PHOTOSYNTHETICA 38 (3): 373-378, 2000

Similar susceptibility to excess irradiance in sun and shade acclimated saplings of Norway spruce [*Picea abies* (L.) Karst.] and stone pine (*Pinus cembra* L.)

R. GAMPER, S. MAYR, and H. BAUER*

Institut für Botanik, Sternwartestr. 15, A-6020 Innsbruck, Austria

Abstract

We compared the responses of sun and shade acclimated saplings of *Picea abies* and *Pinus cembra* to excess photosynthetic photon flux density (PPFD) equivalently exceeding the level for saturating net photosynthetic rate (P_N). Exposure for 2 h up to 2000 µmol(photon) m^{-2} s^{-1} did not affect radiant energy saturated P_N. Photoinhibition of photosynthesis was indicated by a small (10 %) reduction of the potential efficiency of photosystem 2 as derived from measurements of chlorophyll fluorescence (F_V/F_M). However, the extent of F_V/F_M reduction and half-time for recovery were similar in sun and shade acclimated saplings of both species. Furthermore, the effect on F_V/F_M was not stronger when the plants were exposed to excess PPFD at 5 °C instead of 15 °C. Frost-hardening of plants increased slightly their resistance to excess PPFD. Establishment of these conifer saplings usually acclimated to shade in their natural habitat may hardly be endangered by a sudden increase of PPFD, *e.g.*, by gap formation.

Additional key words: chlorophyll fluorescence; frost hardening; low temperature; net photosynthetic rate.

Introduction

Photosynthesis can be inhibited upon exposure to excess irradiance, when the energy capturing processes in the chloroplasts surmounts the metabolic exploitation of energy (photoinhibition; for reviews see Björkman 1981, Powles 1984, Foyer *et al.* 1994, Osmond 1994, Anderson *et al.* 1997, Srivastava and Strasser 1997, *etc.*). Changes of chlorophyll (Chl) *a* fluorescence indicating photoinhibition (F_V/F_M, nonphotochemical quenching) are usually observed as soon as saturation of net photosynthetic rate (P_N) by PPFD (I_{SAT}) is approached (*e.g.*, Demmig-Adams *et al.* 1989). Since I_{SAT} is reached at lower PPFD in shade than in sun plants, shade plants are more prone to photoinhibition (Powles 1984, Oberhuber and Bauer 1991, Demmig-Adams and Adams 1992, Osmond 1994, Srivastava and Strasser 1997). Shade plants also exhibit lower amounts of protective compounds such as antioxidants (Demmig-Adams and Adams 1992) and carotenoids of the xanthophyll cycle (Oberhuber and Bauer 1991, Demmig-Adams and Adams 1996), and a lower repair activity (Aro *et al.* 1994, Skillman and Osmond 1998, however, cf. Greer and Laing 1988). Since the light reactions of photosynthesis have a lower Q_{10} than assimilation of CO_2 (Baker 1994), photoinhibition is induced by a rather low PPFD at chilling temperatures (Powles 1984, Krause 1994, Sonoike 1998).

In a previous field study, rates of photosynthetic O_2 evolution were equally inhibited in sun exposed and shaded needles of *Picea abies* and *Pinus cembra* during winter (Stecher *et al.* 1999). On the other hand, the potential efficiency of photosystem 2 (PS2) as derived from F_V/F_M was less reduced in shaded needles due to the exposure to low PPFD. The aim of this study was to compare the responses of sun- and shade-acclimated saplings to excess PPFD equivalently exceeding I_{SAT}. To this end—after determining I_{SAT} in sun and shade needles at various temperatures—the needles were exposed to a PPFD somewhat higher than I_{SAT} for 2 or 5 h, afterwards P_N at saturating PPFD (P_{SAT}) was measured as well as F_V/F_M. Recovery of F_V/F_M was also observed.

Received 14 April 2000, *accepted* 29 May 2000.

*Author for correspondence; fax: +43 512 507 2715; e-mail: helmut.bauer@uibk.ac.at

Abbreviations: F_M - maximum chlorophyll fluorescence; F_V - variable chlorophyll fluorescence; I_{SAT} - PPFD saturating P_N; P_N - net photosynthetic rate; P_{SAT} - P_N at saturating PPFD; PPFD - photosynthetic photon flux density, PS2 - photosystem 2.

Materials and methods

Plants: Six-year-old saplings of Norway spruce [*Picea abies* (L.) Karst.] and four-year-old saplings of stone pine (*Pinus cembra* L.) were planted in 4 000 cm^3 pots containing a mixture of garden peat and sandy soil. In March 1996, about one month before bud break, half of the plants was placed at an open stand in the Botanical Garden of the University Innsbruck where the plants were shaded in the late afternoon only. The other half was placed in a dense shade of a hedge where PPFD was attenuated to about 5 % and never exceeded 80 μmol (photon) m^{-2} s^{-1}. Shaded *P. abies* plants formed typical shade twigs (long and thin needles, biserially arranged), whereas exposed plants formed sun twigs (shorter and thicker needles positioned all round the axis). Shaded *P. cembra* plants also developed thinner needles and almost no side-branches. Measurements were performed on fully developed current year needles during end of August and early September 1996 (summer), during November 1996 (winter; these plants were considered to be frost-hardened, cf. Bauer *et al.* 1994), and in mid of April 1997 (spring). Prior to measurements plants were conditioned for one week in a climate chamber at 5/0 °C day/night temperature in winter and 20/15 °C in spring. PPFD was 300 and 50 μmol m^{-2} s^{-1} for sun and shade plants, respectively.

CO_2 exchange was measured in an open system as described by Bauer (1978) with some modifications: The ventilated leaf cuvette was manufactured from nickel plated brass with a glass window (volume 1000 cm^3; boundary layer conductance for H_2O 2.5 mol m^{-2} s^{-1}). CO_2 was mixed with mass flow controllers (*FC 260* and *FC 261*, *Tylan*, Eiching, Germany) using 1 % CO_2 and CO_2-free air. Air-flow rates were measured with mass flow meters (*FM 360*, *Tylan*, Eiching, Germany), and a CO_2 infrared gas analyser (*225 MK3*, *ADC BioScientific*, Hoddesdon, England) was used in differential and absolute modes. Attached twigs of conifers were sealed in the leaf cuvette and P_N was determined under the following conditions: 40 Pa CO_2, 90 % relative humidity, 2.5 to 20 °C leaf temperature, and 100 to 1600 μmol (photon) m^{-2} s^{-1} (light source: 2 tungsten halogen lamps with dichroic reflector 75 W, *Osram*, München, Germany). Response of P_N to PPFD was fitted to a non-rectangular hyperbola (Thornley and Johnson 1990). From this function, PPFDs corresponding to 90 % of the highest P_N were calculated as I_{SAT}.

High-PPFD treatment of enclosed twigs was performed in the temperature controlled leaf cuvette with the tungsten halogen lamps. PPFD and duration of treatments are given in Table 1.

Table 1. PPFD [μmol(photon) m^{-2} s^{-1}] to which twigs were exposed during high-light treatment for 2 h in summer and winter and for 2 and 5 h in spring.

			5 °C	15 °C
Summer	*Picea abies*	sun-exposed	800	1200
		shaded	800	1200
	Pinus cembra	sun-exposed	1200	1600
		shaded	1200	1600
Winter	*Picea abies*	sun-exposed	1200	1200
		shaded	1200	1200
	Pinus cembra	sun-exposed	1600	1600
		shaded	1600	1600
Spring	all plants		2000	2000

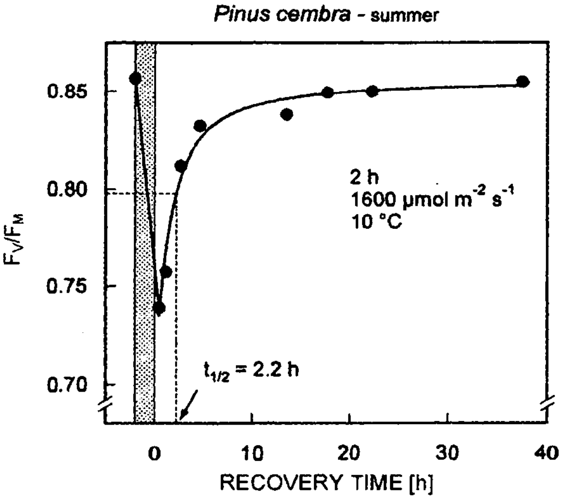

Fig. 1. Recovery of the potential efficiency of photosystem 2 (F_V/F_M) in *Pinus cembra* following the indicated high-light treatment. The shaded area represents the period of treatment. Half time for recovery ($t_{1/2}$) was calculated as time necessary to reach the mean of the value before and the lowest value after treatment.

Chl fluorescence transients were recorded for 2 s with the Plant Efficiency Analyser (*Hansatech Instruments*, King's Lynn, England) at room temperature and 4000 μmol(photon) m^{-2} s^{-1} after darkening needles for 30 min. Measurements were done on attached needles prior to gas exchange measurements and immediately after high-PPFD treatment. Recovery of F_V/F_M (terminology according to Van Kooten and Snel 1990) at 20 °C and 75 μmol(photon) m^{-2} s^{-1} was monitored up to four days after treatment. Maximal depression of F_V/F_M and half time for recovery were evaluated using an asymmetric sigmoid function (Fig. 1).

Projected needle area was determined with a digital video camera (Leaf Area and Analysis System *SI 721*, *Skye Instruments*, Llandron Wells, U.K.).

Number of samples: All values given here are means of two independent samples.

Results

PPFD response of P_N: In summer *P. abies* showed the typical response of P_N to PPFD of sun and shade acclimated plants: P_{SAT} (Fig. 2) and I_{SAT} (Table 2) were higher in sun plants than in shade plants. Furthermore, both parameters increased with temperature in the measured range. In *P. cembra* P_{SAT} responded in the same manner with respect to PPFD acclimation and temperature (Fig. 3, Table 2). However, I_{SAT} was similar in shade and sun acclimated *Pinus* specimens and no distinct effect of temperature was observed.

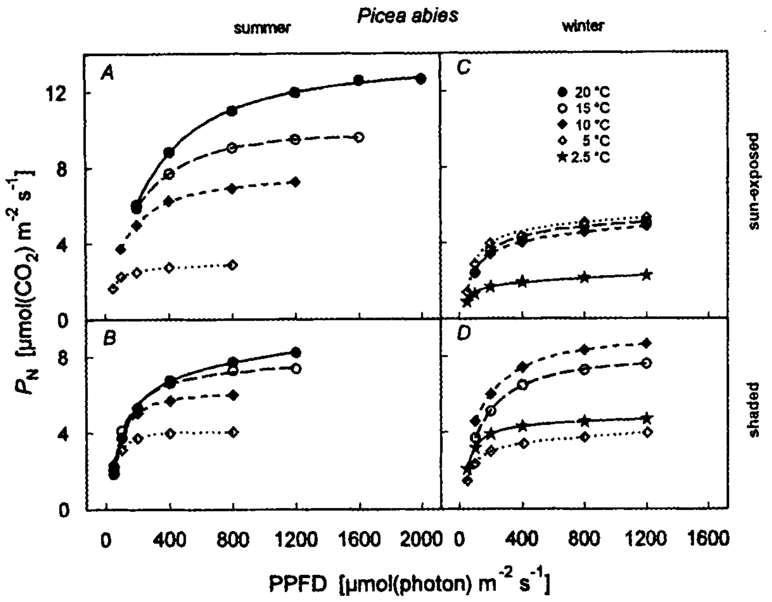

Fig. 2. Photosynthetic photon flux density (PPFD) response of P_N at indicated needle temperatures of sun-exposed (*A, C*) and shaded (*B, D*) saplings of *Picea abies* in summer (*A, B*) and winter (*C, D*).

Table 2. I_{SAT} [μmol(photon) m^{-2} s^{-1}] in sun-exposed and shaded plants of *Picea abies* and *Pinus cembra* at various temperatures during summer and winter.

			2.5 °C	5 °C	10 °C	15 °C	20 °C
Summer	*Picea abies*	sun-exposed		235	515	615	900
		shaded		170	270	430	640
	Pinus cembra	sun-exposed		760	980	860	830
		shaded		605	780	960	960
Winter	*Picea abies*	sun-exposed	640	525	645	540	
		shaded	335	510	580	525	
	Pinus cembra	sun-exposed	1040	1430	1380	1280	
		shaded	1460	1410	1070	740	

Establishment of P_N *versus* PPFD curves was difficult in frost hardened plants, because for measurements the plants must be transferred to room temperature where some recovery of P_N occurred (cf. Bauer *et al.* 1994). Although P_N was taken not before, the twigs were exposed for 60 min to each PPFD starting at low PPFD, P_N at low PPFD could be underestimated as compared to P_N at high PPFD. Therefore, winter values of I_{SAT} have to be interpreted with caution. P_{SAT} values were clearly lower than in summer in all plants except in shade acclimated *P. abies* (Figs. 2 and 3). I_{SAT} showed no clear tendencies in both species and was very high in *Pinus cembra* (Table 2).

After-effects of high-PPFD treatments: In summer and winter twigs were exposed for 2 h to PPFD about 500 to 700 μmol(photon) m^{-2} s^{-1} higher than I_{SAT} determined for the corresponding temperature (cf. Table 1 and Table 2), except in *P. cembra* in winter where the treatment exceeded I_{SAT} not more than about 200 μmol(photon) m^{-2} s^{-1}. Table 3 shows that P_{SAT} was never affected following a 2 h lasting high-PPFD treatment in all samples. When in spring *P. abies* was exposed to 2000 μmol(photon) m^{-2} s^{-1} for 5 h at 5 °C, P_{SAT} was lowered for about 10 to 15 % in shaded and sun-exposed twigs. In *P. cembra* even this treatment hardly affected P_{SAT}.

Table 3. Effects of high-light treatment for 2 or 5 h on P_{SAT} [% of initial rate] and F_V/F_M [% of initial value] immediately after treatment and half time for recovery [h] of F_V/F_M. Mean values of two samples.

			P_{SAT}		F_V/F_M		Half time for recovery of F_V/F_M	
			5 °C	15 °C	5 °C	10 °C	5 °C	10 °C
Summer – 2 h	*Picea abies*	sun-exposed	98.6	98.6	90.0	88.4	1.3	3.3
		shaded	99.0	105.2	89.2	86.9	3.4	4.6
	Pinus cembra	sun-exposed	111.9	103.4	91.2	93.0	1.6	2.8
		shaded	104.0	102.9	88.3	89.7	1.8	2.0
Winter – 2 h	*Picea abies*	sun-exposed	116.5	108.9	92.8	92.0	1.7	1.3
		shaded	109.8	103.6	90.9	93.6	1.9	2.2
	Pinus cembra	sun-exposed	100.0	100.0	91.3	93.0	1.7	2.2
		shaded	113.0	100.0	93.0	93.8	2.4	1.3
Spring – 2 h	*Picea abies*	sun-exposed	100.3	104.7	79.9	84.6	2.8	2.7
		shaded	105.3	104.9	82.2	79.6	2.1	1.8
	Pinus cembra	sun-exposed	105.6	103.4	88.5	85.2	4.3	2.8
		shaded	97.8	112.2	86.2	86.0	2.0	1.6
Spring – 5 h	*Picea abies*	sun-exposed	84.8	95.9	67.5	69.3	6.9	6.2
		shaded	92.6	101.9	65.6	69.8	7.2	4.6
	Pinus cembra	sun-exposed	97.9	102.3	78.3	84.0	7.5	5.7
		shaded	103.4	104.5	77.9	91.0	2.9	6.0

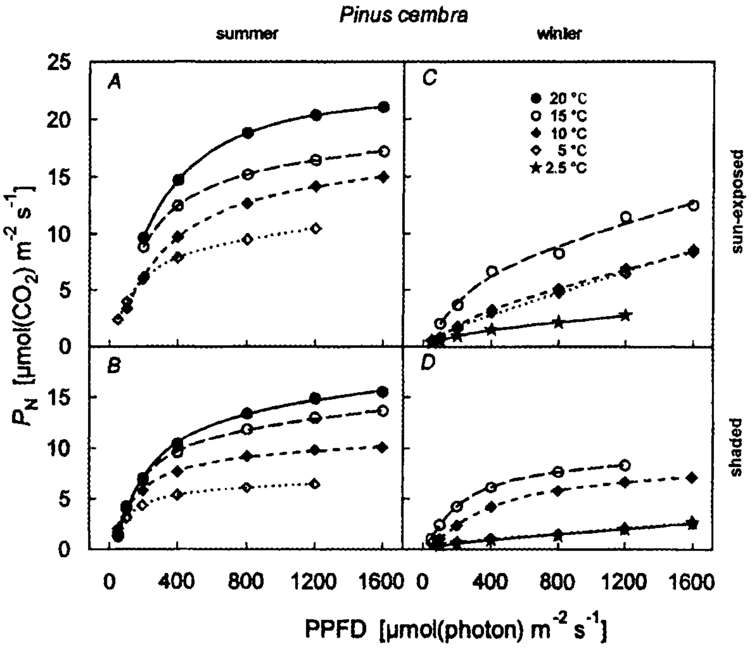

Fig. 3. Photosynthetic photon flux density (PPFD) response of P_N at indicated needle temperatures of sun-exposed (*A, C*) and shaded (*B, D*) saplings of *Pinus cembra* in summer (*A, B*) and winter (*C, D*).

Nevertheless, high-PPFD treatment in summer and winter produced photoinhibition in both species as indicated by a reduction of F_V/F_M of about 10 % (Table 3). There was no clear influence of temperature on the extent of reduction and no clear differences between sun-exposed and shaded plants could be established. Furthermore, recovery of F_V/F_M required nearly the same time in all plants stressed at 5 and 15 °C (Table 3). When the plants were exposed to full sunlight [2000 μmol (photon) m^{-2} s^{-1}] for 5 h in spring, F_V/F_M was reduced for about 32 % in *P. abies* and about 17 % in *P. cembra*, 50 % recovery was reached after about 6 h (Table 3). Again no clear tendencies with respect to PPFD acclimation and treatment temperature could be found.

Discussion

In order to evaluate the influence of PPFD acclimation, low temperature, species, or season on the susceptibility to excess PPFD, mean values of all corresponding measurements are compiled in Table 4 (*e.g.*, mean of all sun-exposed plants *versus* shaded plants or mean of all plants stressed at 5 °C *versus* those stressed at 15 °C and so on). Since the applied high-PPFD treatments did not reduce P_{SAT}, an influence of the above mentioned variables cannot be evaluated. A difference in the effect of excess PPFD on F_V/F_M could only be observed between non-hardened (summer) and frost-hardened (winter) plants (Table 4): in hardened plants reduction was slightly but significantly lower than in non-hardened plants. Lower susceptibility to high PPFD in hardened plants was also demonstrated by a faster (although not statistically significant) recovery of F_V/F_M. Reduced sensitivity to photoinhibition following frost-hardening is well documented from spinach (Somersalo and Krause 1989), winter rye (Hurry and Huner 1992), wheat (Hurry *et al.* 1992), *Eucalyptus* species (Warren *et al.* 1998), and conifers (Krol *et al.* 1995), at least in relation to the degree of PS2 closure (Krivosheeva *et al.* 1996). An increased capacity to keep Q_A oxidised (Öquist *et al.* 1992) and increased phosphate availability (Hurry *et al.* 1993) in frost-hardened rye were related to the reduced sensitivity.

Table 4. Effects of high-PPFD treatment for 2 h on P_{SAT}, F_V/F_M, and half time for recovery of F_V/F_M as depending on PPFD acclimation of plants, treatment temperature, plant species, and season. Mean values ± SE (*n* = 12 or 8). Values of each column not followed by one mutual letter differ significantly at the 0.05 probability level (Student's *t*-test).

	P_{SAT} [% of initial	F_V/F_M value]	Half time for recovery of F_V/F_M [h]
sun-exposed	104.3 ± 1.6^a	89.1 ± 1.2^a	2.38 ± 0.26^a
shaded	104.8 ± 1.4^a	88.3 ± 1.3^a	2.26 ± 0.26^a
5 °C	105.2 ± 1.8^a	88.6 ± 1.2^a	2.25 ± 0.25^a
15 °C	104.0 ± 1.1^a	88.8 ± 1.3^a	2.38 ± 0.27^a
Picea abies	104.6 ± 1.5^a	87.5 ± 1.4^{ac}	2.42 ± 0.28^a
Pinus cembra	104.5 ± 1.5^a	89.9 ± 0.9^a	2.21 ± 0.23^a
summer	103.0 ± 1.6^a	89.6 ± 0.7^a	2.60 ± 0.40^a
winter	106.5 ± 2.3^a	92.6 ± 0.3^b	1.84 ± 0.15^a
spring	104.3 ± 1.5^a	84.0 ± 1.1^c	2.51 ± 0.31^a

A non-expected result of our investigations was that the extent of photoinhibition derived from the reduction of F_V/F_M was not depending on PPFD acclimation of *P. abies* and *P. cembra* (Table 4). Searching 83 related papers dealing with cyanobacteria, algae, lichens, mosses, and higher plants (for reviews see Introduction) we did not find any study where no differences between shade and sun acclimated plants are reported. As described in Materials and methods, the saplings have developed needles morphologically acclimated to the corresponding irradiance. PPFD response of P_N was also typical for shade- and sun-acclimated plants (Fig. 2, Table 2) at least in *P. abies*, so that our plants were really differently acclimated. A reason for the similar responses to high PPFD in sun- and shade-acclimated plants could be that the applied treatment was too faint to affect PS2. According to Anderson *et al.* (1997), 10^6 to 10^7 photons must be delivered to the leaf for an inevitable photoinactivation of one PS2. Assuming a content of Chl (*a*+*b*) of 0.4 g m^{-2} (cf. Bauer *et al.* 2000) and one PS2 per 200 Chl (*a*+*b*) (Björkman 1981), our treatment with 1600 μmol(photon) m^{-2} s^{-1} for 2 h delivered about 5×10^6 photons to one PS2. Even with the treatment of 2000 μmol(photon) m^{-2} s^{-1} for 5 h (*i.e.*, about 1.6×10^7 photons per one PS2) in spring no differences in the response of sun and shade acclimated plants were found (Table 4). Some support to our results comes from Špunda *et al.* (1993) who also report non severe photoinhibition of PS2 photochemistry when saplings of *P. abies* were transferred from low diffuse irradiation to full sun.

A further not expected result of our study was that the effect of a treatment with a comparable high PPFD on F_V/F_M was not stronger at 5 than at 15 °C (for literature see Introduction). This can be possibly explained by the broad optimal temperature range for P_N and by the observation that I_{SAT} did not vary considerably with temperature except in *P. abies* in summer (Table 2). When nordic conifers are exposed to low temperatures and a shortened photoperiod for an extended duration, activity of PS2 will be down-regulated in order to avoid photodamage of the photosynthetic apparatus during winter (*e.g.*, Bauer *et al.* 1994, Ottander *et al.* 1995, Stecher *et al.* 1999). Thereby low temperatures act as a signal rather than as a stressor (cf. Huner *et al.* 1998).

In conclusion, exposure to ecological relevant bright irradiances for a few hours does not affect P_{SAT} in *P. abies* and *P. cembra* and leads only to a small reduction of the potential efficiency of PS2. Thus, establishment of these conifer seedlings, which are usually acclimated to shade in their natural understory habitat, may hardly be endangered by a sudden increase in PPFD, *e.g.*, by a gap formation.

References

Anderson, J.M., Park, Y.-I., Chow, W.S.: Photoinactivation and photoprotection of photosystem II in nature. - Physiol. Plant. **100**: 214-223, 1997.

Aro, E.-M., McCaffery, S., Anderson, J.M.: Recovery from photoinhibition in peas (*Pisum sativum* L.) acclimated to varying growth irradiances. Role of D1 protein turnover. - Plant Physiol. **104**: 1033-1041, 1994.

Baker, N.R.: Chilling stress and photosynthesis. - In: Foyer, C.H., Mullineaux, P.M. (ed.): Causes of Photooxidative Stress and Amelioration of Defense Systems in Plants. Pp. 127-154. CRC Press, Boca Raton 1994.

Bauer, H.: Photosynthesis of ivy leaves (*Hedera helix*) after heat stress. I. CO_2-gas exchange and diffusion resistances. - Physiol. Plant. **44**: 400-406, 1978.

Bauer, H., Nagele, M., Comploj, M., Galler, V., Mair, M., Unterpertinger, E.: Photosynthesis in cold acclimated leaves of plants with various degrees of frost tolerance. - Physiol. Plant. **91**: 403-412, 1994.

Bauer, H., Plattner, K., Volgger, W.: Photosynthesis in Norway spruce seedlings infected by the needle rust *Chrysomyxa rhododendri*. - Tree Physiol. **20**: 211-216, 2000.

Björkman, O.: Responses to different quantum flux densities. - In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (ed.): Physiological Plant Ecology I. Responses to the Physical Environment. Pp. 57-107. Springer-Verlag, Berlin – Heidelberg – New York 1981.

Demmig-Adams, B., Adams, W.W., III: Carotenoid composition in sun and shade leaves of plants with different life forms. - Plant Cell Environ. **15**: 411-419, 1992.

Demmig-Adams, B., Adams, W.W.: The role of xanthophyll cycle carotenoids in the protection of photosynthesis. - Trends Plant Sci. **1**: 21-26, 1996.

Demmig-Adams, B., Winter, K., Krüger, A., Czygan, F.-C.: Light response of CO_2 assimilation, dissipation of excess excitation energy, and zeaxanthin content of sun and shade leaves. - Plant Physiol. **90**: 881-886, 1989.

Foyer, C.H., Lelandais, M., Kunert, K.J.: Photooxidative stress in plants. - Physiol. Plant. **92**: 696-717, 1994.

Greer, D.H., Laing, W.A.: Photoinhibition of photosynthesis in intact kiwifruit (*Actinidia deliciosa*) leaves: Effect of light during growth on photoinhibition and recovery. - Planta **175**: 355-363, 1988.

Huner, N.P.A., Öquist, G., Sarhan, F.: Energy balance and acclimation to light and cold. - Trends Plant Sci. **3**: 224-230, 1998.

Hurry, V.M., Gardeström, P., Öquist, G.: Reduced sensitivity to photoinhibition following frost-hardening of winter rye is due to increased phosphate availability. - Planta **190**: 484-490, 1993.

Hurry, V.M., Huner, N.P.A.: Effect of cold hardening on sensitivity of winter and spring wheat leaves to short-term photoinhibition and recovery of photosynthesis. - Plant Physiol. **100**: 1283-1290, 1992.

Hurry, V.M., Krol, M., Öquist, G., Huner, N.P.A.: Effect of long-term photoinhibition on growth and photosynthesis of cold-hardened spring and winter wheat. - Planta **188**: 369-375, 1992.

Krause, G.H.: Photoinhibition induced by low temperatures. - In: Baker, N.R., Bowyer, J.R. (ed.): Photoinhibition of Photosynthesis - From Molecular Mechanisms to the Field. Pp. 331-348. Bios Scientific Publ., Oxford 1994.

Krivosheeva, A., Tao, D.L., Ottander, C., Wingsle, G., Dube, S.L., Öquist, G.: Cold acclimation and photoinhibition of photosynthesis in Scots pine. - Planta **200**: 296-305, 1996.

Krol, M., Gray, G.R., Hurry, V.M., Öquist, G., Malek, L., Huner, N.P.A.: Low-temperature stress and photoperiod affect an increased tolerance to photoinhibition in *Pinus banksiana* seedlings. - Can. J. Bot. **73**: 1119-1127, 1995.

Oberhuber, W., Bauer, H.: Photoinhibition of photosynthesis under natural conditions in ivy (*Hedera helix* L.) growing in an understory of deciduous trees. - Planta **185**: 545-553, 1991.

Öquist, G., Hurry, V.M., Öquist, M.G., Huner, N.P.A.: Differential resistance of frost-hardened and non-hardened winter rye to photoinhibition of photosynthesis is due to an increased capacity of frost-hardened rye to keep Q_A oxidized under similar irradiance and temperature. - Photosynthetica **27**: 231-235, 1992.

Osmond, C.B.: What is photoinhibition? Some insights from comparisons of shade and sun plants. - In: Baker, N.R., Bowyer, J.R. (ed.): Photoinhibition of Photosynthesis - From Molecular Mechanisms to the Field. Pp. 1-24. Bios Scientific Publ., Oxford 1994.

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

Powles, S.B.: Photoinhibition of photosynthesis induced by visible light. - Annu. Rev. Plant Physiol. **35**: 15-44, 1984.

Skillman, J.B., Osmond, C.B.: Influence of nitrogen supply and growth irradiance on photoinhibition and recovery in *Heuchera americana* (Saxifragaceae). - Physiol. Plant. **103**: 567-573, 1998.

Somersalo, S., Krause, G.H.: Photoinhibition at chilling temperature. Fluorescence characteristics of unhardened and cold-acclimated spinach leaves. - Planta **177**: 409-416, 1989.

Sonoike, K.: Various aspects of inhibition of photosynthesis under light/chilling stress: 'Photoinhibition at chilling temperatures' *versus* 'Chilling damage in the light'. - J. Plant Res. **111**: 121-129, 1998.

Špunda, V., Kalina, J., Nauš, J., Kuropatwa, R., Mašláň, M., Marek, M.: Responses of photosystem 2 photochemistry and pigment composition in needles of Norway spruce saplings to increased radiation level. - Photosynthetica **28**: 401-413, 1993.

Srivastava, A., Strasser, R.J.: Constructive and destructive actions of light on the photosynthetic apparatus. - J. sci. ind. Res. **56**: 133-148, 1997.

Stecher, G., Schwienbacher, F., Mayr, S., Bauer, H.: Effects of winter-stress on photosynthesis and antioxidants of exposed and shaded needles of *Picea abies* (L.) Karst. and *Pinus cembra* L. - Phyton **39**: 205-211, 1999.

Thornley, J.H.M., Johnson, I.R.: Plant and Crop Modelling: A Mathematical Approach to Plant and Crop Physiology. - Oxford University Press, Oxford 1990.

Van Kooten, O., Snel, J.F.H.: The use of chlorophyll fluorescence nomenclature in plant stress physiology. - Photosynth. Res. **25**: 147-150, 1990.

Warren, C.R., Hovenden, M.J., Davidson, N.J., Beadle, C.L.: Cold hardening reduces photoinhibition of *Eucalypts nitens* and *E. pauciflora* at frost temperatures. - Oecologia **113**: 350-359, 1998.