ELSEVIER

Scientia Horticulturae 98 (2003) 71–84

SCIENTIA HORTICULTURAE

www.elsevier.com/locate/scihorti

Domestication of the Chilean guava (*Ugni molinae* Turcz.), a forest understorey shrub, must consider light intensity

C. Pastenes*, E. Santa-María, R. Infante, N. Franck

Depto. Producción Agrícola, Facultad de Ciencias Agronómicas, Universidad de Chile, Casilla 1004, Santiago, Chile

Accepted 3 December 2002

Abstract

A Chilean guava ecotype (*Ugni molinae* Turcz.) was cultivated in Santiago during the summer of 1999/2000 in order to assess the effect of shading on photosynthesis. Plants were grown under either 50% shading or full sunlight and chlorophyll fluorescence, net assimilation rates of CO_2, photosynthetic pigment contents, were measured 2 months after planting, in each light regime, during the day. The capacity to recover the photochemical efficiency of photosystem II in light grown plants, measured as F_v/F_m after 30 min dark adaptation was markedly reduced, reaching values lower than 0.5 at midday, with a sunlight PPFD of 1600 μmol m^{-2} s^{-1}. On the other hand, the shaded plants showed a nearly complete recovery of the parameter. The photochemical quenching of chlorophyll fluorescence, reached a value of 0.47, also at midday, in full light grown plants, nearly half that observed in the shade, indicating a high PSII excitation pressure in the former. The light saturated net CO_2 assimilation rates, measured in controlled conditions of temperature, were markedly lower in the full light plants compared to the shade ones. It is concluded that the Chilean guava is not able to cope with the light intensities characteristic of many Mediterranean climates, resulting in chronic photoinhibition.

Keywords: Chilean guava; Chlorophyll fluorescence; Photoinhibition; Photosynthesis; Shading; *Ugni molinae*

1. Introduction

Plants in the field are permanently exposed to changes in photosynthetic photon flux density (PPFD), together with other environmental conditions such as temperature and air

* Corresponding author. Tel.: +56-2-6785840; fax: +56-2-6785805.
E-mail address: cpastene@uchile.cl (C. Pastenes).

0304-4238/03/$ – see front matter
doi:10.1016/S0304-4238(02)00224-8

humidity. Such changes in PPFD occur during the day and in the long term, during the growing season, and plants must adapt their physiology to such changes. Even though there is no evidence that photosynthetic CO_2 assimilation rate correlates with biomass production, it has been commonly observed that the capacity of plants to grow and develop in regimes contrasting with their original habitats, depends on the capacity of such plants to acclimatize at the level of photosynthesis, particularly in the case of temperature and light (Björkman et al., 1974, 1975; Pearcy, 1977).

It has been generally observed that photosynthesis responds proportional by to light intensity, up to a point where further increases in light are followed by constant CO_2 assimilation rate, i.e. photosynthesis becomes light saturated. Therefore, light becomes absorbed in excess of the capacity of leaves to use it in photochemistry. Plants nearly saturate at about 900 μmol photons m^{-2} s^{-1}, well bellow the midday intensity reached in most Mediterranean climates during the summer. When plants are unable to adapt to a condition of excess absorbed energy by the photosynthetic apparatus, photoinhibition, defined as the light dependent reduction of the efficiency of the photosynthetic electron transport, may occur (Jahns and Miehe, 1996; Osmond et al., 1993). The primary site of damage during photoinhibition is photosystem II, particularly the reaction center protein, D1. The loss of the photosynthetic activity will depend on the relative rate to which D1 proteins are damaged compared to the rate to which they are synthesized and integrated again into the PSII complex (Baker, 1991). When severe damage occurs, reductions in quantum yield are not reversible in the short term, and even light saturated photosynthetic rates are decreased, being therefore referred to as ''chronic'' photoinhibition (Osmond, 1994). Photosynthetic organisms, however, have evolved mechanisms to protect themselves against photodamage. Non-photochemical energy dissipation has been described as the most important form of protection, resulting in a lower quantum yield of photosynthesis, similar to photo-induced damage, except that this is rapidly reversible and no maximal photosynthetic rate reduction is observed (Demmig-Adams and Adams, 1996; Horton et al., 1996; Osmond et al., 1993). Therefore, it has been referred to as ''dynamic'' photo-inhibition (Osmond, 1994). Other mechanisms for protection consist of chlorophyll concentration changes in order to reduce the extent of the absorbed light (Giardi et al., 1996; Murchie and Horton, 1997); chloroplast movements, reducing the organelle and photosynthetic complexes exposure to light (Haupt, 1990); increases in the capacity for scavenging the active oxygen species by means of increases in scavenging enzyme activity and/or concentration of non-enzymatic antioxidants (Bowler et al., 1992; Foyer et al., 1994); and leaf movement or paraheliotropism, avoiding direct exposure to sun, therefore avoiding light and heat (Ludlow and Björkman, 1984).

Plants have been classified, according to their natural growing environment and CO_2 assimilation rate as shade or sun plants. However, no conclusion can be drawn, regarding the capacity of such plants to adapt to different light regimes. This is particularly relevant for the domestication of wild species for agricultural purposes. The Chilean guava, also known as *murtilla* or *murta* (*Ugni molinae*) is a Myrthaceae species native from south Chile, growing in woodland edges and forest understorey characterized by low PPFD. This shrub has been gaining attention from farmers in Chile, for jam, tea and liquor production, and has been introduced in the UK and Australia, also for ornamental use. Domestication of

this species, however, has been mainly practised in full light conditions and in warmer climates compared to that of its origin.

The aim of the present study was to assess the capacity of Chilean guava plants to adapt, at the level of photosynthesis, to the light environment of central Chile, characteristic of many Mediterranean climates. Shading was considered as a means of alleviating a possible photoinhibitory condition in plants.

2. Materials and methods

The experiments were conducted in 1999–2000 at the Agronomical Research and Experimental Station (Antumapu) at the Faculty of Agronomical Sciences of the University of Chile in Santiago, Chile, 33°40′S, 70°38′W. The experimental design was a randomized complete block with four replications. Each block consisted of two plots, corresponding to shade and full light treatments, with six plants, 0.6 m apart in the row. Plots were 3.6 m from one each other. Shade condition was achieved by means of black mesh of 50% transmittance, placed 1 m above ground.

Plants were asexually propagated through cuttings and rooted during the winter, after which they were planted in November 1999, when a strong root system was already formed. Irrigation was by controlled drip (NAAN, Israel) at 4.7 l m^{-1} h^{-1}.

Photochemical (q_P) and non-photochemical quenching (q_N) of chlorophyll fluorescence were determined during the day. Leaves were dark adapted the afternoon before measurements by means of leaf clips. Early in the morning, in the dark-adapted leaves, the minimal (F_0) and maximal (F_m) emitted fluorescence were recorded with a modulated fluorimeter (Hansatech FMS1, UK), and the leaf clips immediately removed after marking the position on the leaf, in order to measure F_s, F_m' and F_0' in exactly the same spot during the day. Measurements were done with care not to disturb the leaf position and light exposure on the leaf. After the steady state fluorescence, F_s, was measured, F_m' was recorded by means of a 3500 μmol photons m^{-2} s^{-1} PAR light flash and the leaf darkened with a black cloth for 30 s after measuring F_0' using far red light. All measurements were done with the same hardware configuration. The parameters q_P and q_N were calculated according to van Kooten and Snell (1990) in which $q_P = (F_m' - F_s')/(F_m' - F_0')$ and $q_N = 1 - (F_m' - F_0')/(F_m - F_0)$. Recovery of the maximum quantum yield, measured as F_v/F_m, in which $F_v = F_m - F_0$ was determined, dark adapting leaves for 30 min with leaf clips, on the same leaves during the day. Different leaves were used for the fluorescence quenching parameters and F_v/F_m, with three and five replications per plot every measuring time, respectively.

Net CO_2 assimilation rates and stomatal conductance were determined by means of an Infrared Gas Analyser (IRGA) (ADC-1, UK). Measurements were carried out in laboratory conditions on detached leaves collected immediately before measurement and kept in humid petri dishes. Leaves were detached in order to increase the leaf area by measuring two leaves from the same plant, simultaneously inside the photosynthetic chamber. Measurements were carried out at different light intensities, supplied from a cold light source (Schott, Germany), and measuring from darkness to the highest intensity. Four plants per plot were measured.

Leaf temperature was measured with an infrared thermometer (Extech, USA) using the same leaves as for fluorescence measurements, and same intervals.

Ambient PAR light was measured by means of a PAR light meter (Licor, Li-182, USA) positioning the sensor perpendicular to the sunlight and parallel to the ground. Air temperature and relative humidity were obtained from a higrothermometer (Exctech 445900, USA), measured 1 m above ground.

Four leaf discs of 5 mm diameter were taken from every plant and macerated in a mortar with 1 ml ethanol 80% v/v. The homogenate was taken to a volume of 1.5 ml with ethanol 80% and centrifuged at 12,000 rpm for 2 min. Total carotenoids, chlorophyll *a* and *b* were determined according to Lichtenthaler and Wellburn (1983), measuring 470, 649 and 665 nm absorbance in a double beam spectrophotometer (Shimadzu, UV-1601, Japan).

Measurements of plant height and internode length were carried out once per week. Each measurement was made to every plant in each plot.

Standard analysis of variance techniques were used to assess the significance of treatment means based on a completely randomized design. The data shown are mean values ± S.E. Significance was represented by $*P < 0.05$.

3. Results

As expected, the period from January to February 2000 was characterized by clear skies, with average PPFD recordings of 800 and 1600 μmol m^{-2} s^{-1} PAR at 13:00 h in shade and full light, respectively (Fig. 1A). Fluorescence measurements were performed on 25 and 26 January, both days with identical PPFD (Fig. 1B). The lowest PPFD was observed early in the morning, at 8:30, with values of 90 μmol m^{-2} s^{-1} and 620 m^{-2} s^{-1} PAR in the shade and full light, respectively (Fig. 1B), and reaching the highest values at 13:00, similar to

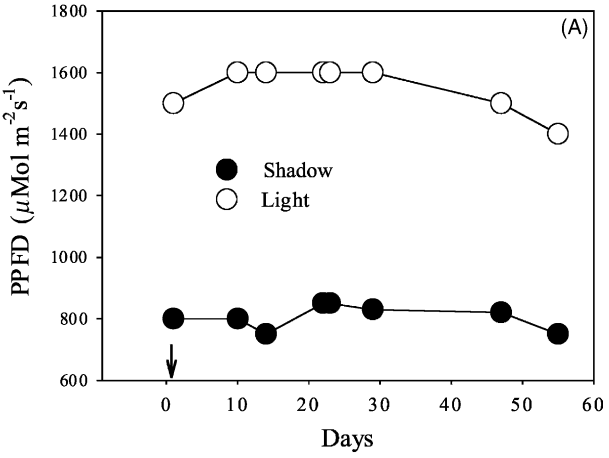

Fig. 1. Environmental parameters during the season and the day of fluorescence measurement. (A) Recorded PAR during the 2 months of measurements at 13:00 h, arrow indicating 4 January; (B) PAR light; (C) relative humidity; and (D) air temperature, taken during the day of fluorescence measurements, from 8:30 to 18:30 h.

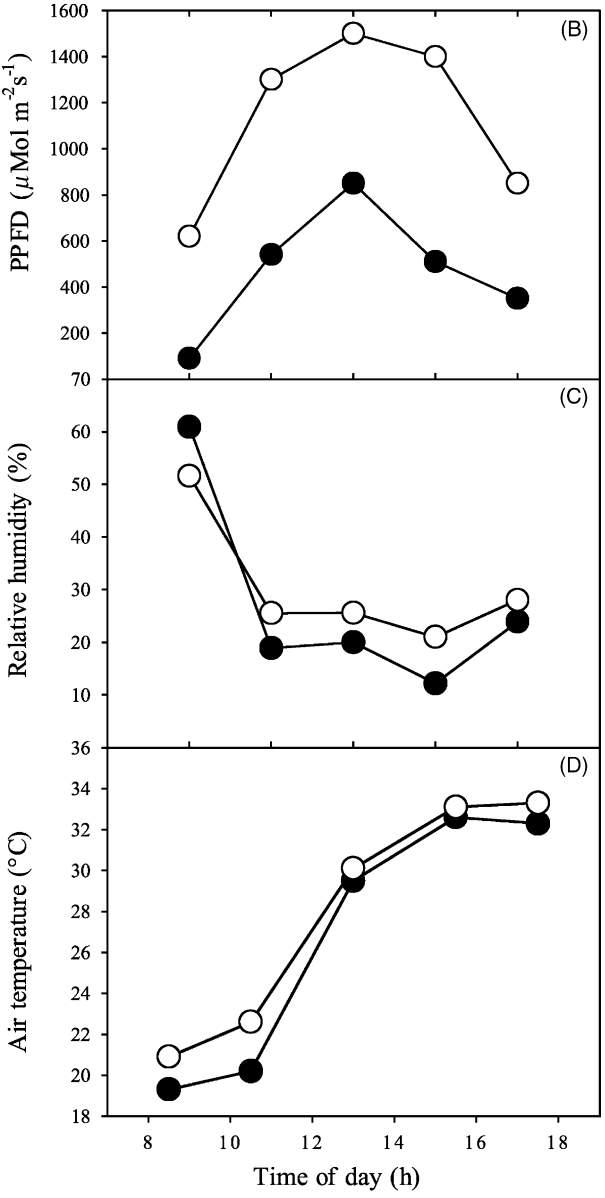

Fig. 1. (*Continued*).

that already mentioned as the 2 months average (Fig. 1A). At 17:30, in the afternoon, the PPFD declined to 350 and 850 m^{-2} s^{-1} in shade and full light, respectively. In the afternoon and, particularly, early morning, the PPFD values in shade plots were less than 50% of that in full light, as a result of the lower angle of incident light reaching the mesh,

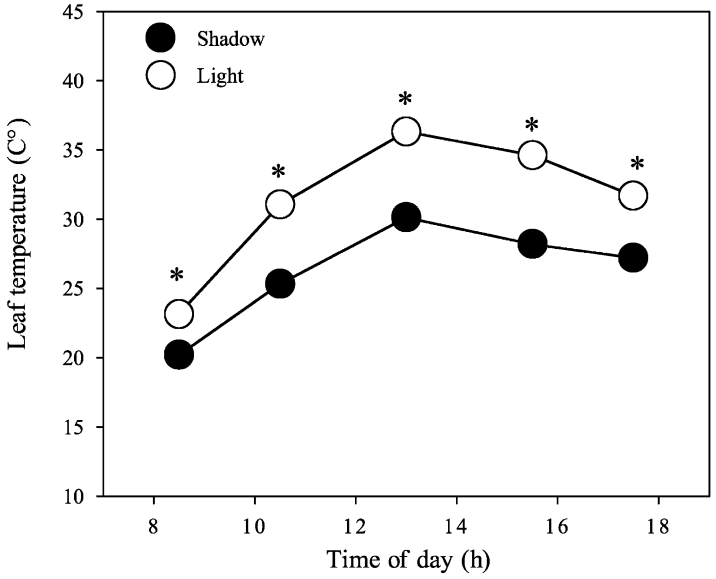

Fig. 2. Leaf temperature from light and shade plants measured from 8:30 to 18:30 h. Asterisk (*) represents significant differences between light conditions for every hour ($P \leq 0.05$).

compared to midday. Air humidity, on the other hand, strongly decreased during the day for the shade and full light, from 60.9 and 51.6% at 8:30 h to 12.2 and 21% at 15:30 h, respectively (Fig. 1C). Air temperature followed the light intensity, reaching 35.2 and 33.9 °C in full light and shade, respectively, at 15:30 h, slightly decreasing later (Fig. 1D). The lowest temperatures were observed at 8:30 h with values of 20 and 19.3 °C in full light and shade plots, respectively (Fig. 1D). The temperature difference between shade and full light never exceeded 2 °C.

Shading resulted in a significant by lower leaf temperature compared to full light plants throughout the day (Fig. 2). Also, leaf temperature measured from 13:00 to 17:30 h in leaves from shade plants was the same or lower than air temperature, in contrast to full light grown plants with higher leaf temperature compared to air (Figs. 1D and 2).

PPFD higher than that saturating for photosynthesis, induces non-radiative de-excitation mechanisms at the chlorophyll level in the PSII complexes, resulting in a decreased maximum quantum yield of photosynthesis. Such changes are partially or totally reversed in darkness, and the extent up to which the maximum quantum yield is recovered, has been used as a probe for photoinhibition in leaves (Adams et al., 1990). The F_v/F_m parameter has been correlated with the maximum quantum yield of photosynthesis (Björkman and Demmig, 1987; Bolhar-Nordenkampf and Öquist, 1993; Cornic and Briantais, 1991; Genty et al., 1989) reaching a maximum theoretical value of 0.85 (Bolhar-Nordenkampf et al., 1991). It is suggested, from Fig. 3, that plants grown in shade conditions nearly recovered to the maximum quantum yield for photochemistry in 30 min of dark adaptation throughout the day. In contrast, plants grown under full sunlight recovered the F_v/F_m

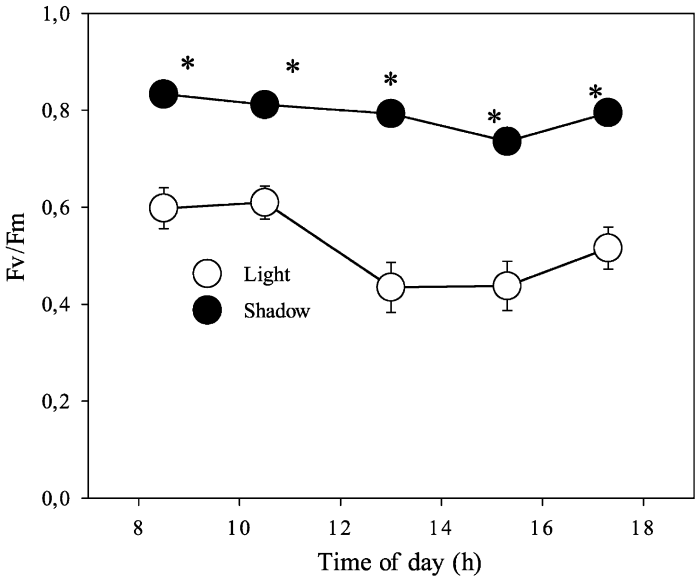

Fig. 3. F_v/F_m measured in leaves from light and shade plants during the day, from 8:30 to 18:30 h, after 30 min dark adaptation, except for the first measurement, for which leaves were dark adapted from the 19:00 h the afternoon before. Asterisk (*) represents significant differences between light conditions for every hour ($P \leq 0.05$). Bars represent S.E.

parameter to a maximum of about 0.6 at 10:30, and values lower than 0.5 were observed at 13:00 and 15:30 h (Fig. 3).

The parameter q_P, which represents the proportion of PSII reaction centers in an open state, i.e. capable of charge separation, remains highly constant and close to 0.9 in the shaded plants during the day (Fig. 4A). As for the full light grown plants, q_P was always lower on average compared to the former, such difference being significant from midday onwards. The lowest value, of about 0.47 occurs in full light leaves at 13:00 (Fig. 4A). As expected, q_N, which is proportional to the absorbed energy re-emitted as heat from the PSII complexes, followed changes opposite to q_P (Fig. 4B). Highest values were observed in full light grown plants, particularly at 13:00 h with a value of 0.8, nearly double than that observed for the shaded plants at the same hour. Similar to q_P, differences in q_N were significant in the afternoon (Fig. 4B).

The light regime also induced changes in pigment composition of leaves, resulting in significantly higher contents for the shade plants (Fig. 5). Pigment content in the shade plants was higher than the full light, with 68% more total carotenoids, and 70 and 48% more chlorophyll *a* and *b*, respectively, compared to the full light. The chlorophyll *a*/*b* ratio was also significantly different between treatments, being 33% higher in shade compared to full light grown plants.

Leaves from full light plants shows a lower capacity for photosynthesis for PPFD higher than 200 μmol m^{-2} s^{-1} (Fig. 6). Independently of the light regime, the assimilation rates were low, reaching less than 4 μmol CO_2 m^{-2} s^{-1} under the highest intensity measured (Fig. 6). The observed differences in carbon assimilation does not seem to be related to

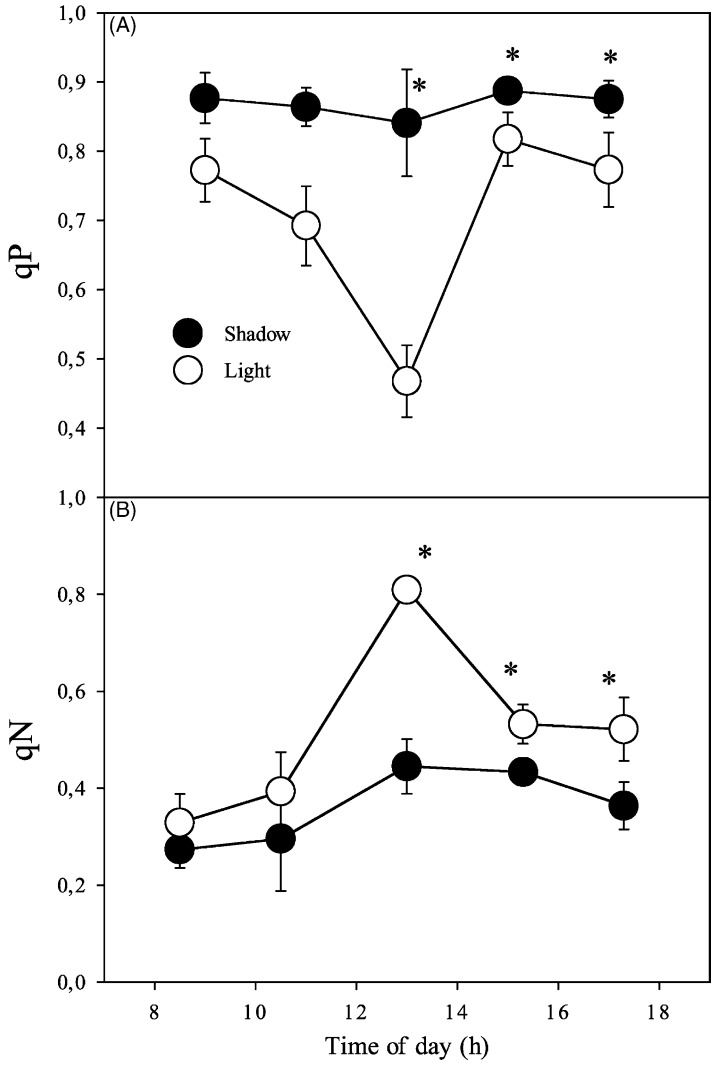

Fig. 4. Photochemical (A) and non-photochemical (B) chlorophyll fluorescence quenching, measured from 8:30 to 18:30 h in leaves from light and shade plants. Asterisk (*) represents significant differences between light conditions for every hour ($P \leq 0.05$). Bars represent S.E.

stomatal characteristics since no difference in stomatal conductance, nor pore width or stomatal density were observed between treatments (data not shown).

Three weeks from transplanting, shade plants reached greater height on average than those in full light reaching, 20 and 10 cm, respectively (Fig. 7A). The taller plants grown in shade, however, were not necessarily a consequence of higher dry mass accumulation, but for the known effect of low PPFD on plant elongation. The shaded plants, in fact, had longer internodes than full light grown plants (Fig. 7B) (data not shown).

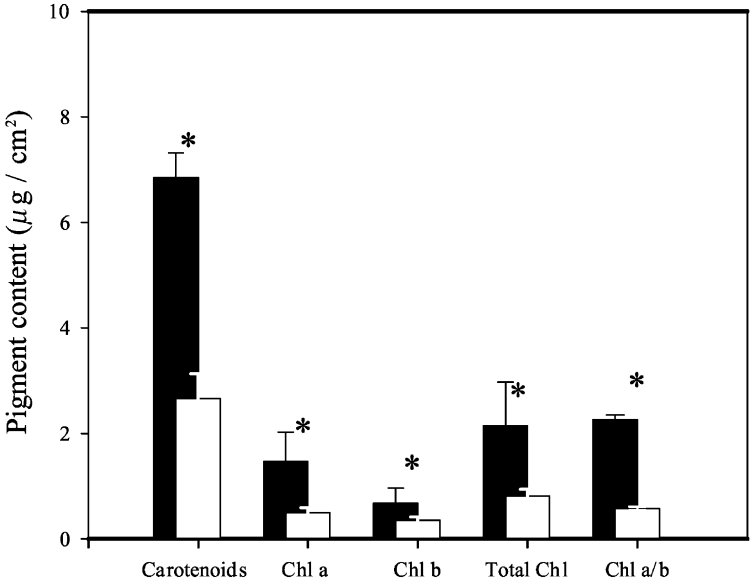

Fig. 5. Total carotenoids, chlorophyll *a*, chlorophyll *b*, total chlorophyll and the chlorophyll *a*/*b* ratio in leaves from light and shade plants, taken 1 February. Asterisk (*) represents significant differences between light conditions for every hour ($P \leq 0.05$). Bars represent S.E.

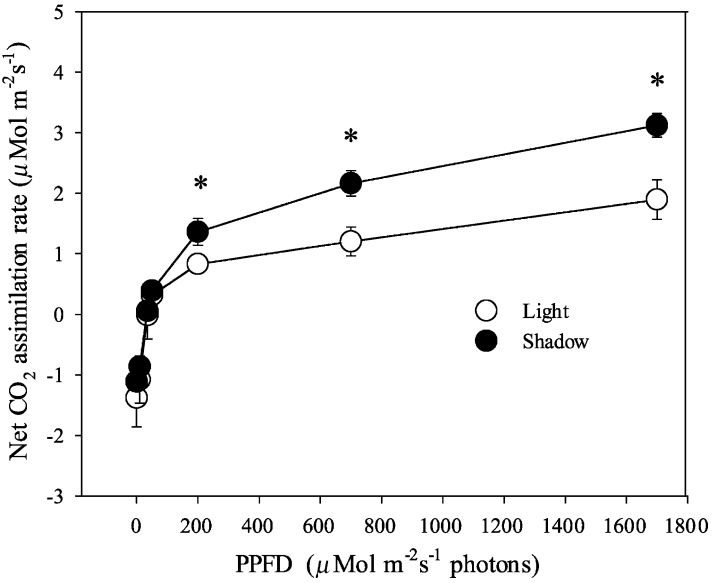

Fig. 6. Net CO_2 assimilation in leaves from light and shade plants, collected on 1 January, at different light intensities, from darkness up to 1750 μmol m^{-2} s^{-1} PAR photons. Asterisk (*) represents significant differences between light conditions for every hour ($P \leq 0.05$). Bars represent S.E.

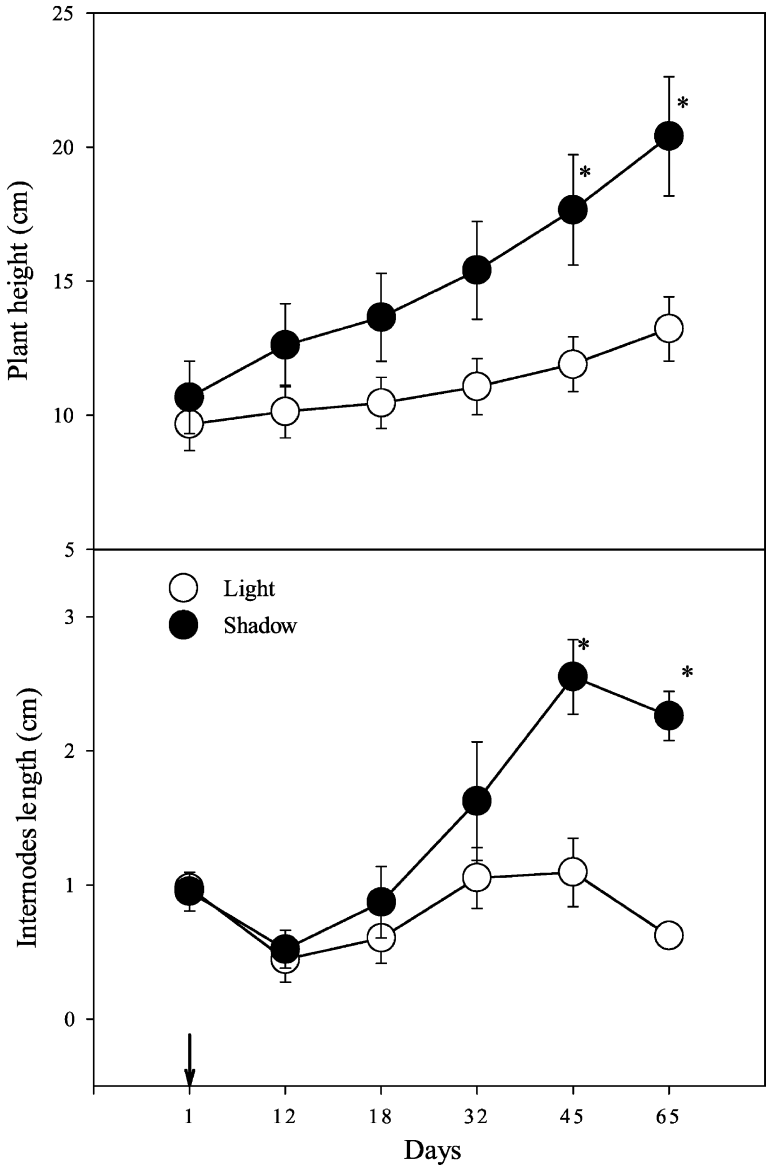

Fig. 7. (A) Plant height and (B) average internode length, measured during the growing season in light and shade plants; arrow indicates 4 January. Asterisk (*) represents significant differences between light conditions for every hour ($P \leq 0.05$). Bars represent S.E.

4. Discussion

The PPFD and air temperature observed in the present study (Fig. 1A and D) may constitute a strong limitation for some species to the functioning of the photosynthetic

carbon metabolism, inducing photoinhibition (Long and Humphries, 1994). High PPFD from sunlight may not only induce over-excitation of the photosynthetic apparatus as it is suggested in the present study from the poor capacity for F_v/F_m recovery (Fig. 3), but the extremely low q_P values and concomitant high q_N during midday in full light grown plants (Fig. 4), may also be linked to increases in temperature of leaf tissues. Leaf temperature of full sunlight plants was 5 °C higher than air temperature at midday (Figs. 1D and 2). High temperature is responsible for alterations on the functioning and organization of the photosynthetic apparatus particularly PSII components (Melis, 1991; Pastenes and Horton, 1996a,b) and electron transport in chloroplasts (Pastenes and Horton, 1999), also in carbon metabolism through increases in photorespiration because of changes in gas solubility and the Rubisco enzyme activity (Crafts-Brander and Salvucci, 2000; Jensen, 2000). The latter effect is also induced by transient water vapor deficits, in turn induced by heat. As a consequence stomatal closure occurs, reducing the CO_2 concentration readily available for reduction (Hsiao, 1973; Mott and Parkurst, 1991; Pugnaire et al., 1999; Weise et al., 1990) and, therefore, inducing an over-excitation of the photosynthetic apparatus, particularly photosystem II (PSII) with loses of photosynthetic quantum yield (Ludlow and Björkman, 1984).

The full light grown plants, in fact, were unable to recover the photochemical efficiency of photosystem II, measured as F_v/F_m, to values close to the theoretical maximum of 0.83 after 30 min dark adaptation. It is known that such reductions correspond to both: non-radiative dissipation of the energy absorbed by PSII complexes as a result of down-regulation of PSII photochemistry (Björkman and Demmig-Adams, 1994; Horton and Ruban, 1994), and to direct damage to PSII (Andersson and Barber, 1996; Aro et al., 1993). The decline in F_v/F_m in the full sunlight plants, was a minimum at midday, but even early in the morning the parameter was not higher than 0.6. The F_v/F_m measurements carried out at 8:30 resulted from dark adaptation throughout the night, from 19:00 h the previous, to 8:30 h the following day, as necessary for calculations of q_N during the day (see Section 2). The poor capacity to recover F_v/F_m, even for such a long time in darkness is, therefore, an indication that long-term photoinhibition affects leaves from those plants. In contrast, shaded plants show complete recovery of the parameter with values higher than 0.8, most of the day, characteristic of healthy dark-adapted leaves of C3 plants (Demmig and Björkman, 1987).

It is evident that light intensity exceeds the capacity of leaves to use that energy in photochemistry in the exposed plants, since the extent of open PSII reaction centers, represented by q_P, is remarkably depressed during midday (Fig. 4). The light driven electron transport in chloroplasts, couples the acidification of the lumen, necessary for ATP synthesis. Also, lumen pH mediates the activation of non-photochemical energy dissipation mechanisms at the PSII antenna level (Horton and Ruban, 1994; Horton et al., 1994), the extent of which is represented by q_N. Non-photochemical energy dissipation has been described as the most important form of protection against excess light, resulting in a lower quantum yield of photosynthesis, similar to photo-induced damage, except that no maximal photosynthetic rate reduction is observed (Demmig-Adams and Adams, 1996; Horton et al., 1996; Osmond et al., 1993). q_N contributes to maintain PSII reaction centers in an open state, i.e. capable of performing electron transport and, therefore, avoiding over-excitation of antenna chlorophylls. q_N, in the shaded plants (Fig. 4) only slightly increased during midday, reflecting a more balanced light excitation to reducing power and energy

demand ratio. On the fully exposed plants, however, q_N increased up to 0.8 at midday. Such a high value was unable to maintain PSII reaction centers. It has been suggested, in fact, that q_P values close to 0.5 would be a threshold for long-term photoinhibition in many species and growth conditions (Öquist et al., 1992). Therefore, the decrease in the F_v/F_m ratio in light plants, which indicates a loss of the photochemical efficiency, clearly correlates with the low q_P values (Fig. 4).

Photosynthetic pigment content in leaves has been correlated with the capacity of plants to acclimate to a different light environment (Allen, 1992; Jahns and Miehe, 1996; Färber et al., 1997), thus smaller chlorophyll contents imply a lower excitation pressure on PSII (Baker, 1991; Demmig-Adams and Adams, 1992; Krause, 1988). Even though full light plants resulted in lower chlorophyll *a* and *b* content (Fig. 5), this is not necessarily a consequence of acclimation. High temperatures, in fact, as well as high light are known to induce senescence in leaf tissues, and to shorten the life of leaves (Lawlor, 1994). In the present study, leaf temperature of light grown plants was even higher than air temperature from early morning to midday (Figs. 1D and 2). Also, acclimation has been suggested to occur, decreasing preferentially PSII antenna size, therefore increasing the chlorophyll *a*/*b* ratio (Leong and Anderson, 1984). In the present study, the pigment content in light grown plants, characterized by a low chlorophyll *a*/*b* ratio, suggests that no acclimation to light occurred, but possibly damage to the photosynthetic apparatus. It is well known that non-reversible photoinhibition in plants is partly the consequence of active oxygen species formed in the chloroplasts (Demmig-Adams and Adams, 1996; Foyer et al., 1994) responsible for cell toxicity and loss of cell components, like photosynthetic complexes associated with light harvesting pigments (Asada, 1994).

Photoinhibition in plants implies a lowered photosynthetic capacity, in many cases associated with a lower capacity for plant dry mass accumulation (Ögren and Sjöstrom, 1990; Winter and Königer, 1991). Plants grown in the shade reached higher net photosynthetic rates upon illumination with light intensities higher than 200 $\mu mol\ m^{-2}\ s^{-1}$, compared to full light grown plants. Such differences might have been even higher in the field, where leaf temperature and, therefore, water vapor pressure deficit and stomatal conductance are very likely unfavorable for light plant photosynthesis. Therefore, in addition to: (a) the poor capacity to recover F_v/F_m, even after overnight darkness; (b) q_P values during midday close to 0.5; and (c) general loss of photosynthetic pigments and the decline in light saturated CO_2 assimilation, further suggests that the Chilean guava is sensitive to high light intensities, being seriously photoinhibited. While the smaller size of light grown plants results from shorter internodes, but no assessment of plant dry mass was carried out to be correlated with the light effects on photosynthesis. Shading has already been used in horticulture in Mediterranean climates, in order to increase yield and fruit quality. Even though shading might not be an economical option at present, Chilean guava could be produced as an intercrop under tree canopies, increasing the profitability of land.

References

Adams III, W.W., Demmig-Adams, B., Winter, K., Schreiber, U., 1990. The ratio of variable to maximum fluorescence from photosystem II, measured in leaves at ambient temperature and at 77 K, as an indicator of the photon yield of photosynthesis. Planta 180, 166–174.

Allen, J.F., 1992. Protein phosphorylation in regulation of photosynthesis. Biophys. Acta 1098, 275–335.

Andersson, B., Barber, J., 1996. Mechanisms of photodamage and protein degradation during photoinhibition of photosystem II. In: Baker, N.R. (Ed.), Photosynthesis and the Environment. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 101–121.

Aro, E.-M., Virgin, I., Andersson, B., 1993. Photoinhibition of photosystem II. Inactivation, protein damage and turnover. Biochim. Biophys. Acta 1143, 113–134.

Asada, K., 1994. Production and action of active oxygen species in photosynthetic tissues. In: Foyer, C., Mullineaux, P.M. (Eds.), Causes of Photooxidative Stress and Amelioration of Defense Systems in Plants. CRC Press, Boca Raton, FL, pp. 77–104.

Baker, N.R., 1991. A possible role for photosystem II environmental perturbations of photosynthesis. Plant Physiol. 81, 563–570.

Björkman, O., Demmig-Adams, B., 1994. Regulation of photosynthetic light energy capture, conversion and dissipation in leaves of higher plants. In: Schulze, E.-D., Caldwell, M.M. (Eds.), Ecophysiology of Photosynthesis. Springer, Berlin, pp. 17–47.

Björkman, O., Demmig, B., 1987. Photon yield of evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. Planta 170, 489–504.

Björkman, O., Mahall, B., Nobs, M., Ward, W., Mooney, F.N.H., 1974. Growth response of plants from habitats with contrasting thermal environments: an analysis of the temperature dependence under controlled conditions. Carnegie Inst. Washington Yearb 73, 757–767.

Björkman, O., Mooney, F.N.H., Ehleringer, J., 1975. Photosynthetic responses of plants from habitats with contrasting thermal environments. Carnegie Inst. Washington Yearb 74, 743–748.

Bolhar-Nordenkampf, H.R., Hofer, M., Lechner, E.G., 1991. Analysis of light-induced reduction of the photochemical capacity in field-grown plants. Evidence for photoinhibition. Photosynth. Res. 27, 31–39.

Bolhar-Nordenkampf, H.R., Öquist, G., 1993. Chlorophyll fluorescence as a tool in photosynthesis research. In: Hall, D.O., Scurtock, I.M.O., Bolhar-Nordenkampf, H.R., Leegood, R.C., Long, S.P. (Eds.), Photosynthesis and Production in a Changing Environment: A Field Laboratory Manual. Chapman & Hall, London, Chapter 12, pp. 193–206.

Bowler, C., van Montagu, M., Inzé, D., 1992. Superoxide dismutase and stress tolerance. Ann. Rev. Plant Phys. Plant Mol. Biol. 43, 83–116.

Cornic, G., Briantais, J.M., 1991. Partitioning of photosynthetic electron flow between CO_2 and O_2 reduction in a C_3 leaf (*Phaseolus vulgaris* L.) at different CO_2 concentration and during drought stress. Planta 183, 178–184.

Crafts-Brander, S.J., Salvucci, M.E., 2000. Rubisco activase constrains the photosynthetic potential of leaves at high temperature and CO_2. Proc. Natl. Acad. Sci. USA 97, 13430–13435.

Demmig-Adams, B., Adams, W.W., 1992. Photoprotection and other responses of plants to high light stress. Ann. Rev. Plant Physiol. Plant Mol. Biol. 43, 599–626.

Demmig-Adams, B., Adams, W.W., 1996. The Role of Xanthophyll Cycle Carotenoids in the Protection of Photosynthesis, vol. 1. Elsevier, Amsterdam, pp. 21–26.

Demmig, B., Björkman, O., 1987. Comparison of the effect of excessive light on chlorophyll fluorescence (77 K) and photon yield of O_2 evolution in leaves of higher plants. Planta 171, 171–184.

Färber, A., Young, A.J., Ruban, A.V., Horton, P., Jahns, P., 1997. Dynamics of the xanthophyll cycle in different antenna sub-complexes in the photosynthetic membranes of higher plants. Plant Physiol. 115, 1609–1618.

Foyer, C.H., Lelandais, M., Kunert, K.J., 1994. Photooxidative stress in plants. Physiol. Plant. 92, 626–717.

Genty, B., Briantais, J.M., Baker, N.R., 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim. Biophys. Acta 990, 87–92.

Giardi, M.T., Cona, A., Geiken, B., Kucera, T., Masojidek, J., Matoo, A.K., 1996. Long-term drought stress induces structural and functional reorganization of photosystem II. Planta 99, 118–125.

Haupt, W., 1990. Chloroplast movement. Plant Cell. Env. 13, 595–614.

Horton, P., Ruban, A., 1994. The role of light harvesting complex II in energy quenching. In: Baker, N.R., Bowyer, J.R. (Eds.), Photoinhibition of Photosynthesis: From Molecular Mechanisms to the Field. Bios Scientific Publishers, Oxford, UK, pp. 111–128.

Horton, P., Ruban, A.V., Walters, R.G., 1994. Regulation of light harvesting in green plants. Indication by nonphotochemical quenching of chlorophyll fluorescence. Plant Physiol. 106, 415–420.

Horton, P., Ruban, A.V., Walters, R.G., 1996. Regulation of light harvesting in green plant. Physiol. Plant Mol. Biol. 47, 665–684.

Hsiao, T.C., 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24, 519–570.

Jahns, P., Miehe, B., 1996. Kinetic correlation of recovery from photoinhibition and zeaxanthin epoxidation. Planta 98, 202–210.

Jensen, R.G., 2000. Rubisco activase constrains the photosynthetic potential of leaves at high temperature and CO_2. Proc. Natl. Acad. Sci. USA 97, 12937–12938.

Krause, G.H., 1988. Photoinhibition of photosynthesis. An evaluation of damaging and protective mechanisms. Physiol. Plant. 74, 566–574.

Lawlor, D.W., 1994. The effects of water deficit on photosynthesis. In: Baker, N.R., Bowyer, J.R. (Eds.), Photoinhibition of Photosynthesis from Molecular Mechanisms to the Field. Bios Scientific Publishers, Oxford, UK, pp. 129–160.

Leong, T.Y., Anderson, J.M., 1984. Adaptation of the thylakoid membranes of pea chloroplasts to light intensities. II. Regulation of electron transport capacities, electron carriers, coupling factor (CF_1) activity and rates of photosynthesis. Photosynth. Res. 5, 117–128.

Lichtenthaler, H.K., Wellburn, A.R., 1983. Determination of total carotenoids and chlorophyll *a* and *b* of leaf extract in different solvents. Biochem. Soc. Trans. 603, 591–592.

Long, S.P., Humphries, S., 1994. Photoinhibition of photosynthesis in nature. Ann. Rev. Plant Physiol. Plant Mol. Biol. 45, 633–662.

Ludlow, M.M., Björkman, O., 1984. Paraheliotropic leaf movements in *Siratro* as a protective mechanism against drought-induced damage to primary photosynthetic reactions: damage by excessive light and heat. Planta 161, 505–516.

Melis, A., 1991. Dynamics of photosynthetic membrane composition and function. Biochim. Biophys. Acta 1058, 87–106.

Mott, K.A., Parkurst, D.F., 1991. Stomatal responses to humidity in air and helox. Plant Cell Environ. 14, 509–515.

Murchie, E.H., Horton, P., 1997. Acclimation of photosynthesis to irradiance and spectral quality in British plant species: chlorophyll content, photosynthetic capacity and habitat preference. Plant Cell Environ. 20, 438–448.

Ögren, E., Sjöstrom, M., 1990. Estimation of the effect of photoinhibition on the carbon gain in leaves of a willow canopy. Planta 181, 560–567.

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

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

Osmond, C.B., Ramus, J., Levavasseur, G., Franklin, L.A., Henley, W.J., 1993. Fluorescence quenching during photosynthesis and photoinhibition of *Ulva rotundata* Blind. Planta 190, 97–106.

Pastenes, C., Horton, P., 1996a. Effect of high temperature on photosynthesis in beans. I. Oxygen evolution and chlorophyll fluorescence. Plant Physiol. 112, 1245–1251.

Pastenes, C., Horton, P., 1996b. Effect of high temperature on photosynthesis in beans. II. CO_2 assimilation and metabolite contents. Plant Physiol. 112, 1253–1260.

Pastenes, C., Horton, P., 1999. Resistance of photosynthesis to high temperature in two bean varieties (*Phaseolus vulgaris* L.). Photosynth. Res. 62, 197–203.

Pearcy, R.W., 1977. Acclimation of photosynthetic and respiratory CO_2 to growth temperatures in *Atriplex lentiformis* (Torr) Wats. Plant Physiol. 59, 795–799.

Pugnaire, F.I., Serrano, L., Pardos, J., 1999. Constraints by water stress on plant growth. In: Pessarakli, M. (Ed.), Handbook of Plant and Crop Stress. Marcel Dekker, New York, pp. 271–283.

van Kooten, O., Snell, J.F.H., 1990. The use of chlorophyll fluorescence nomenclature in plant stress physiology. Photosynth. Res. 25, 147–150.

Weise, R.R., Frederick, J.R., Alm, D.M., Kramer, D., Hesketh, J.D., Crofts, A.R., Ort, D.R., 1990. Investigation of the limitations to photosynthesis induced by leaf water deficit in field grown sunflower (*Helianthus annuus* L.). Plant Cell Environ. 13, 923–931.

Winter, K., Königer, M., 1991. Dry matter production and photosynthetic capacity in *Gossypium hirsutum* L. under conditions of slightly suboptimum leaf temperatures and high levels of irradiance. Oecologia 87, 190–197.