Species-specific acclimation to strong shade modifies susceptibility of conifers to photoinhibition

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Abstract

Photoinhibitory processes in the photosynthetic apparatus of the seedlings of Abies alba (Mill.), Picea abies (Karst.), and Pinus mugo (Turra) growing under strong shade (5 % of full solar irradiance) or full irradiance conditions were investigated in winter and spring using chlorophyll a fluorescence techniques. The extent of photoinhibition in needles as indicated by a decrease in maximum quantum yield of PS II photochemistry (Fv/Fm) depended on species, air temperature and acclimation to the light environment. Unexpectedly, shade-tolerant Abies alba was less affected by low-temperature photoinhibition compared to the other species. Fv/Fm recovered with increasing air temperature. During winter, the seedlings of Picea abies growing in shade showed higher Fv/Fm than those from full light. Non-photochemical quenching of fluorescence (NPQ) measured at the same levels of actinic light was higher in needles acclimated to full light except for Abies alba in February. Photosynthetic performance in term of ETR (apparent electron transport rate) was also higher in full light-acclimated needles. In April, at ambient temperature, recovery of PS II efficiency from the stress induced by illumination with saturating light was faster in the needles of Picea abies than in those of Abies alba. The shade-acclimated needles of Abies alba and Picea abies showed greater down-regulation of PS II induced by high light stress.

List of abbreviations: ETR – apparent electron transport rate (µmol m⁻² s⁻¹); ETRmax – maximum value of ETR; Fv/Fm – maximum quantum yield of photosystem II photochemistry; Fm – maximum fluorescence yield; F' m – maximum fluorescence in the light; F0 – minimum fluorescence yield; Fs – steady-state fluorescence yield; NPQ – non-photochemical quenching of fluorescence; PPFD – photosynthetic photon flux density (µmol m⁻² s⁻¹); PPFDsat - saturation level of photosynthetic photon flux density; PSII – photosystem II; ΦPSII – quantum yield of PSII photochemistry.

Introduction

Low air temperature and bright light are conducive to photoinhibitory processes in a leaf. The diurnal depression in maximum quantum yield of PS II (Fv/Fm) at midday is usually related to high incident light level (Krause et al. 2001, Jifon and Syversten 2003, Senevirathna et al. 2003, Robakowski and Wyka 2004). In winter, evergreen plants experience reversible or persistent photoinhibition, indicated as a decrease in Fv/Fm, which usually recovers in spring and into early summer (Adams III, Demmig-Adams 1994, Verhoeven et al. 1996, Pocock et al. 2001, Han et al. 2004). This may play either a photoprotective or photodestructive role in plants. Reversible photoinhibition (down-regulation of PS II) related to dissipation of
excessive energy in xanthophyll cycle serves to protect the photosynthetic apparatus from gross destruction i.e. damage to the D1 protein of the PS II reaction centre by low temperature and/or excessive light (Somersalo and Krause 1990, Groom et al. 1991). Excess light increases accumulation of protons in the thylakoid lumen. The acidification induces de-epoxidation of the carotenoid violaxanthin into antheraxanthin and zeaxanthin (VAZ cycle). The excess energy is dissipated as heat and can be estimated by the measure of non-photochemical quenching of fluorescence (Adams III, Demmig-Adams 1994, Lambers et al. 1998). Low-temperature induced photoinhibition in needles of the evergreen conifers Pinus ponderosa, Pseudotsuga menziesii, and Picea pungens was due to a down-regulation of PS II that involved sustained xanthophyll cycle-associated energy dissipation (Adams III, Demmig-Adams 1994). Nevertheless, in winter, xanthophyll cycle-associated energy dissipation may not operate effectively. Then, the rhodoxanthin and lutein may play a more important photoprotective role than the VAZ cycle, as it was shown in leaf of Thuja plicata Donn. ex D. Don and Cryptomeria japonica D. Don. (Weger et al. 1993, Han et al. 2004). However, rhodoxanthin is a significant light screening compound in certain members of the Cupressaceae and the Taxaceae, but not the Pinaceae (Weger et al. 1993). Energy dependent down-regulation of PS II usually recovers to the dark-adapted state within a few minutes, but due to partial reversion of photoinhibition it may last longer (Somersalo and Krause 1990, van Wijk and van Hasselt 1993).

Low air temperature and light of high intensity may cause irreversible or slowly relaxing (within hours or days) photoinhibition that is related to destruction of D1 protein in reaction centre of PS II. The magnitude of photooxidative damage depends on the turn-over of D1 protein. Its resynthesis leads to a slow recovery of quantum efficiency of PS II (Kitao et al. 2000). In such case, photoinhibition plays a photoprotective role together with pH-dependent quenching under high light and/or low air temperature (Verhoeven et al. 1996, Krause et al. 2001). Adams et al. (2004) argued that destruction of D1 protein is part of downregulation of photosynthesis and upregulation of photoprotection. D1 degradation is not correlated with insufficient supply of carbohydrate, and decrease in growth and productivity. Moreover, decreases in the level of D1 protein and oxygen-evolving complex may decrease the likelihood of photooxidative damage (Adams et al. 2004). Photoinhibition often represents an important protective strategy which allows plants to sustain photochemical activity at the lowest costs (Anderson et al. 1997).

Plant response to the factors inducing photoinhibition depends on the species successional status and acclimation to irradiance conditions of growth. Pioneer, light-demanding trees from a neotropical forest showed lower decrease in Fv/Fm than shade-tolerant species (Krause et al. 2001). Nevertheless, a pioneer Betula platyphylla var. japonica acclimated to strong shade sustained greater photodamage than shade-tolerant species after exposure to light stress (Kitao et al. 2000). In leaves of Ilex aquifolium from the shaded side of the tree, Fv/Fm was higher than from the sun-exposed side (Groom et al. 1991). Similarly, in Cryptomeria japonica, the needles growing in shade were characterised by higher Fv/Fm but lower NPQ and apparent electron transport rate (ETR) from August until April in comparison to sunlit needles (Han et al. 2004). These results showed that photoinhibition is deeper in leaf exposed to both high light and low temperature than in leaf growing in shade. On the other hand, leaves acclimated to higher irradiance have a larger pool of xanthophyll cycle pigments, increased chlorophyll a/b ratio, and more rhodoxanthin produced in winter (the Cupressaceae and the Taxaceae), opposite to shaded leaves (Krause et al. 2001, Han et al. 2004).

In the present study, it was hypothesised that the conifer seedlings acclimated to strong shade are more susceptible to low-temperature and light-induced photoinhibition. The pioneer, light-demanding Pinus mugo and mid-successional, moderately shade-tolerant Picea abies were expected to be less susceptible to photoinhibition than the late-successional, shade-tolerant Abies alba. In addition, it was presumed that a recovery of PS II efficiency from the post-illumination stress can be faster in Picea abies than in Abies alba and more effective in sun-acclimated than in shade-acclimated needles.