M. 1992. Photoinhibition of photosynthesis represents a mechanism for the long-term regulation of photosystem II. Planta 186: 450–460.

Öquist, G. & Huner, N.P.A. 2003. Photosynthesis of overwintering evergreen plants. Annual Review of Plant Biology 54: 329–355.

Öquist, G. & Malmberg, G. 1989. Light and temperature dependent inhibition of photosynthesis in frost-hardened and un-hardened seedlings of pine. Photosynthesis Research 20: 261–277.

Öquist, G. & Wass, R. 1988. A portable, microprocessor operated instrument for measuring chlorophyll fluorescence kinetics in stress physiology. Physiologia Plantarum 73: 211–217.

Ort, D.R. & Baker, N.R. 2002. A photoprotective role for O2 as an alternative electron sink in photosynthesis. Current Opinion in Plant Biology 5: 193–198.

Ottander, C., Campbell, D. & Öquist, G. 1995. Seasonal changes in photosyntem II organisation and pigment composition in *Pinus sylvestris*. Planta 197: 176–183.

Ottander, C. & Öquist, G. 1991. Recovery of photosynthesis in winter-stressed Scots pine. Plant, Cell and Environment 14: 345–349.

Pagter, M., Hausman, J.-F. & Arora, R. 2010. Deacclimation kinetics and carbohydrate changes in stem tissues of *Hydrangea* in response to an experimental warm spell. Plant Science 180: 140–148.

Park, Y.-I., Chow, W.S. & Anderson, J.M. 1996. Chloroplast movement in the shade plant *Tradescantia albiflora* helps protect photosystem II against light stress. Plant Physiology 111: 867–875.

Parker, J. 1953. Photosynthesis of *Picea excelsa* in winter. Ecology 34: 605–609.

Parker, J. 1961. Seasonal trends in carbon dioxide absorption, cold resistance, and transpiration of some evergreens. Ecology 42: 372–380.

Paul, M.J. & Foyer, C.H. 2001. Sink regulation of photosynthesis. Journal of Experimental Botany 52: 1383–1400.

Pearce, R.S. 2001. Plant freezing and damage. Annals of Botany 87: 417–424.

Pelkonen, P. & Hari, P. 1980. The dependence of the springtime recovery of CO_2 uptake in Scots pine on temperature and internal factors. Flora 169: 398–404.

Persson, H.A. & Gustavsson, B.A. 2001. The extent of clonality and genetic diversity in lingonberry (*Vaccinium vitis-idaea* L) revealed by RAPDs and leaf-shape analysis. Molecular Ecology 10: 1385–1397.

Pisek, A. & Winkler, E. 1958. Assimilationsvermögen und Respiration der Fichte (*Picea excelsa* Link) in Verschiedener Höhenlage und der Zirbe (*Pinus cembra* L) an der Alpinen Waldgrenze. Planta. 51: 518–543.

Pomeroy, J. & Brun, E. 2001. Physical properties of snow. In: Jones, H., Pomeroy, J., Walker, D. & Hoham, R. (eds). Snow ecology. Cambridge University Press. Cambridge (UK). p. 45–126.

Pomeroy, J.W & Dion, K. 1996. Winter radiation extinction and reflection in a boreal pine canopy: measurements and modelling. Hydrological processes 10: 1591–1608.

Pomeroy, J.W., Gray, D.M., Hedström, N.R. & Janowicz, J.R. 2002. Predictions of seasonal snow accumulation in cold climate forests. Hydrological processes 16: 3543–3558.

Quarmby C. & Allen S.E. 1989. Organic constituents. In S.E. Allen (ed.): Chemical analysis of ecological materials. Blackwell Scientific Publications. Oxford (UK). p. 160–200.

Raines, C.A. 2003. The Calvin cycle revisited. Photosynthesis Research 75: 1–10.

Räisänen, J. 2008. Warmer climate: less of more snow? Climate Dynamics 30: 307–319.

Rasmus, S. 2005. Snow pack structure characteristics in Finland - measurements and modelling. Report Series in Geophysics (University of Helsinki) 48: 1–238. [Ph.D. thesis].

Rasmus, S., Grönholm, T., Lehning, M., Rasmus, K. & Kulmala, M. 2007. Validation of the SNOWPACK model in five different snow zones in Finland. Boreal Environment Research 12: 467–488.

Raunkiaer, C. 1934. The life forms of plants and statistical plant geography. Oxford University Press (Clarendon Press), Oxford. 632 pp.

Rautiainen, M., Stenberg, P. & Nilson, T. 2005. Estimating canopy cover in Scots pine stands. Silva Fennica 39: 137–142.

Regehr, D.L. & Bazzaz, F.A. 1976. Low temperature photosynthesis in successional winter annuals. Ecology 57: 1297–1303.

Repo, T., Leinonen, I., Wang, K.-Y. & Hänninen, H. 2006. Relation between photosynthetic capacity and cold hardiness in Scots pine. Physiologia Plantarum 126: 224–231.

Resco, V., Hartwell, J. & Hall, A. 2009. Ecological implications of plants' ability to tell the time. Ecology Letters 12: 583–592.

Richardson, S.G. & Salisbury, F.B. 1977. Plant responses to the light penetrating snow. Ecology 58: 1152–1158.

Ritchie, J.C. 1955. Biological flora of the British Isles. *Vaccinium vitis-idaea* L. Journal of Ecology 43: 701–708.

Rixen, C., Stoeckli, V. & Ammann, W. 2003. Does artificial snow production affect soil and vegetation of ski pistes? A review. Perspectives in Plant Ecology, Evolution and Systematics 5: 219–230.

Rochaix, J.-D. 2010. Regulation of photosynthetic electron transport. Biochimica et Biophysica Acta 1807: 375–383.

Rohde, A. & Bhalerao, R. 2007. Plant dormancy in the perennial context. Trends in Plant Science 12: 217–223.

Rokka, A., Suorsa, M., Saleem, A., Battchikova, N. & Aro, E.-M. 2005. Synthesis and assembly of thylakoid protein complexes: multiple assembly steps of photosystem II. Biochemical Journal 388: 159–168.

Rouhier, N., Lemaire, S.D. & Jacquot, J.-P. 2008. The role of glutathione in photosynthetic organisms: emerging functions for glutaredoxins and glutathionylation. Annual Review of Plant Biology 59: 143–166.

Ruelland, E., Vaulthier, M.-N., Zachowski, A. & Hurry, V. 2009. Cold signalling and cold acclimation in plants. Advances in Botanical Research 49: 35–150.

Sarvikas, P., Tyystjärvi, T. & Tyystjärvi, E. 2010. Kinetics of prolonged photoinhibition revisited: photoinhibited photosystem II centres do not protect the active ones against loss of oxygen evolution. Photosynthesis Research 103: 7–17.

Savitch, L.V., Leonardos, E.D., Krol, M., Jansson., S., Grodzinski, B., Huner, N.P.A. & Öquist, G. 2002. Two different strategies for light utilization in photosynthesis in relation to growth and cold acclimation. Plant, Cell and Environment 25: 761–771.

Saxe, H., Cannell, M.G.R., Johnsen, Ø., Ryan, M.G. & Vourlitis, G. 2001. Tree and forest functioning in response to global warming. New Phytologist 149: 369–399.

Schaberg, P.G. 2000. Winter photosynthesis in red spruce (*Picea rubens* Sarg.): limitations, potential benefits, and risks. Arctic, Antarctic and Alpine Research 32: 375–380.

Schaberg, P.G., Snyder, M.C., Shane, J.B. & Donnelly, J.R. 2000. Seasonal pattern of carbohydrate reserves in red spruce seedlings. Tree Physiology 20: 549–555.

Schaberg, P.G., Wilkinson, R.C., Shane, J.B., Donnelly, J.R. & Cali, P.F. 1995. Winter photosynthesis of red spruce from three Vermont seed sources. Tree Physiology 15: 345–350.

Scheller, H.V. & Haldrup, A. 2005. Photoinhibition of photosystem I. Planta 221: 5–8.

Schulze, E.D., Mooney, H.A. & Dunn, E.L. 1967. Wintertime photosynthesis of Bristlecone pine (*Pinus aristata*) in the White Mountains of California. Ecology 48: 1044–1047.

Sevanto, S., Suni, T., Pumpanen, J., Grönholm, T., Kolari, P., Nikinmaa, E., Hari, P. & Vesala T. 2006. Wintertime photosynthesis and water uptake in a boreal forest. Tree Physiology 26: 749–757.

Šiffel, P. & Šantruček, J. 2005. Diurnal course of photochemical activity of winter-adapted Scots pine at subzero temperatures. Photosynthetica 43: 395–402.

Simons, A.M., Goulet, J.M. & Bellehumeur, K.F. 2010. The effect of snow depth on overwinter survival in *Lobelia inflata*. Oikos 119: 1685–1689.

Slaney, M., Wallin, G., Medhurst, J. & Linder, S. 2007. Impact of elevated carbon dioxide concentration and temperature on bud burst and shoot growth of boreal Norway spruce. Tree Physiology 27: 301–312.

Solantie, R. & Drebs, A. 2006. Kova pakkanen ja ohut lumipeite - tuhoisa yhdistelmä matalille kasveille ja puiden juurille. Sorbifolia 37: 99–105.

Sonoike, K. 2011. Photoinhibition of photosystem I. Physiologia Plantarum 142: 56–64.

Starr, G. & Oberbauer, S.F. 2003. Photosynthesis of arctic evergreens under snow: implications for tundra ecosystem carbon balance. Ecology 84: 1415–1420.

Steponkus, P.L. 1984. Role of the plasma membrane in freezing injury and cold acclimation. Annual Review of Plant Physiology and Plant Molecular Biology 35: 543–584.

Stewart, W.S. & Bannister, P. 1973. Seasonal changes in carbohydrate content of three *Vaccinium* spp with particular reference to *V. uliginosum* L. and its distribution in the British Isles. Flora 162: 134–155.

Stitt, M. & Hurry, V. A. 2002. A plant for all seasons: alterations in photosynthetic carbon metabolism during cold acclimation in *Arabidopsis*. Current Opinion in Plant Biology 5: 199–206.

Strand, Å., Hurry, V., Henkes, S., Huner, N., Gustafsson, P., Gardeström P. & Stitt, M. 1999. Acclimation of *Arabidopsis* leaves developing at low temperatures. Increasing cytoplasmic volume accompanies increased activities of enzymes in the Calvin cycle and in the sucrose-biosynthesis pathway. Plant Physiology 119: 1387–1397.

Streb, P., Shang, W., Feierabend, J. & Bligny, R. 1998. Divergent strategies of photoprotection in high mountain plants. Planta 207: 313–324.

Strimbeck, G.R., Schaberg, P.G., DeHayes, D.H., Shane, J.B. & Hawley, G.J. 1995. Midwinter dehardening of montane red spruce during a natural thaw. Canadian Journal of Forest Research 25: 2040–2044.

Sturm, M. 1992. Snow distribution and heat flow in the taiga. Arctic and Alpine Research 24: 145–152.

Sturm, M. & Benson, C.S. 1997. Vapor transport, grain growth and depth-hoar development in the subarctic snow. Journal of Glaciology 43: 42–59.

Sturm, M., Holmgren, J., König, M. & Morris, K. 1997. The thermal conductivity of seasonal snow. Journal of Glaciology 43: 26–41.

Sturm, M., McFadden, J., Liston, G.E., Chapin, S.III, Racine, C.H. & Holmgren, J. 2001. Snow-shrub interactions in Arctic tundra: A hypothesis with climatic implications. Journal of Climate 14: 336–344.

Suni, T., Berninger, F., Vesala, T., Markkanen, N., Hari, P. Mäkelä, A., Ilvesniemi, H., Hänninen, H., Nikinmaa, E., Huttula, T., Laurila, T., Aurela, M., Grelle, A., Lindroth, A., Arneth, A., Shibistova, O. & Lloyd, J. 2003. Air temperature triggers the recovery of evergreen boreal forest photosynhesis in spring. Global Change Biology 9: 1–17.

Sutinen, M-L., Palta, J.P. & Reich, P.B. 1992. Seasonal differences in freezing stress resistance of needles of *Pinus nigra* and *Pinus resinosa*: evaluation of the electrolyte leakage method. Tree Physiology 11: 241–254.

Suzuki, N. & Mittler, R. 2006. Reactive oxygen species and temperature stresses: A delicate balance between signalling and destruction. Physiologia Plantarum 126: 45–51.

Sveshnikov, D., Ensminger, I., Ivanov, A.G., Campbell, D., Lloyd, J., Funk, C., Hüner, N.P.A. & Öquist, G. 2006. Excitation energy partitioning and quenching during cold acclimation in Scots pine. Tree Physiology 26: 325–336.

Takahashi, S. & Badger, M.R. 2011. Photoprotection in plants: a new light on photosystem II damage. Trends in Plant Science 16: 53–60.

Takahashi, S., Milward, S.E., Yamori, W., Evans, J.E., Hillier, W. & Badger, M.R. 2010. The solar action spectrum of photosystem II damage. Plant Physiology 153: 988–993.

Takahashi, S. & Murata, N. 2008. How do environmental stresses accelerate photoinhibition? Trends in Plant Science 13: 178–182.

Tanaka, A. 2007. Photosynthetic activity in winter needles of the evergreen tree *Taxus cuspidata* at low temperatures. Tree Physiology 27: 641–648.

Tanino, K., Kalcsits, L., Silim, S., Kendall, E. & Gray, G.R. 2010. Temperature-driven plasticity in growth cessation and dormancy development in deciduous woody plants: a working hypothesis suggesting how molecular and cellular function is affected by temperature during dormancy induction. Plant Molecular Biology 73: 49–65.

Taulavuori, K., Bauer, E. & Taulavuori, E. 2011. Overwintering stress of *Vaccinium vitis-idaea* in the absence of snow cover. Environmental and Experimental Botany: [In Press].

Taulavuori, K., Laine, K., Taulavuori, E., Pakonen, T. & Saari, E. 1997. Accelerated dehardening in bilberry (*Vaccinium myrtillus* L) induced by a small elevation in air temperature. Environmental Pollution 98: 91–95.

Thomashow, M.F. 1999. Plant cold acclimation: freezing tolerance genes and regulatory mechanisms. Annual Review of Plant Physiology and Plant Molecular Biology 5: 571–99.

Thornley, J.H.M. 1998. Dynamic model of leaf photosynthesis with acclimation to light and nitrogen. Annals of Botany 81: 421–430.

Tieszen, L.L. 1974. Photosynthetic competence of the subnivean vegetation of an Arctic tundra. Arctic and Alpine Research 6: 253–256.

Tikkanen, M., Grieco, M. & Aro, E.-M. 2011. Novel insights into plant light-harvesting complex II phosphorylation and 'state transitions'. Trends in Plant Science 16: 126–131.

Tikkanen, M., Grieco, M., Kangasjärvi, S. & Aro, E.-M. 2010. Thylakoid protein phosphorylation in higher plant chloroplasts optimizes electron transfer under fluctuating light. Plant Physiology 152: 723–735.

Tikkanen, M., Piippo, M., Suorsa, M., Sirpiö, S., Mulo, P., Vainonen, J., Vener, A.V., Allahverdiyeva, Y. & Aro, E.-M. 2006. State transitions revisited - a buffering system for dynamic low light acclimation of Arabidopsis. Plant Molecular Biology 62: 779–793.

Tyystjärvi, E. 2008. Photoinhibition of Photosystem II and photodamage of the oxygen evolving manganese cluster. Coordination Chemistry Reviews 252: 361–376.

Uemura, S. 1989. Snowcover as a factor controlling the distribution and speciation of forest plants. Vegetatio 82: 127–137.

Uemura, M., Tominaga, Y., Nakagawara, C., Shigematsu, S., Minami, A. & Kawamura, Y. 2006. Responses of the plasma membrane to low temperatures. Physiologia Plantarum 126: 81–89.

Ungerson, J & Scherdin, G. 1965. Untersuchungen über Photosynthese und Atmung unter natürlichen Bedingungen während des Winterhalbjahres bei *Pinus silvestris* L., *Picea excelsa* Link. und *Juniperus communis* L. Planta (Berl.) 67: 136–167.

Valladares, F., Gianoli, E. & Gómez, J.M. 2007. Ecological limits to plant phenotypic plasticity. New Phytologist 176: 749–763.

Vass, I. 2011. Role of charge recombination processes in photodamage and photoprotection of the photosystem II complex. Physiologia Plantarum 142: 6–16.

Veatch, W., Brooks, P.D., Gustafson, J.R. & Molotch, N.P. 2009. Quantifying the effects of forest canopy cover on net snow accumulation at a continental, mid-latitude site. Ecohydrology 2: 115–128.

Vegis, A. 1964. Dormancy in higher plants. Annual Review of Plant Physiology 15: 185–224.

Venäläinen, A., Tuomenvirta, H., Heikinheimo, M., Kellomäki, S., Peltola, H., Strandman, H. & Väisänen, H. 2001. Impact of climate change on soil frost under snow cover in a forested landscape. Climate Research 17: 63–72.

Verhoeven, A.S., Adams, W.W.III & Demmig-Adams, B. 1998. Two forms of sustained xanthophyll cycle-dependent energy dissipation in overwintering *Euonymus kiautschovicus*. Plant, Cell and Environment 21: 893–903.

Verhoeven, A.S., Adams, W.W.III & Demmig-Adams, B. 1999. The xanthophyll cycle and acclimation of *Pinus ponderosa* and *Malva neglecta* to winter stress. Oecologia 118: 277–287.

Verhoeven, A., Osmolak, A., Morales, P. & Crow, J. 2009. Seasonal changes in abundance and phosphorylation status of photosynthetic proteins in eastern white pine and balsam fir. Tree Physiology 29: 361–374.

Vogg, G., Heim, R., Gotschy, B., Beck, E. & Hansen, J. 1998a. Frost hardening and photosynthetic performance of Scots pine (*Pinus sylvestris* L.) needles. II. Seasonal changes in the fluidity of thylakoid membranes. Planta 204: 201–206.

Vogg, G., Heim, R., Hansen, J., Schäfer, C. & Beck, E. 1998b. Frost hardening and photosynthetic performance of Scots pine (*Pinus sylvestris* L.) needles. I. Seasonal changes in the photosynthetic apparatus and its function. Planta 204: 193–200.

Wada, M., Kagawa, T. & Sato, Y. 2003. Chloroplast movement. Annual Review of Plant Biology 54: 455–468.

Wahren, C.-H.A., Walker, M.D. & Bret-Harte, M.S. 2005. Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. Global Change Biology 11: 537–552.

Walker, D.A., Halfpenny, J.C., Walker, M.D. & Wessman, C.A. 1993. Long-term studies of snow-vegetation interactions. BioScience 43: 287–301.

Wang, X., Arora, R., Horner, H.T. & Krebs, S.L. 2008. Structural adaptations in overwintering leaves of thermonastic and nonthermonastic *Rhododendron* species. Journal of the American Society for Horticultural Science 133: 768–776.

Warren, C.R. & Adams, M.A. 2004. Evergreen trees do not maximize instantaneous photosynthesis. Trends in Plant Science 9: 270–274.

Welling, A. & Palva, E.T. 2006. Molecular control of cold acclimation in trees. Physiologia Plantarum 127: 167–181.

Welling, A., Rinne, P., Viherä-Aarnio, A., Kontunen-Soppela, S., Heino, P. & Palva, E.P. 2004. Photoperiod and temperature differentially regulate the expression of two dehydrin genes during overwintering of birch (*Betula pubescens* Ehrh.). Journal of Experimental Botany 55: 507–516.

Widén, B. 2002. Seasonal variation in forest floor CO2 exchange in a Swedish coniferous forest. Agricultural and Forest Meteorology 111: 283–297.

Wildi, B. & Lütz, C. 1996. Antioxidant composition of selected high alpine plant species from different altitudes. Plant, Cell and Environment 19: 138–146.

Wipf, S. & Rixen, C. 2010. A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. Polar Research 29: 95–109.

Wipf, S., Rixen, C., Fischer, M., Schmid, B. & Stoeckli, V. 2005. Effects of ski piste preparation on alpine vegetation. Journal of Applied Ecology 42: 306–316.

Wipf, S., Rixen, C. & Mulder, C.P.H. 2006. Advaned snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community. Global Change Biology 12: 1496–1606.

Wipf, S., Stoeckli, V. & Bebi, P. 2009. Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. Climatic Change 94: 105–121.

Wisniewski, M., Bassett, C. & Gusta, L.V. 2003. An overview of cold hardiness in woody plants: seeing the forest through the trees. HortScience 38: 952–959.

Woolgrove, C.E. & Woodin, S.J. 1996. Ecophysiology of a snow-bed bryophyte *Kiaeria starkei* during snowmelt and uptake of nitrate from meltwater. Canadian Journal of Botany 74: 1095–1103.

Xin, Z. & Browse, J. 2000. Review: Cold comfort farm: the acclimation of plants to freezing temperatures. Plant, Cell and Environment 23: 893–902.

Yoshioka, M. & Yamamoto, Y. 2011. Quality control of Photosystem II: Where and how does the degradation of the D1 protein by FtsH proteases start under light stress? - Facts and hypotheses. Journal of Photochemistry and Photobiology B: Biology 104: 229–235.

Zarter, C.R., Adams, W.W.III, Ebbert, V., Adamska, I., Jansson, S. & Demmig-Adams, B. 2006a. Winter acclimation of PsbS and related proteins in the evergreen *Arctostaphylos uva-ursi* as influenced by altitude and light environment. Plant, Cell and Environment 29: 869–878.

Zarter, C.R., Adams, W.W.III, Ebbert, V., Cuthbertson, D.J., Adamska, I. & Demmig-Adams, B. 2006b. Winter down-regulation of intrinsic photosynthetic capacity coupled with up-regulation of Elip-like proteins and persistent energy dissipation in a subalpine forest. New Phytologist 172: 272–282.

Zarter, C.R., Demmig-Adams, B., Ebbert, V., Adamska, I. & Adams, W.W.III. 2006c. Photosynthetic capacity and light harvesting efficiency during the winter-to-spring transition in subalpine conifers. New Phytologist 172: 283–292.

Zeller, O. 1951. Über Assimilation und Atmung der Pflanzen im Winter bei tiefen Temperaturen. Planta 39: 500–526.

Zhu, X.B., Cox, R.M. Bourque, C.-P.A. & Arp, P.A. 2002. Thaw effects on cold-hardiness parameters in yellow birch. Canadian Journal of Botany 80: 390–398.