J. Ginseng Res.
Vol. 22, No. 2, 102~113(1998)

The effect of irradiance during leaf development on photoinhibition in *Panax ginseng* C. A. Meyer

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(Received March 24, 1998)

Abstract : This experiment used chlorophyll fluorescence techniques to assess the effect of irradiance during leaf development on photoinhibition of photosynthesis in *Panax ginseng*. Seedlings of *P. ginseng* were grown in the glasshouse at four shade levels. The maximum mid-day irradiance in each treatment between emergence (January 4) and completion of the experiment (February 25) was 1220, 485, 235, 125 μmol/m²/s. To assess the rapidity of photosynthetic readaptation to changes in light levels, fluorescence parameters (Fo, F, Fm, Fm', ΔF/Fm', Fv/Fm) were measured for three days before and after transfer of plants (on February 21) from each light treatment into each of the other light treatments. Before transfer, dark adapted values of Fv/Fm in the 1220 (0.699) and 485 (0.739) treatments were different from each other and lower than values in the 235 (0.764) and 125 (0.768) treatments, indicating mild photoinhibition. Patterns of change in F during the day also differed between treatments, with low light treatments tracking irradiance levels, but F in the high light treatment (1220) declined in the morning, presumably due to fluorescence quenching. Although plants grown at high irradiance had relatively low photosynthetic efficiency, relative electron transport rate was greater than in lower irradiance treatments. After transfer, plants adopted the daily pattern of change in F of the treatment to which they were moved with little change in absolute levels of F, except in plants transferred from the highest (1220) to the lowest light level (125), where F increased over the course of the three days following transfer. After plants were transferred, Fm' converged on values similar to those in plants raised in the treatments to which they were moved. Values of Fv/Fm in plants moved from low to high light declined dramatically, but there was no decline in plants from 485 moved to 1220. Values of Fv/Fm in plants that were moved from high light to lower light increased to values above those recorded in plants raised in the lower light treatments. Reductions in quantum efficiency caused by photoinhibition at high irradiance may be more than compensated for by higher electron transport rates, although evidence suggests that under high irradiance this tends to be balanced by reduced leaf area and earlier senescence. Chlorophyll fluorescence techniques appear capable of indicating effects of irradiance induced stress in ginseng, yielding results comparable to those obtained with gas exchange techniques but in less time and with greater replication.

Key words : Ginseng, *Panax ginseng*, photosynthesis, photoinhibition, chlorophyll fluorescence.

Introduction

Ginseng (Araliaceae) is an obligate shade plant with a natural habitat on the floor of broad-leaved forests in Asia and North America.[1] There are a number of species in the genus but the two which are important commercially are *Panax ginseng* C.A. Meyer and *Panax quinquefolium* L. Dried root from these two species is used extensively in traditional Asian medicines.[2,3]

Ginseng is an herbaceous perennial. A single trifoliate leaf on a short (40~80 mm) petiole is produced from the seed. During the first season of growth a terminal bud is formed on a short rhizome. This requires a period of chilling over winter before producing a single aerial stem (70~

400 mm) in spring (rarely two). The stem emerges in early spring, bearing a whorl of leaves (3~5 leaflets) which increase in size and number each year as the plant ages. No more leaves are produced during the season. The production of new root during a season depends, therefore, entirely on the set of leaves produced in spring. This makes the fate of that set of leaves of particular importance for the future productivity of the plant.

Ginseng leaves have long been known to require high levels of shade.[4] In an early attempt to define optimal light intensity for growth of *Panax ginseng*,[5] it was concluded that 8% light was optimal for survival, but that 19% produced similar dry matter yield. Subsequent attempts to define optimal shade levels have produced a wide range of recommendations. Low irradiances are indicated in a number of studies: 5~10% gave greatest root weights 6); 8~13% (but perhaps higher) produced light saturation of photosynthesis 7); 6~8% gave maximum photosynthesis.[8] All of these studies were on two-year-old plants. Other studies[9,10] have indicated that higher irradiances give greater yields. They have concluded that 10~20% gave greatest root yields after three years and that 20~30% gave the highest photosynthesis rates and the greatest root yields after four years.

A level of shade fixed for an entire season may avoid leaf damage or death caused by periods of high irradiance at mid-day in mid-summer, but is likely to lead to sub-optimal irradiance during spring and autumn, and during the morning and afternoon. From a practical point of view there is often little alternative to fixed levels of shade throughout the season. Nevertheless shade structure design or the forest canopy used to shade ginseng can be manipulated to ensure maximum rates of photosynthesis for the greatest possible time during the day, or season. Traditional Korean shade structures, although acknowledged to be too shaded,[7] produce relatively high irradiance in the morning and afternoon by being narrow and open on the sides.[11] Other attempts to maintain more uniform irradiance throughout the day have been proposed.[12]

The light environment during leaf development in spring is likely to have a substantial effect on the photosynthetic capacity of the leaf.[13,14] Physical characteristics like leaf area and thickness and stomatal density will be effectively fixed by the time leaf development is concluded. Other physical characteristics which affect photosynthesis, like leaf orientation or chloroplast distribution, may change rapidly.[15] There is no evidence of rapid leaf movement in ginseng although differences in leaf orientation between low and high irradiance treatments have been measured (Parmenter unpublished). Other leaf characteristics like chlorophyll concentration and granal stacking adapt to ambient irradiance[16] but are reversible over the course of hours to days.

A number of studies describe the response of ginseng photosynthesis to varying growth or measurement irradiances. Many of the light response studies of ginseng[8,17,11] describe CO_2 gas exchange light response curves on material grown under traditional levels of shade (about 5%[10]). This may not always be appropriate unless ginseng lacks the capacity to adapt its photosynthetic system to its growth irradiance, for photosynthetic rates at saturating irradiance are likely to be lower in plants grown at 5% than in plants grown at higher irradiance.[14]

In other studies growth irradiance has been observed to affect light response curves. *P. ginseng* had the highest rates of photosynthesis when grown at 30% of ambient irradiance,[7] even at low (35 $\mu mol/m^2/s$) measurement irradiance. In another study photosynthetic rate of plants grown at 10 or 15% of ambient irradiance was higher than in plants grown at 20 or 25%.[18] However, in this study maximum measurement irradiance was low at only 165 $\mu mol/m^2/s$. If measured at higher irradiances, photosynthesis of plants grown at 20~25% could be expected to improve relative to those grown at lower irradiances.

Photosynthesis of ginseng grown at 5, 15 or 20%[11] demonstrated no significant difference bet-

ween 15 and 20% over the course of a sunny or a shady day, implying that photosynthesis is operating at close to saturation irradiances at these shade levels. In another study,[10] photosynthesis rates were greater in ginseng grown at 15% than those grown at 10 or 20% but measurement conditions were not specified.

All of these studies used gas exchange techniques to estimate rates of photosynthesis. These techniques are relatively time consuming and consequently involve few plants. The recent development of techniques for measuring chlorophyll fluorescence,[19,20] provides a means of rapidly assessing photosynthetic efficiency. In the experiment reported here we use this technique to assess the optimal irradiance for ginseng photosynthesis and the effect of irradiance during leaf development on subsequent photosynthetic performance when plants are transferred to different light levels.

The fluorescence parameters Fo, Fm, Fv and Fv/Fm are all measurements made on plants in a dark adapted state, when all non-photochemical quenching of fluorescence is assumed to be at a minimum. The fluorescence parameters F, Fm' and Δ/Fm' are made on plants which are in a light adapted state in which some of the fluorescence is quenched by non-photochemical processes.[21]

Fo is the level of fluorescence measured after exposure of dark adapted leaves to a weak modulated measuring beam. It is assumed that all PSII reaction centres are open and the photosynthetic membrane is in a non-energized state. Fm is the maximal fluorescence measured after dark adapted leaves are exposed to a saturating pulse of light which is assumed to close all PSII reaction centres. The difference between Fm and Fo, is called variable fluorescence (Fv), and the ratio of variable to maximal fluorescence (Fv/Fm) is a measure of the maximal efficiency of photosynthesis.

F is the fluorescence signal recorded from a leaf exposed to ambient light levels. Fm' is the fluorescence signal generated when a leaf exposed to ambient light receives a light pulse which closes all reaction centres. The parameter Δ/Fm' is the equivalent of Fv/Fm but measured under ambient light levels (Δ=Fm'-F) sometimes called yield and represents the actual photosynthetic efficiency or the "effective" quantum yield.[22]

Under non-photorespiratory conditions the relationship between quantum yield for CO_2 fixation and the quantum efficiency of PSII is linear, but under photorespiratory conditions it is non-linear.[23,24] The measurements reported here were made at ambient levels of CO_2 and O_2 (i.e. photorespiratory conditions) which means caution needs to be exercised in interpreting changes in relative quantum efficiency of electron transport as indicating comparable effects on carbon fixation. Nevertheless these measurements provide a useful indication of how plants react to different levels of irradiance, and are particularly helpful in identifying irradiances which begin to strain the limits of the plant to adjust to high irradiance.

Methods

1. Plant production

Seed from Korean ginseng (*Panax ginseng* C.A. Meyer) grown at Redbank research station, Clyde, was harvested from three years old plants in February 1994. On 23 December 1994 single seeds with an emergent radicle were planted in pots (70×70×90 mm) containing a mix of screened bark, peat, and sand (4:4:1), which had been steam sterilized for two hours, with lime later added to raise pH to 6. Pots were placed in the glasshouse, and on 4 January 1995 plants began to emerge and pots were separated into one of four shade treatments, each containing 12-15 plants (Table 1). Plants were watered daily and once each week were watered to saturation with a nutrient solution (0.5 g Phostragen per litre of water-10%N, 4.4%P, 22.4%K). By 6 January 1995, over 50% of plants in each treatment had emerged and by 9 January 1995 all plants had em-

Table 1. The maximum and mean 'brightest hour' irradiance (μmol/m²/s) for the period from leaf emergence (4 January) until the experiment concluded (24 February) in each of the four irradiance treatments

Treatment	Maximum	Mean
1	1220	630
2	485	250
3	235	120
4	125	65

erged.

2. Treatments

There were four shade treatments, three created by draping black shade cloth (10%, 20% or 40% transmittance) over a frame, the fourth was unshaded. Unshaded irradiance in the glasshouse was substantially lower than ambient irradiance outside the glasshouse. Between 0700 and 2000 NZST the irradiance inside the glasshouse was 0.47 that outside. Maximum unshaded irradiance (inside the glasshouse) during the experiment was about 1200 μmol/m²/s although average mid-day values were closer to 600 μmol/m²/s (Fig. 1a). A single tray of 12~15 plants was placed in each shade treatment. Irradiance in each treatment was measured with quantum sensors (Lambda Instruments Inc) placed at leaf height in the centre of each tray. These were recorded every three seconds and stored as five minute averages. The irradiance in each treatment is described by the average daily irradiance and the maximum irradiance (Jan 4-Feb 24) during the brightest hour in the day (Table 1).

Plants were grown in the four irradiance treatments until 2100 on 21 February, when 2~3 plants were moved from each treatment into each of the other treatments.

3. Glasshouse climate

Air temperature in the glasshouse was measured in a gill screen at plant height every minute and recorded as 5-minute means. Although minimum air temperatures in the glasshouse were controlled to keep air temperature above 10℃, control of maximum temperatures was poor. During the experimental period, air temperature was,

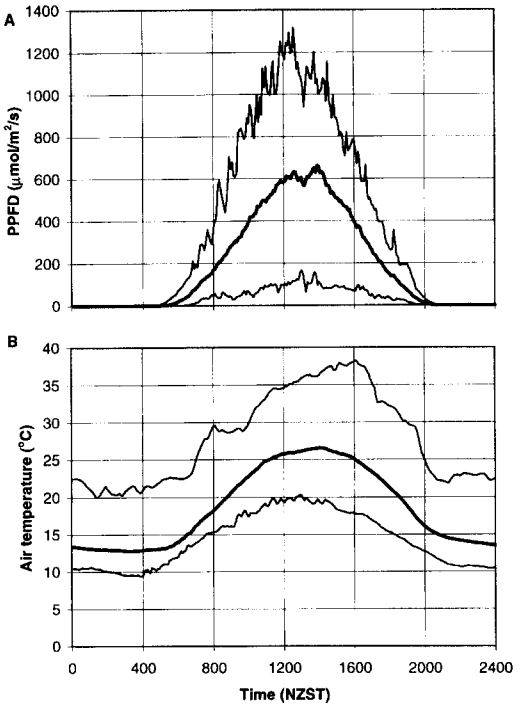

Fig. 1. Mean daily course of irradiance and air temperature for the period between *P. ginseng* emergence and completion of post-transfer fluorescence measurements (4 January to 24 February). A; Mean, maximum and minimum irradiance during the brightest hour of the day in the unshaded treatment. B; Mean, maximum and minimum air temperature for the same period.

on average, 13℃ at night, rising to an average of 26℃ at mid-day (Fig. 1b). Maximum air temperature varied between 20℃ at night to as much as 38℃ during the day. Minimum temperatures varied between 10 and 20℃.

Mean daily irradiance declined during the experiment from maximum values of around 300 μmol/m²/s on 4 January to values of about 200 by 24 February. Daily mean air temperature was consistently between 16 and 20℃ during the experiment although there were occasions when it was as much as 25℃.

4. Measurements

Chlorophyll fluorescence measurements were made on all plants for 3 days (13-16 Feb) before and 3 days (22-24 Feb) after transfer between

treatments on 21 February.

On 13 February, measurements of fluorescence parameters began on all plants at 1300 (NZST) and were repeated at intervals of 2~3 hours each day, ending at 2000 and beginning at 0600, until measurements ceased at 1400 on 16 February.

On the evening of 21 February plants were transferred to new shade treatments and fluorescence measurements started the following day at 0600 and continued at hourly intervals that day and at 2-hourly intervals the following two days until 2000 on 24 February.

Chlorophyll fluorescence measurements were made with an OS100 fluorometer (Opti Sciences Inc). Measurements at 0600 and 2000 were made in darkness and provided estimates of minimal fluorescence (Fo), maximal fluorescence (Fm) and the dark adapted fluorescence ratio (Fv/Fm). Measurements at other times were made under ambient irradiance and provided estimates of fluorescence intensity (F), maximal fluorescence (Fm') and $\Delta F/Fm'$ (van Kooten and Snel 1990, Genty *et al* 1989). Fluorescence measurements were made with the beam housing attached to a leaf clip to ensure all measurements were made at a standard distance from (12 mm) and angle to (45°) the leaf. Irradiance was measured with a quantum sensor attached to the leaf clip in the same plane as the measured leaf. Modulated beam irradiance was approximately 0.25 $\Delta mol/m^2/s$ and saturation pulse length was 0.7 seconds for all measurements.

5. Statistics

Curves were fitted to graphs of relative electron transport rate (Fig. 4) using the Michaelis-Menton equation :

$$R=\phi R_m I/(R_m+\phi I)$$

where R is relative electron transport rate, I is irradiance, ϕ and R_m are the parameters for initial slope (maximum quantum efficiency) and upper asymptote of the curve (maximum relative electron transport rate at saturating irradiance). This was done using a gamma generalized linear model with reciprocal link function,[25] fitting separate slopes and intercepts for each treatment from which ϕ and R_m were calculated.

Results

1. Before transfer

During fluorescence measurements, maximum irradiance in the unshaded treatment was 600~700 $\mu mol/m^2/s$ (Fig. 2a) and the daily temperature cycle on each day of measurement was very

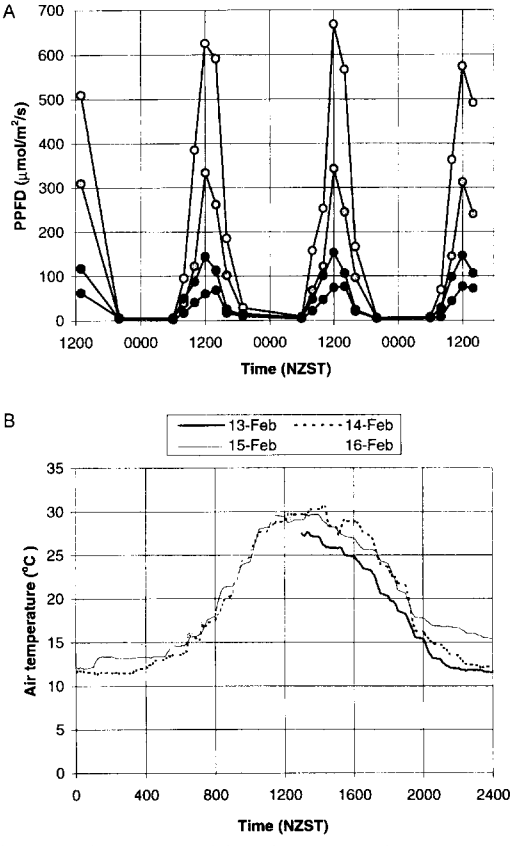

Fig. 2. Daily course of irradiance and air temperature during the measurement of *P. ginseng* chlorophyll fluorescence before plant transfer, for the period 1300 on 13 February to 1400 on 16 February. A; Mean irradiance in each treatment at the time of fluorescence measurement. In this and all subsequent figures, the irradiance treatment in which plants were raised is indicated by the density of shading in the symbols: treatment 1 (white circles) to treatment 4 (black circles). B; Air temperature during the course of each day of measurement of chlorophyll fluorescence.

similar (Fig. 2b).

(1) Fluorescence intensity (F)

Values of F were lower in treatment 1 (Table 1) than in other treatments (Fig. 3a) and showed a pattern of change during the day which was different from the other treatments. F in all treatments rose during the morning from night-time levels before falling later in the day. But the fall in treatment 1 was first apparent at the 1000 measurement, reaching lowest levels at mid-day before recovering to night-time levels during the afternoon. In treatments 3 and 4, F reached maximum values at mid-day, before returning to night-time levels. There is some evidence that the behaviour of treatment 2 was intermediate between that of treatment 1 and treatments 3 and 4, with F falling before treatments 3 and 4 on 15-16 February.

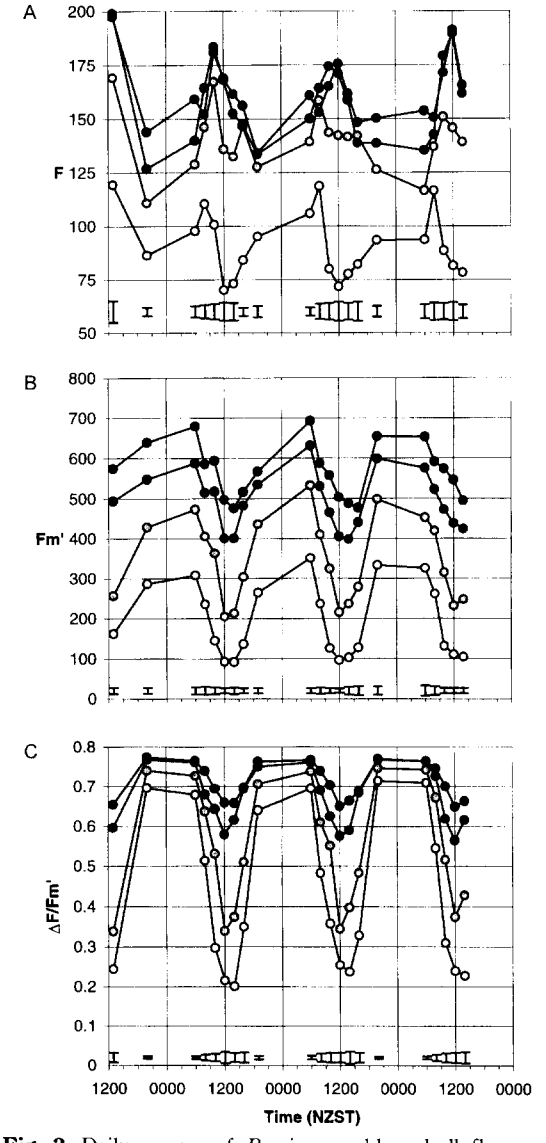

Fig. 3. Daily course of *P. ginseng* chlorophyll fluorescence parameters before plant transfer in each of the four irradiance treatments for the period 1300 on 13 February to 1400 on 16 February. A; Fluorescence intensity at ambient irradiance (F). B; Maximal fluorescence at ambient irradiance after a saturation pulse (Fm'). C; The relative efficiency of photosynthesis at ambient irradiance (ΔF/Fm').

(2) Maximal fluorescence (Fm')

Maximal fluorescence appeared to be driven principally by irradiance, falling to a mid-day minimum before rising to maximal values at the end of the day. In treatment 4, minimum Fm' values were recorded at 1400 or 1600 which was also when maximum irradiance occurred in this treatment (Fig. 2a). Fm' changed little between the last value in the day and first value the following morning. These values of Fm' are assumed to represent Fm, the value produced when the plant is in a dark adapted state. Low values of Fm' at the end of the day on 14 February were due to measurements being made an hour earlier (1900) than usual when irradiance was 29, 16, 11, 9 μmol/m²/s in treatments 1, 2, 3, 4 (i.e. not yet completely dark).

(3) μF/Fm'

There was a difference between treatments in dark adapted values of ΔF/Fm' measured at 0600 and 2000 (i.e. Fv/Fm) . Treatment 1 (0.699) and treatment 2 (0.739) were significantly different from each other (P<.001, SED 0.007) and from treatments 3 and 4 (0.764 and 0.768) which were not significantly different.

(4) Relative electron transport rate

Using the analysis of Schreiber[22] relative electron transport rate of each treatment was assessed at a range of light intensities. Plants showed characteristic saturation curves before transfer (Fig. 4). There were differences between the fitted curves for each light treatment. Treat-

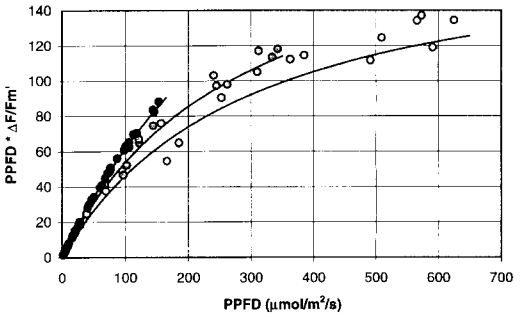

Fig. 4. Relative electron transport rate of *P. ginseng* plotted against irradiance for each of the four irradiance treatments before transfer. Parameters for fitted curves are shown in Table 2.

Table 2. The parameter values of the Michaelis-Menton equation used to fit curves to data in Fig. 4. for the four irradiance treatments. Standards errors of difference between means are for comparisons between the mean above the SED with the mean in the column to the left

Treatment	1	2	3	4
Φ	0.668	0.735 ***	0.762 ns	0.762 ns
SED		.016	.016	.016
R_m	201	217 ns	336 ***	344 ns
SED		9.2	21.6	45.3

*** $p<0.001$.

ment 1 had significantly lower values ($P<0.001$) of ϕ than the other treatments (Table 2). Treatments 1 and 2 had significantly ($P<0.001$) lower R_m values than treatments 3 and 4.

2. After transfer

Plants were transferred to new irradiance treatments after 2000 on 21 February. Maximum irradiance levels at the time of measurement during the following three days were 900~1000 μmol/m²/s in the unshaded treatment (Fig. 5a), and air temperatures were similar on all days of measurement, with mid-day maxima in the range 25~28℃ (Fig. 5b).

Plants shifted to a new light level rapidly adopted the daily pattern of change in F typical of plants which had been grown in that light level e. g. plants from treatments 3 and 4 shifted to treat-

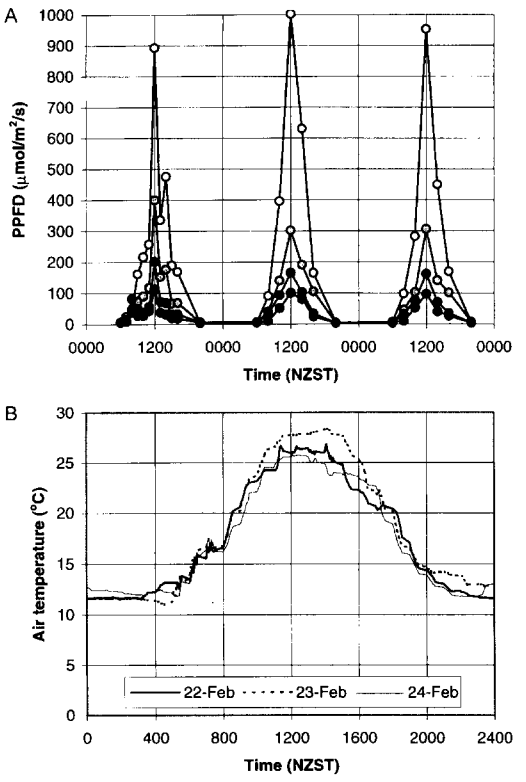

Fig. 5. Daily course of irradiance and air temperature during the measurement of chlorophyll fluorescence of *P. ginseng* after plant transfer, for the period 0600 on 22 February to 2000 on 24 February. A; Marimum PPFD in each treatment at the time of measurement of fluorescence. B; Air temperature during the course of each day of measurement of chlorophyll fluorescence.

ment 1, began to show a decline in F before midday on the first day , which became even more pronounced on the second day after transfer, with F values peaking in all treatments at 0800 before declining. Although shifting to a new light level altered the daily pattern of change in F, it did not greatly alter the absolute level of F. An exception to this occurred in plants shifted from treatment 1 into treatments 3 or 4. F in these plants rose relative to F in plants which remained in treatment 1 (Fig. 6).

Fm' in plants transferred between treatments converged on values typical of the irradiance treatment into which they were moved. This convergence was most apparent in plants transferred

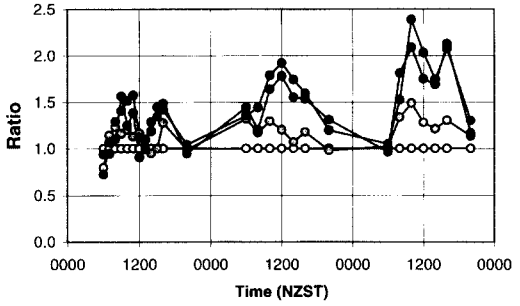

Fig. 6. Ratio of F in *P. ginseng* plants transferred from treatment 1 (1220) to each of the four light treatments (1220, 485, 235, 125) to the value of F in untransferred plants for the three days following transfer, demonstrating progressive increase in F in the more shaded treatments.

to treatment 1 although Fm' in these plants never quite fell to values as low as those in plants which remained in treatment 1. Fm' in plants transferred from treatment 1 to treatment 4 reached midday minima which were substantially greater than minimum values in plants which remained in treatment 1, although even after three days, midday Fm' values in treatment 1 plants transferred to treatment 4 were not as high as in plants which remained in treatment 4.

Fv/Fm values after transfer (Fig. 7) indicate the severe photoinhibition that developed in plants transferred from treatments 3 and 4 to treatment 1 (Fig. 7A) and treatment 2 (Fig. 7B). Plants transferred from treatment 2 to treatment 1 (Fig. 7A) showed no sign of photoinhibition. Plants transferred from treatments 1 and 2 to more shaded treatments, showed a rapid (1~3 days) recovery from mild photoinhibition (Figs. 7C and D). Plants transferred to treatment 3 from treatments 1 and 2 had higher Fv/Fm values than plants which remained in treatment 3 (Fig. 7C).

(1) Relative electron transport rate (RETR)

Plants showed characteristic saturation curves before transfer (Fig. 4 reproduced in Fig. 8). Plots of relative electron transport rate after transfer showed clearly the effects of photoinhibition in plants transferred to the highest irradiance level

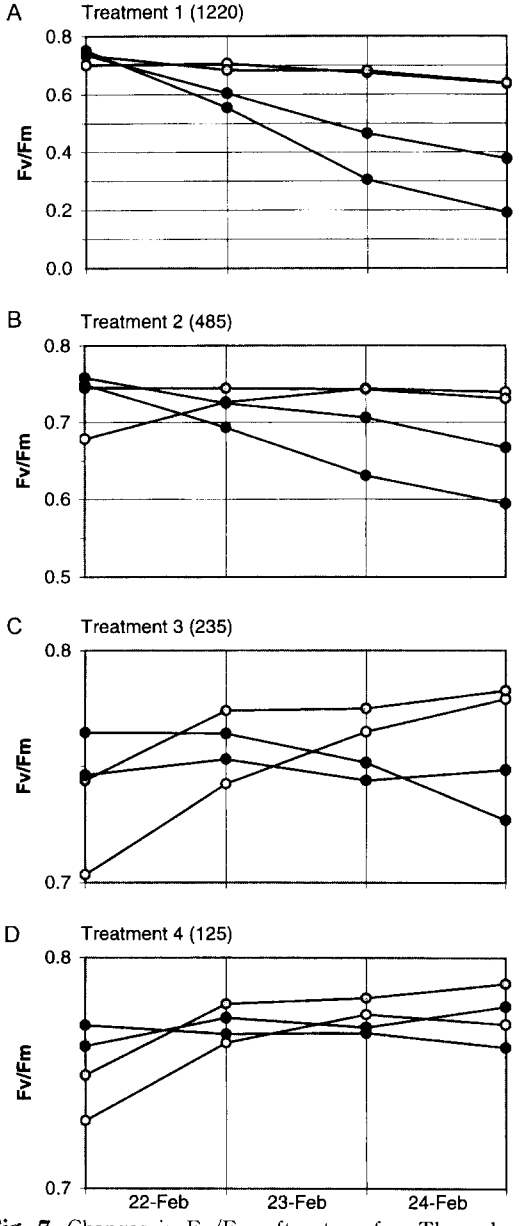

Fig. 7. Changes in Fv/Fm after transfer. The values for the dark period before 22 February were made at 0600 NZST and those for the dark period after 24 February were made at 2200 NZST. The values for the dark period between 22-23 February and between 23-24 February are means of (very similar) measurements taken at 2100 NZST and 0600 NZST.

(Fig. 8A). Plants transferred to treatment 1 from treatments 3 and 4 had RETRs which were far

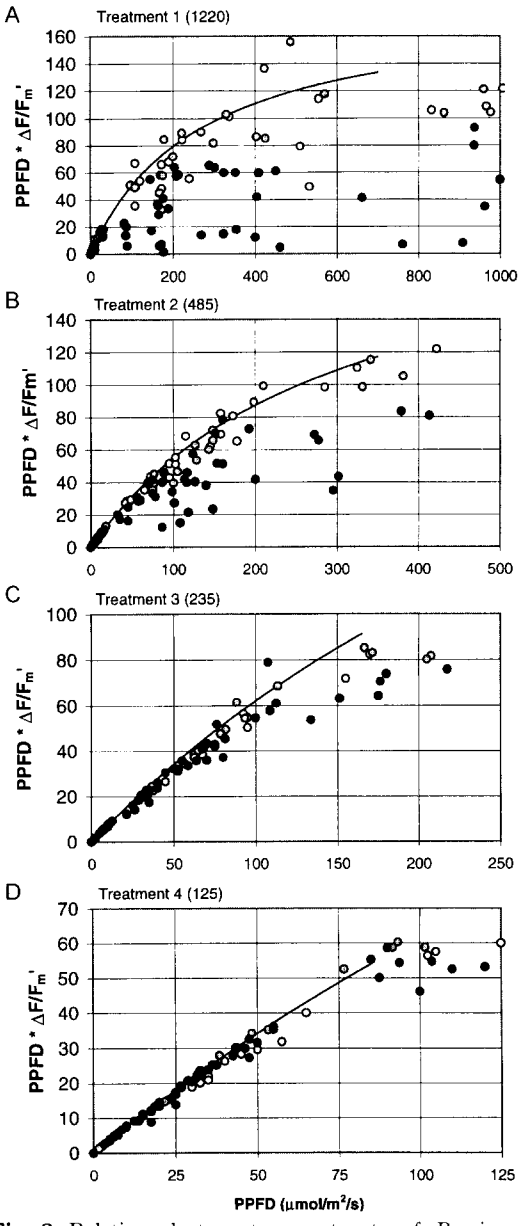

Fig. 8. Relative electron transport rate of *P. ginseng* plotted against irradiance after transfer from each of the four irradiance treatments. Curves fitted to pre-transfer RETRs in Fig. 4. are reproduced in this figure. A; Transfer into treatment 1 (1220). B; Transfer into treatment 2 (485). C; Transfer into treatment 3 (235). D; Transfer into treatment 4 (125).

lower than those recorded in plants from treatments 1 and 2.

Transfer to treatment 2 (Fig. 8B) was still enough to reduce RETR in plants from treatments 3 and 4. Plants in treatments 1 and 2 maintained rates only slightly lower than those recorded in treatment 2 plants before transfer.

Plants transferred to treatments 3 and 4 (Fig. 8C and 8D) had RETRs little different from plants which remained in those treatments.

Discussion

1. F and Fm'

The higher the treatment irradiance the lower the fluorescence intensity (F) (Fig. 3). This is probably an indication of reduction in chlorophyll antenna size in the chloroplasts of plants grown at high irradiance[16] although there may also be a component of fluorescence quenching in this signal, which could be expected to reduce fluorescence in proportion to the ambient irradiance.[26] But during the course of each day, fluorescence intensity tracks irradiance, rising to maximum values at midday and returning to minimal values during darkness.

Although shifting to a new light level altered the daily pattern of change in F, it did not greatly alter the absolute level of F. The stable differences in F between treatments after transfer imply that different irradiances during leaf development affect this fluorescence parameter and are not readily reversed. There were two exceptions to the general observation that F was little affected by transfer between different irradiance treatments. One was the progressive increase of F in treatment 1 plants moved to treatment 4 (Fig. 6). The other was the very rapid adoption by all plants moved to treatment 1 of the daily pattern of F characteristic of plants in the high light treatment i.e. a decline in F from early morning, rather than from midday as in other treatments. The different time course of these responses suggests that perhaps two different processes are involved. The early morning decline in F in plants in high light may be the result of energy dependent quenching.[26] The slow recovery of plants removed from high light ap-

pears to be more characteristic of a physical readaptation, such as a change in chlorophyll antenna size.

From measurement of Fm' after transfer it is apparent that the Fm' signal is determined to some extent by adaptation of the plant to irradiance during growth, although it can readjust rapidly after a change in light conditions. There are many factors determined by irradiance level which are likely to affect this signal, including chloroplast orientation in the cell,[27] chlorophyll concentration,[28] and protein phosphorylation.[29] Some of these are known to react very rapidly to changes in irradiance (chloroplast orientation, protein phosphorylation), others, such as chlorophyll concentration, take longer. It appears that at least in the treatment 1 plants some changes may be irreversible.

2. Dark adapted Fv/Fm

The similarity of Fv/Fm values at the end of one day and the beginning of the next provides confirmation that plants are effectively dark adapted for these measurements. Maximum dark adapted values of Fv/Fm of 0.75~0.80 recorded in this experiment are relatively low compared with those recorded for other plants i.e. 0.80~0.85,[30] but are comparable with the lowest values recorded by those authors, and similar to those recorded elsewhere for *P. ginseng*,[31]

Although photoinhibition occurred in treatment 2 (250/485) at what is a comparatively high irradiance level for ginseng (probably equivalent to about 20~25% of ambient levels), the degree of photoinhibition was mild. Mean dark adapted Fv/Fm ratios were 0.74 in treatment 2 and 0.76 in treatments 3 and 4, which appears to be close to the maximum levels obtainable in this species. Shade levels recommended for *P. ginseng* typically range from 5~20% of ambient levels.[5,6,9,10,11,18] At the upper end of this range (20% of ambient levels), it appears likely that only very mild photoinhibition would occur.

Even in the high irradiance treatment in this experiment Fv/Fm ratios were not greatly reduced; they were as much as 0.699. This treatment experienced exceptionally high irradiance for ginseng. The mean irradiance during the brightest hour of the day was 630 μmol/m²/s (Table 1) with maximum 'brightest hour' levels of irradiance between 4 January and 24 February, of 1220 μmol/m²/s. This is close to 60% of maximum ambient irradiance. Plants not only survived this irradiance but recorded the highest RETRs (Figs. 4 and 8).

3. Relative electron transport rates

Although some photoinhibition occurred in treatments 1 and 2, it is clear from plots of RETR (Figs. 4 and 8) that the higher irradiances in these treatments may allow higher electron transport rates than are possible in more shaded treatments. For example, using the curves in Fig. 4 it is possible to calculate that at any time during the day RETR will be greatest in the treatment with the highest irradiance. In fact, while irradiance in treatment 4 was 10% of that in treatment 1 throughout the day, RETR in treatment 4 varied from about 12% of treatment 1 in the morning and evening to about 35% of treatment 1 in the middle of the day (when irradiances were at their highest and relative quantum efficiencies in treatment 1 were at their lowest). To assess how different shade levels affect photosynthetic performance it is necessary therefore to measure performance at irradiances as high as those in the least shaded treatment. Plants grown at high irradiances will not demonstrate higher photosynthetic rates than ginseng grown in more shaded conditions unless irradiance levels during measurement are at least as high those in the brightest treatment.

Comparisons of photosynthesis rates of ginseng grown at different irradiances have usually shown higher rates in the most shaded treatments,[32] or at intermediate irradiances.[18] In the latter study, using shade of 5, 10, 15, 20 and 25%, the highest rates of photosynthesis were obtained at 10 and 15% with lowest rates at 25% (and, curiously, 5%). Measurement illuminance in both studies went no higher than 10 klux or about 8% of maximum ambient levels.[7]

But maximum measurement irradiances were much lower than the maximum irradiances plants were exposed to in these studies. Maximum midday illuminance is probably around 120 klux[7,11] and 10 klux represents only about 8% of midday levels. Plants grown at 15, 20 and 25%[18] experienced substantially higher levels than this, perhaps as much as 30 klux. If photosynthesis in these treatments had been measured at illuminances higher than 10 klux, they are likely to have had photosynthetic rates higher than the maximum levels indicated by measurement up to 10 klux.

The conclusion that ginseng grown in low light produces the highest photosynthetic rates could also have been drawn from Fig. 4 if measurement irradiance had been limited to 150~200 μmol/m²/s (i.e. 8~10% of maximum unshaded levels). At that irradiance, plants from the most shaded treatments (treatments 3 and 4) have the greatest RETRs. But measuring RETR in different treatments at the same time of day in this experiment would always have given higher RETR the higher the irradiance treatment.

Many factors influence the relationship between photosynthesis and root growth, but perhaps more than for most plants one may expect the relationship in ginseng to be relatively close. Since no more leaf is produced after plant emergence in spring, since seed is a relatively small proportion of plant mass, and since leaves on a ginseng plant are rarely self shading, the link between leaf photosynthetic rate and root growth is likely to be strong. For these reasons the high RETR in the high irradiance treatment here could be expected to be correlated with high root growth rates. There are, however, inevitably balancing acts performed by the plant which negate these apparent advantages of growth in high light. For example, in a large field trial we have measured root growth at an irradiance of 35%, which was only 2% less than at an irradiance of 8% (Parmenter and Littlejohn unpublished). Higher irradiances during leaf development also produce smaller leaves. In a previous experiment[31] in which seedling plants were grown under constant irradiance (12 hour day) ranging from 245 to 900 μmol/m²/s, leaf areas varied from a maximum of 1240 mm² at 345 μmol/m²/s to 840 mm² at 900 μmol/m²/s, a reduction of 30% with increased irradiance. This is comparable with reductions of 20~30% recorded in other studies.[5,9,10] Coupled with this is the observation, yet to be satisfactorily quantified, that leaf senescence occurs earlier the higher the growth irradiance[9,10] (Parmenter unpublished) reducing the period of effective photosynthesis. There are also risks associated with high irradiance. For example, it is apparent from Fig. 8 that during the period after transfer irradiance was relatively high. This produced some very low RETRs, even in treatment 1 plants which had not been transferred. For plants already experiencing some degree of photoinhibition this sort of increase in irradiance produced dangerous reductions in quantum efficiency. The effect was extreme in the case of plants transferred from low light into high light (Fig. 8a) and several of these plants died soon after the completion of the experiment. There is also evidence that increased levels of irradiance can increase incidence of Alternaria infection in the leaf,[10] possibly due to increased light stress in these plants.

Chlorophyll fluorescence techniques used in this study are both simple to execute and rapid, and have yielded useful information about the effect of irradiance level on photoinhibition of photosynthesis in ginseng. The results obtained concur with the higher estimates of maximum tolerable irradiance produced using gas exchange techniques. The fluorescence parameters also offer a useful tool for investigating the plant processes involved in adaptation of ginseng to different irradiance levels.

Acknowledgements

Thanks to Brian Swanney for climate measurements.

References

1. Fountain, M. S. : *Castanea* **51**(1), 42 (1986).

2. Bensky, D., Gamble, A. : *Chinese Herbal Medicine, Materia Medica*, Eastland Press, Seattle (1993).
3. Bissett, N. G. (ed.) *Herbal Drugs and Phytopharmaceuticals*, Medpharm, Stuttgart (1994).
4. Harding A. R. : *Ginseng and other medicinal plants*. Published by A.R. Harding. Re-issued with additions by Emporium Publications, Boston, Mass., 1972. (1908).
5. Kim, J. H. : *Seoul Uni. J.* (B), 95 (1964).
6. Kuribayashi, T., Ohashi, H. : *Syoyakugaku Zasshi* **25**(2), 110 (1971).
7. Park, H. : *Proceed. 3rd Int. Ginseng Symp.*, 151 (1980).
8. Jo, J. S., Won, J. Y. : *Korean J. Crop Sci.* **29**(1), 89 (1984).
9. Choi, S. Y., Cheon, S. K., Yang, D. J., Ahn, Y. J. : *Seoul Nat. Uni. Coll. Ag. Bull.* **7**(1), 241 (1982).
10. Cheon, S. K., Mok, S. K., Lee, S. S., Shin, D. Y. : *Korean J. of Ginseng Sci.* **15**(1), 21 (1991).
11. Lee, S. S., Cheon, S. K., Mok, S. K. : *Korean J. Crop Sci.* **32**(3), 256 (1987).
12. Yang, J., Liu, S., Du, E. : *Korean J Ginseng Sci.* **16**(1), 75 (1992).
13. Boardman, N. K. : *Ann. Rev. Plant Physiol.*, **28**, 355 (1977).
14. Anderson, J. M., Osmond, C. B. : *In* Kyle, D. J., Osmond, C. B., Arntzen, C. J. (eds) *Photoinhibition, Elsevier Science Publishers*, B. V., p. 1 (1987).
15. Bjorkman, O., Demmig, B. : *Planta* **170**, 489 (1987).
16. Chow, W. S., Quian, L., Goodchild, D. J., Anderson, J. M. : *Australian J. Plant Physiol.* **15**, 107 (1988).
17. Jo, J. S., Mok, S. K., Won, J. Y. : *Korean J Crop Sci.* **40**(4) 398 (1985).
18. Jo, J. S., Won, J. Y., Mok, S. K. : *Korean J Crop Sci.* **31**(4), 408 (1986).
19. Schreiber, U. : *Photosyn. Res.* **9**, 261 (1986).
20. Krause, G. H., Weis, E. : *Ann. Rev. Plant Physiol.* **42**, 313 (1991).
21. Van Kooten, O., Snel, J. F. H. : *Photosyn. Res.* **25**, 147 (1990).
22. Schreiber, U., Bilger, W., Neubauer, C. : *In* Schulze E-D., Caldwell, M. (eds.) *Ecophysiology of Photosynthesis*, Springer-Verlag, Berlin, p. 49 (1994).
23. Genty, B., Briantais, J.-M., Baker, N. R. : *Biochim. et Biophy. Acta* **990**, 87 (1989).
24. Harbinson, J., Genty, B., Baker, N. R. : *Photosyn. Res.* **25**, 213 (1990).
25. Nelder, J. A. : *Biometrics* **47**, 1605. (1991).
26. Demmig-Adams, B., Adams, W. W. III. : *Ann. Rev. Plant Physiol.* **43**, 599 (1992).
27. Haupt, W., Scheuerlein, R. : *Plant Cell Environ.* **13**, 595 (1990).
28. Adamson, H. Y., Chow, W. S., Anderson, J. M., Vesk, M., Sutherland, M. W. : *Physiol. Plant.* **82**, 353 (1991).
29. Allen, J. F. : *Trends in Biochemistry and Science* **17**, 12 (1992).
30. Bjorkman, O., Demmig-Adams, B. : *In* Schulze, E-D., Caldwell, M. (eds.) *Ecophysiology of Photosynthesis*, Springer Verlag, Berlin (1994).
31. Parmenter, G. A. : *Photoinhibition in ginseng*. New Zealand Inst. C. & F. Res., Research Report, Invermay (1994).
32. Wang, H., Fan, J., Yang, X., Liou, Q., Dai, H. : *In* Bailey, W.G., Whitehead, C., Proctor, J.T.A., Kyle, J.T. (eds.) *Proceedings of the International Ginseng Conference*, Simon Fraser University, Burnaby, p. 452 (1995).