Acclimation of Photosynthetic Activity of *Zantedeschia* ‘Best Gold’ in Response to Temperature and Photosynthetic Photon Flux

Keith A. Funnell¹ and Errol W. Hewett

Institute of Natural Resources, Massey University, Private Bag 11-222, Palmerston North, New Zealand

Julie A. Plummer

Plant Sciences, Faculty of Agriculture, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia

Ian J. Warrington

The Horticulture and Food Research Institute of New Zealand Ltd., Private Bag 11030, Palmerston North, New Zealand

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ABSTRACT. Photosynthetic activity of individual leaves of *Zantedeschia* Spreng. ‘Best Gold’ aff. *Z. pentlandii* (Wats.) Wittm. [syn. *Richardia pentlandii* Wats.] (‘Best Gold’), were quantified with leaf expansion and diurnally, under a range of temperature and photosynthetic photon flux (PPF) regimes. Predictive models incorporating PPF, day temperature, and percentage leaf area expansion accounted for 78% and 81% of variation in net photosynthetic rate (P_n) before, and postattainment of, 75% maximum leaf area, respectively. Minimal changes in P_n occurred during the photoperiod when environmental conditions were stable. Maximum P_n ($10.9 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ or $13.3 \mu\text{mol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$) occurred for plants grown under high PPF ($694 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and day temperature (28°C). Acclimation of P_n was less than complete, with any gain through a greater light-saturated photosynthetic rate (P_{max}) at high PPF also resulting in a reduction in quantum yield. Similarly, any gain in acclimation through increased quantum yield under low PPF occurred concurrently with reduced P_{max} . It was concluded that *Zantedeschia* ‘Best Gold’ is a shade tolerant selection, adapted to optimize photosynthetic rate under the climate of its natural habitat, by not having obligate adaptation to sun or shade habitats.

Production of *Zantedeschia* Spreng. sp. (calla) as a potted flowering plant or cut flower is now established world wide, including Africa, Australasia, both North and South America, India, and Europe (Funnell, 1993; Kuehny, 2000). *Zantedeschia* represented 20% (U.S. \$4.5 million) of New Zealand’s export earnings from all cut flowers in 2000 (New Zealand Department of Statistics, 2000). They are the second largest export earner of cut flowers for New Zealand after orchids (*Cymbidium* Swartz sp.) and, together with sales of *Zantedeschia* tuber products, continue to increase in importance as an economically important crop. Despite this importance, very little is known of the eco-physiology of the crop. As a result, understanding of environmental factors influencing productivity and development of appropriate production technologies is limited. Photosynthesis is an important process relevant to productivity and is strongly influenced by the environment (Bai and Kelly, 1999; van Iersel and Lindstrom, 1999), but it has not been examined in *Zantedeschia*.

The photosynthetic photon flux (PPF) at which net photosynthetic rate (P_n) becomes light saturated varies among species and after acclimation to growing environment, with P_n acclimating to the environment in which leaves have grown (Bjorkman, 1981). In shade tolerant plants, including those of the Araceae, P_n is greater in leaves grown under shade compared with full sun

(Schaffer and O’Hair, 1987). As a member of the Araceae this raises the possibility that *Zantedeschia* may also be shade tolerant. Obligate shade plants have an intrinsically low potential for PPF acclimation and, particularly, a low ability to increase their capacity for effective utilization of high PPF (Bjorkman, 1981). They are, however, more efficient at using low PPF and hence have greater apparent quantum yield, than plants adapted to full sun habitats (Bjorkman and Demmig, 1987).

Both short-term and long-term preconditioning effects of temperature on P_n of leaves have been noted in many species (Bennett et al., 1982; Caulfield and Bunce, 1988; van Iersel and Lindstrom, 1999). However, while minor differences exist among species in the relationship between P_n and day and night temperatures, temperature at time of measurement has been shown to have the greatest single effect on P_n (Bennett et al., 1982). Under constant environment, P_n for some species remains constant during the daily period of light (Mortensen and Moe, 1983; Pallas, 1973). In contrast, a constant environment can result in a diurnal decline in P_n for some plant species (Pallas, 1973; Warrington et al., 1977). P_n also increases as the individual leaf develops and expands. Typically, leaves must reach at least 70% of their full expansion before maximum P_n values can be reached (Giaquinta, 1978; Sato et al., 1978).

The cultivar of *Zantedeschia* used in this study, ‘Best Gold’, is most likely derived from *Zantedeschia pentlandii* which occurs in open grassland or forest margins of the eastern mountainous regions of southern Africa (Letty, 1973). The objectives of this research were, therefore, to 1) determine the photosynthetic characteristics of ‘Best Gold’, 2) determine how these change with the diurnal lighting period, leaf area expansion, temperature and PPF, 3) determine any relationship between these photosyn-

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¹Corresponding author; k.funnell@massey.ac.nz.

thetic characteristics and the plant's original habitat, and 4) provide commercial recommendations for optimizing photosynthetic rate.

Materials and Methods

Experiments reported here were part of a larger experiment as described by Funnell et al. (1998) where plants of *Zantedeschia* 'Best Gold' were grown at one of six day/night (daily mean) temperatures: 16/10 (13), 22/10 (16), 22/16 (19), 28/16 (22), 28/22 (25), and 28/28 (28) °C ± 0.5 °C. In all treatments, day/night vapor pressure deficit was 1.0/0.4 kPa. Photoperiod and individual day and night temperatures were 12 h duration. Day/night and night/day temperature and vapor pressure changeovers were each of 2 h duration, with lights switching off and on at the midpoint of each respective changeover.

Plants were grown in individual 1.2-L pots containing a 5 peat : 3 pumice (by volume) growing medium containing 3 kg·m⁻³ dolomite lime. Each pot was supplied with enough nutrient solution (5 × 100 mL applications daily of half-strength Hoagland's A modified with chelated iron, type ONC; Brooking, 1976) to ensure drainage at each application and prevent moisture stress.

The treatments were imposed using controlled environment facilities in the National Climate Laboratory at The Horticulture and Food Research Institute of New Zealand Ltd, at Palmerston North. Photoperiod was provided by four 1000-W high-pressure multivapor-lamps (Sylvania Metalarc) and four 1000-W Philips quartz halogen lamps in the ceiling of the plant growth room, separated by a plate glass and a water thermal barrier. The *PPF* at pot height, measured using a light meter (LI-185; LI-COR Inc., Lincoln, Nebr.) with a quantum sensor (LI 190S; LI-COR) attached, was 694 ± 20 μmol·m⁻²·s⁻¹ (high *PPF*). Within the same controlled environment room a *PPF* of 348 ± 10 μmol·m⁻²·s⁻¹ (low *PPF*) was achieved for half the plants, by covering four of the eight trolleys per room with a spectrally neutral woven polypropylene shade cloth of nominal 50% density. At weekly intervals, trolleys were relocated within each room and rotated 180° about their own axis, to minimize any influence of environmental gradients within the growth rooms.

Plants were placed in the treatments when sprouts on tubers were emerging but before any leaf emergence had occurred. Successive leaves were tagged as they appeared to allow leaves of similar morphological development and ontogeny to be compared. For all experiments listed, plants were maintained in each controlled environment treatment until the monitored leaves, typically the second leaf on each plant, had become fully expanded. The duration of this period ranged between 20 and 40 d, for the warmest and coldest mean temperature treatments, respectively.

For all experiments, P_n was measured using an open system infrared gas analyzer (LCA-2; ADC Ltd., Hoddesdon, United Kingdom) with air obtained from outside the building for the inlet supply (350 ± 10 μmol CO₂/mol). All measurements were carried out at the relevant treatment day temperature and *PPF* and, unless stated otherwise, between 6 and 8 h following the beginning of the daily lighting period. Air supply was dried to a constant 20% relative humidity and pumped into the assimilation cuvette (Parkinson leaf chamber, ADC Ltd.) at a rate of 0.625 L·min⁻¹, reducing to 0.356 L·min⁻¹ when negative or minimal P_n values occurred. Incident *PPF* at the leaf surface was measured using the sensor on the LCA-2 apparatus. At each measurement, the assimilation cuvette was placed in the middle of a leaf and covered 6.25 cm².

P_n AS A FUNCTION OF LEAF EXPANSION. Values of P_n and leaf area were monitored during expansion of the first leaf produced from plants grown under three treatments. Treatments consisted of a day/night regime of 22/16 °C under both high and low *PPF*, and 28/22 °C under the high *PPF* regime. Leaf area expansion was determined nondestructively by tracing the outline of selected leaves on paper after each determination of P_n , and measuring the traced area using a LI-COR model 3100 leaf area meter (LI-COR Inc.). Within each temperature × light treatment, plants were arranged in a completely randomized design. P_n was measured on each of a randomly selected sample of six leaves (i.e., one leaf per plant) at 2-d intervals, beginning when a leaf lamina was free from enveloping protective sheath leaves, and continuing until further increases in leaf expansion were minimal.

Partial correlations between P_n , day temperature, night temperature, *PPF*, and proportion (percentage) of maximum leaf area, were examined for formulation of predictive models. Models were determined by regression analysis using the stepwise selection method of the REG procedure of SAS (SAS Inst. Inc., 1988). A minimum significance level of $P < 0.15$ was used to determine which of the above factors were included in the model.

P_n AS A FUNCTION OF DURATION FROM COMMENCEMENT OF DAILY LIGHTING. Values of P_n of recently mature leaves were obtained during a daily period of lighting, from plants grown under three treatments. Recently mature was defined as the stage when a leaf had attained a minimum of ≈75% of expected maximum expansion. Treatments consisted of 12 h each of days/nights of 16/10, 22/16, and 28/22 °C under the high *PPF* regime. P_n was measured on each of a randomly selected sample of six leaves (one leaf per plant), initially at 30 min intervals commencing 15 min before the commencement of lighting, and subsequently at more infrequent intervals through the entire 12 h period of lighting. Before the commencement of lighting, incident *PPF* at the leaf surface was 0 μmol·m⁻²·s⁻¹. All subsequent measurements were conducted at an incident *PPF* of 694 ± 20 μmol·m⁻²·s⁻¹.

In each treatment environment, leaves were monitored on plants arranged in a completely randomized design. To avoid potential inherent problems arising from repeated measures, a different sample of six leaves (one per plant) was used from each treatment population at each time of measurement. Rates of change in P_n with time were determined by regression analysis using the REG procedures of SAS (SAS Inst., Inc., 1988).

P_n AS A FUNCTION OF *PPF*. Using recently mature leaves, response curves for P_n as a function of *PPF* were determined for plants grown in different environments. Treatments consisted of 12 h each of days/nights of 16/10, 22/10, 22/16, 28/16, 28/22, and 28/28 °C, under both high and low *PPF*. Data were recorded from a random sample of six leaves (one per plant) per treatment. The *PPF* was adjusted in increments using layers of spectrally neutral mesh screens to reduce *PPF*, and by raising the plants closer to the light source to increase *PPF*. In each case, one of the *PPF* levels included that which the plants were originally grown under (i.e., either 348 or 694 μmol·m⁻²·s⁻¹), resulting in a P_n known as P_{grow} . Respiration was measured in the dark using black cloth to eliminate light from the cuvette, with reduced air flow rates as discussed previously. Recorded values of P_n and *PPF* were fitted to a hyperbolic tangent function (Eq. [1]; Jassby and Platt, 1976). Specifically, if P_n is the net photosynthetic rate, P_{max} is the photosynthetic rate at saturating *PPF*, $\tanh$ the hyperbolic tangent, α the initial slope (i.e., apparent quantum yield), *PPF* the photosynthetic photon flux, and R the respiration rate, then

$$P_n = P_{max} \times \tanh [(\alpha/P_{max}) \times PPF] - R \quad [1]$$

Specific leaf area (SLA, Eq. [2]) was calculated from destructive harvests carried out subsequent to recording photosynthetic rates of the same leaf, as described by Funnell, et al. (1998). Specifically, if SLA is the specific leaf area, LA is the leaf area measured using a leaf area meter (LI-3100; LI-COR), and LW the dry weight of the leaf recorded after being vacuum dried to constant mass at 0.3 kPa and 40 °C, then

$$SLA = LA/LW \quad [2]$$

SLA data were subjected to analysis of variance (ANOVA) using the general linear models procedure of SAS (SAS Inst., Inc., 1988). Photosynthetic rate data, both on a leaf area and leaf dry weight basis, were fitted by nonlinear regression analysis using the NLIN procedure of SAS (SAS Inst., Inc., 1988). All six replicates from a given treatment were mathematically fitted individually. Derived parameters from the curve fitting procedure were subjected to ANOVA, as well as linear and quadratic contrasts, using the general linear models procedure of SAS (SAS Inst., Inc., 1988). With only three day temperatures treatments, significance of either linear and quadratic contrasts for trend analysis was considered preferable to using regression analysis.

In addition to measuring rates of dark respiration as part of determining the *PPF* response curves, dark respiration was also measured commencing 2 h after termination of the lighting period. Rates of change in respiration rate as a function of actual leaf temperature, were determined by regression analysis using the REG procedure of SAS (SAS Inst., Inc., 1988). In addition, rates were subjected to ANOVA using the general linear models procedure of SAS (SAS Inst., Inc., 1988).

Results

P_n AS A FUNCTION OF LEAF EXPANSION. Values of P_n increased with expansion of the leaf in all treatments (Fig. 1). Maximum P_n did not occur until leaves had reached $\approx 90\%$ of their full expansion regardless of temperature and *PPF*. At the stage of expansion subsequently defined as recently mature (i.e., 75% expansion), leaves had achieved 81% of the maximum P_n .

Across all treatments, P_n was positively correlated with the following variables: day temperature (DTEMP), night temperature (NTEMP), *PPF*, and percentage of maximum leaf area (PLA). The relative contribution made by each factor in determining P_n over the entire period of expansion could be assessed by the magnitude of the standardized multiple regression coefficients (beta coefficients), i.e., $PLA = 0.56$, $PPF = 0.37$, and $DTEMP = 0.34$. Addition of NTEMP did not meet the significance level of $P < 0.15$ required for entry into the model. A single predictive model including the above parameters was developed (Eq. [3], $P \leq 0.001$) which accounted for 78% of the variation in P_n throughout the entire period of expansion.

$$P_n = 0.122 \times PLA + 0.011 \times PPF + 0.53 \times DTEMP - 18 \quad [3]$$

Over the entire period of leaf expansion, a strong partial correlation existed between P_n and PLA ($r = 0.76$). However, once leaves reached 75% maximum leaf area this partial correlation was reduced to $r = 0.46$. During this later stage of leaf expansion the partial correlation between P_n and *PPF* was $r = 0.72$ and, P_n and DTEMP was $r = 0.66$. Beta coefficients for the prediction of P_n at this later stage of expansion were $PLA = 0.22$, $PPF = 0.55$, and $DTEMP = 0.45$. Again, addition of NTEMP did not meet the significance level of $P < 0.15$ for entry into the model. A single predictive model for leaves that were $> 75\%$ of their potential

expansion (Eq. [4], $P \leq 0.001$) accounted for 81% of the variation in P_n .

$$P_n = 0.06 \times PLA + 0.013 \times PPF + 0.55 \times DTEMP - 14 \quad [4]$$

P_n AS A FUNCTION OF DURATION FROM COMMENCEMENT OF DAILY LIGHTING. P_n increased rapidly during the first hour of lighting (Fig. 2). Subsequent variation in P_n was minor for the remaining period of stable temperature, vapor pressure deficit, and *PPF* conditions. Over this period of stable environment, values of P_n averaged 10.5 ± 0.7 , 9.1 ± 0.3 , and $5.3 \pm 0.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at days of 28, 22, and 16 °C, respectively. Across the duration of stable environment, P_n declined linearly ($P \leq 0.05$) and $\approx 10\%$ at the two higher temperatures from 1 h to 11 h of photoperiod. However the magnitude of this decline was less than the estimated accuracy of the equipment, i.e., $0.7 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

P_n AS A FUNCTION OF *PPF*. Under all treatments, the increasing value of P_n with increasing *PPF* was described by a family of Tanh functions on a basis of both leaf area (Fig. 3A and B) and leaf

Fig. 1. Net photosynthetic rate (P_n) as a function of individual leaf area expansion, at selected day/night temperature and *PPF* regimes. Measurement conditions were same as treatment conditions. Each symbol represents the mean of six observations and vertical bars $\pm$ SE. $\downarrow$ represents 75% maximum leaf area.

Fig. 2. Net photosynthetic rate (P_n) as a function of duration from commencement of daily lighting, at selected day/night temperature regimes and high *PPF*. Each symbol represents the mean of six observations and vertical bars $\pm$ SE. Broken lines indicate limits of diurnal temperature changeovers.

dry weight (Fig. 3C and D). As an indication of the goodness of fit, mean square error values for fitting the Tanh function for individual leaf replicates ranged between 0.1 and 0.49. Data from plants grown at a common *PPF* and day temperature were pooled, as differences in magnitude of the fitted parameters (as per Eq. [1]) between treatments with the same day temperature were not significant ($P \leq 0.05$).

Differences in P_n due to temperature were substantially greater for leaves grown under high *PPF* than for those grown under the low *PPF* conditions independent of measurement *PPF* (Fig. 3). Further, rates of P_n were consistently higher for leaves grown under a particular temperature regime under the higher *PPF* growth conditions. Differences in P_n among temperature treatments were always greater when P_n was expressed on a unit leaf area basis than on a unit leaf dry weight basis (Fig. 3).

At all temperatures, light-saturated photosynthetic rate ($P_{\max}$) was greater in leaves from plants grown under high *PPF* than those at low *PPF* when expressed on either a unit leaf area or leaf dry weight basis ($P \leq 0.001$, Fig. 4A and B). For plants from the

high *PPF* regime, $P_{\max}$ per unit leaf area increased following a linear trend with increasing temperature, resulting in a 40% increase across the temperature range examined ($P \leq 0.001$). In contrast, for plants from the low *PPF* regime, differences among temperatures in $P_{\max}$ per unit leaf area were minimal, indicating a relatively flat response to temperature. When expressed on a leaf dry weight basis, $P_{\max}$ increased following a linear trend with increasing temperature under both *PPF* regimes ($P \leq 0.001$, Fig. 4B). This response of $P_{\max}$ with temperature resulted in a 53% and 31% increase across the temperature range, under high and low *PPF* regimes, respectively.

When grown under low *PPF*, light saturation of photosynthesis (i.e., 90% to 100% $P_{\max}$) was estimated from the modelled data to occur between 600 and 700 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Table 1). For plants grown under high *PPF*, light saturation was achieved between an estimated *PPF* of 1100 and 1300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

When expressed on the basis of both unit leaf area and unit leaf dry weight, apparent quantum yield (α) was greater from plants grown under low *PPF* than under high *PPF* ($P \leq 0.001$, Fig. 4C and D). For plants from the high *PPF* regime, the reduced value of α per unit leaf area at 16 °C resulted in a quadratic trend between apparent quantum yield and increasing day temperature ($P \leq 0.01$). However, on a unit leaf area basis, for plants grown under the low *PPF* regime, α declined following a linear trend with increasing day temperature ($P \leq 0.05$). On a unit leaf dry weight basis, under the high *PPF* regime, the quadratic trend between α and temperature was very pronounced, while under the low *PPF* regime, α was independent of temperature (Fig. 4D).

On a leaf area basis, rates of dark respiration measured during the day, were marginally greater for leaves grown under high than low *PPF* ($P \leq 0.05$, Table 1). Both the measured dark respiration rates and those determined from fitting Eq. [1] appeared to be lower at days of 28 °C compared with either 22 or 16 °C. This reduction in respiration rate ($0.5 \pm 0.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was only marginally greater than the accuracy of measurement of the equipment ($\pm 0.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) even with a reduced rate of air flow.

Dark respiration measurements did not vary between day and night. Leaf temperature under the measurement conditions varied between 13 and 28 °C, but differences in actual rates of dark respiration between temperatures were not detected ($P = 0.10$).

Specific leaf area (SLA) increased with increasing day temperature and under the lower

Fig. 3. (A and B) Net photosynthetic rate (P_n) per unit leaf area, and (C and D) per unit leaf dry weight, as a function of photosynthetic photon flux (*PPF*), for plants of *Zantedeschia* 'Best Gold' grown at days of 16, 22, and 28 °C, under (A and C) high or (B and D) low *PPF* regimes. ↓ represents *PPF* at which plants were grown before recording P_n . Each symbol represents the mean of either six or 18 observations; function = Eq. [1]. Mean square error values for fitting the function for leaves from each of the environments averaged 0.25.

PPF ($P \leq 0.01$, Table 2). Differences in SLA were most evident under the low PPF regime, resulting in an approximate increase of 26% between 16 and 28 °C. In contrast, under the high PPF regime, SLA increased by only $\approx 6\%$.

Discussion

Photosynthetic rates of leaves of *Zantedeschia* 'Best Gold' were similar to those reported for other members of the Araceae (Schaffer and O'Hair, 1987; Valenzuela et al., 1991). However, in comparison with other plant species (non-Araceae) these values of P_n were in the low to intermediate range (Bjorkman, 1981; Connor and Sadras, 1992).

The synchrony of changes in P_n with increases in leaf area expansion (Fig. 1), with an apparent maximum at 90% of full expansion, was within the range reported for other crop species where maximum P_n occurred anywhere between 70% to 100% of full expansion (Giaquinta, 1978; Ho et al., 1984; Sato et al., 1978; Schaffer and O'Hair, 1987).

As expected, the proportion of full expansion attained was a

primary determinant of P_n during initial leaf expansion. However, at and beyond the 75% expansion stage, inclusion of proportion of full expansion in the predictive model only accounted for small (5%) variation in P_n not already accounted for by the combined effects of day temperature and PPF. Since this stage of expansion was used for subsequent investigations, it was assumed that P_n values were primarily a function of growing environment. Furthermore, changes in P_n during the daily period of lighting were small enough to be within the margin for measurement error ($0.7 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). It is therefore concluded that in contrast to crops such as soybean [*Glycine max* (L.) Merrill] and cotton (*Gossypium hirsutum* L.) (Pallas, 1973; Warrington et al., 1977), there was minimal decline in P_n in leaves of *Zantedeschia* 'Best Gold' with photoperiod during this early stage of crop establishment.

Rates of P_n responded to the day temperature and PPF conditions exposed to during growth (Fig. 3). In all treatments, this acclimation to temperature and PPF resulted in P_n values measured at the PPF under which they were grown originally (i.e., P_{grow}) reaching an average 85% of the light-saturated rate (i.e., P_{max}). While being similar to other shade-tolerant species (Niinemets and Tenhunen, 1997), the ability of leaves of *Zantedeschia* 'Best Gold' to respond to PPF is substantial compared with species adapted to sun habitats. Doubling PPF from 348 or 694 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during growth of plants at 28 °C, resulted in a 70% increase in light-saturated P_n per unit leaf area (Fig. 4A). In contrast, doubling PPF during growth of two species adapted to sun habitats, i.e. Italian ryegrass (*Lolium multiflorum* L.) and goldenrod (*Solidago virgaurea* L.), resulted in increases in light-saturated $P_n \leq 25\%$ (Prioul and Bourdu, 1973).

Irrespective of temperature, when grown under low PPF, light saturation of photosynthesis was reached between 600 and 700 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. In contrast, for plants grown under high PPF, light saturation was achieved between an estimated 1100 and 1300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Light saturation at PPF regimes close to that experienced during growth is common for many plant species, but not all species respond in the same manner (Pallas and Samish, 1974). In contrast to the results in the present study for *Zantedeschia*, shade grown plants of other members of the Araceae attained higher P_n values than those grown under full sunlight (Schaffer and O'Hair, 1987). Given that PPF on a clear summer day frequently exceeds 1200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, it would appear that *Zantedeschia* 'Best Gold' is able to optimize photosynthetic activity at an early stage of growth when planted without shade.

Increased apparent quantum yield (α) from plants grown under low PPF (Fig. 4C and D)

Fig. 4. (A and B) maximum photosynthetic rate at saturating PPF (P_{max}), and (C and D) apparent quantum yield (α), as a function of day temperature, for plants of *Zantedeschia* 'Best Gold' grown under high and low PPF. (A and C) are expressed in units of leaf area, and (B and D) in units of leaf dry weight. Each symbol represents the fitted value from the relevant parameter in Eq. [1] and vertical bars = $\pm$ SE.

Table 1. Estimated gas exchange parameters for leaves of *Zantedeschia* 'Best Gold' grown at differing day temperatures and under high or low *PPF* regimes. *PPF* parameters were estimates derived from fitted lines presented in Fig. 3 and respiration rates were those determined experimentally. Values are presented on the basis of both leaf area and leaf dry weight (DW).

Day temp (°C)	<i>PPF</i>	Dark respiration rate ^z		<i>PPF</i> at compensation point ^y		<i>PPF</i> saturation range ^x	
		Leaf area ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Leaf DW ($\mu\text{g}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$)	Leaf area ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Leaf DW ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Leaf area ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Leaf DW ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)
16	High	-0.9	-1	56	53	1200-1400	1200-1300
	Low	-0.7	-1	24	26	600-700	600-700
22	High	-0.9	-1.1	41	35	1100-1400	1200-1300
	Low	-0.6	-0.9	23	23	600-700	600-700
28	High	-0.4	-0.5	19	19	1200-1300	900-1200
	Low	-0.3	-0.5	13	13	600-800	600-800

^zGas exchange at a *PPF* of 0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

^y*PPF* at which gas exchange rate was 0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

^x*PPF* at which P_n ranged between 90% and 100% of P_{max} .

allows for a high rate of CO_2 fixation at low *PPF*, typical of plant species able to acclimate to shade habitats. However the actual values obtained (ranging between 0.016 and 0.029 mol CO_2 /mol *PPF*) were low compared with those for other plant species acclimated to shade habitats (Fahl et al., 1994). For plants grown under low *PPF*, the decline in per unit leaf area with increased temperature (Fig. 4C) was similar to that reported for other C_3 plant species (Ehleringer and Pearcy, 1983). Temperature optima for photosynthetic rates reported herein are similar to those reported for other members of the Araceae (Sato et al., 1978). Under high *PPF*, the temperature at which photosynthesis per unit leaf area was maximum was 28 °C (Fig. 4A). However, for plants grown under low *PPF*, the inability to detect differences in photosynthetic rate per unit leaf area with increasing temperature was a result of increased specific leaf area (Table 2). When expressed on a leaf dry weight basis, the temperature at which photosynthesis was greatest was 28 °C regardless of the *PPF* under which the plant was grown (Fig. 4B).

Rates of dark respiration were within the bounds reported for other species (Zelitch, 1971). In addition, the greater rate of dark respiration under high *PPF* compared with low *PPF* was similar to that reported for other species (Bjorkman 1981). However, the expected increase in respiration rate with increased day temperature, as reported for other plant species (Jiao et al., 1991; Miura and Osada, 1981; Sato et al., 1978) was not detected. With roses (*Rosa* L.), lowering the night temperature from 27 to 17 °C increased daily carbon gain due to a reduction in dark respiration (Jiao et al., 1991). If in the current experiment respiration rates of

leaves are representative of the entire plant, growers of *Zantedeschia* 'Best Gold' are less likely to achieve any significant improvement in net carbon gain by reducing night temperatures.

The ability of *Zantedeschia* 'Best Gold' to alter P_n in response to both *PPF* and temperature under which it was cultivated has its parallel in the natural habitat of the suggested parent species, *Zantedeschia pentlandii*, which occurs in open grassland and forest margins of the eastern mountainous regions of Africa (Letty, 1973). These habitats would have either full sun or partial shade, and would result in an incident *PPF* as high as 1200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (i.e., close to that estimated as achieving light saturation). As daily maximum/minimum air temperature during the growing season averages 25.4/14.3 °C (Union of South Africa Department of Transport, 1954), it is apparent this *Zantedeschia* selection is well adapted to optimize photosynthetic activity under the temperature regimes of its natural habitat.

In summary, P_n of recently mature leaves of *Zantedeschia* 'Best Gold' have the ability to acclimate to different *PPF* and temperature conditions during growth. However, acclimation to any one environment is less than complete as any gain from the ability to acclimate to high *PPF*, through greater P_{max} , must be contrasted with a simultaneous reduction in quantum yield. Also, any gain from the ability to acclimate to low *PPF*, through increased quantum yield, must be contrasted with a simultaneous reduction in P_{max} . From this it is concluded that *Zantedeschia* 'Best Gold' is a shade tolerant selection, having neither an obligate adaptation to sun or shade habitats. Therefore, during the early stages of crop growth examined herein, cultivating this crop in full sun and days of 28 °C is likely to result in achieving the maximum photosynthetic rate.

Table 2. Specific leaf area (SLA) as affected by day temperature and *PPF* regime during determination of *PPF* response curves.

Day temp (°C)	SLA ($\text{m}^2\cdot\text{kg}^{-1}$)	
	High <i>PPF</i>	Low <i>PPF</i>
16	26.4 ^z	29.6
22	25.5	35.0
28	27.9	37.2
LSD _{0.05}	1.3	
Significance of F		
Temperature (T)	**	
<i>PPF</i>	**	
T × <i>PPF</i>	**	

^zMean separation between any two values by lsd, $P = 0.05$ ($n = 6$).

**Significant at $P \leq 0.01$.

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