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

**Abstract.** Photosynthetic activity of individual leaves of *Zantedeschia* Spreng. ‘Best Gold’ aff. *Z. pentlandii* (Watts.) W. Schaffer & O’Hair, 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 (Pn) before, and postattainment of, 75% maximum leaf area, respectively. Minimal changes in Pn occurred during the photoperiod when environmental conditions were stable. Maximum Pn (10.9 µmol·m–2·s–1 or 13.3 µmol·g–1·s–1) occurred for plants grown under high PPF (694 µmol·m–2·s–1) and day temperature (28 °C). Acclimation of Pn was less than complete, with any gain through a greater light-saturated photosynthetic rate (Pmax) 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 Pmax. 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 increase, 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 (Pn) becomes light saturated varies among species and after acclimation to growing environment, with Pn acclimating to the environment in which leaves have grown (Bjorkman, 1981). In shade tolerant plants, including those of the Araceae, Pn 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 Pn 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 Pn and day and night temperatures, temperature at time of measurement has been shown to have the greatest single effect on Pn (Bennett et al., 1982). Under constant environment, Pn 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 Pn for some plant species (Pallas, 1973; Warrington et al., 1977). Pn also increases as the individual leaf develops and expands. Typically, leaves must reach at least 70% of their full expansion before maximum Pn 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-
thetistic characteristics and the plant’s original habitat, and 4) provide commercial recommendations for optimizing photosynthetic rate.

Materials and Methods

Experiments reported here were in 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 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 cm thick peat moss 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 Inc.), 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, Pn 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⁻¹). 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 night/day temperature and PPF changeovers were each 2 h duration, with lights switching off and on at the midpoint of each respective changeover.

Pn as a function of leaf expansion. Values of Pn 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 Pn, 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. Pn 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 Pn, 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.

Pn as a function of duration from commencement of daily lighting. Values of Pn 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. Pn 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 Pn with time were determined by regression analysis using the REG procedures of SAS (SAS Inst., Inc, 1988).

Pn as a function of PPF. Using recently mature leaves, response curves for Pn 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, 22/16, 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 Pn known as Pgrow. 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 Pn and PPF were fitted to a hyperbolic tangent function (Eq. [1]; Jassby and Platt, 1976).

\[ P_n = P_{\text{max}} \times \tanh \left( \frac{\alpha}{P_{\text{max}}} \times \text{PPF} \right) - R \]

Specifically, if Pn is the net photosynthetic rate, Pmax is the photosynthetic rate at saturating PPF, Tanh the hyperbolic tangent, \( \alpha \) the initial slope (i.e., apparent quantum yield), PPF the photosynthetic photon flux, and R the respiration rate, then

J. Amer. Soc. Hort. Sci. 127(2):290–296. 2002.
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

\[ SLA = \frac{LA}{LW} \]  

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**

**Pn as a function of leaf expansion.** Values of Pn increased with expansion of the leaf in all treatments (Fig. 1). Maximum Pn did not occur until leaves had reached >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 Pn.

Across all treatments, Pn 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 Pn 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 Pn throughout the entire period of expansion.

\[ P_n = 0.122 \times \text{PLA} + 0.011 \times \text{PPF} + 0.53 \times \text{DTEMP} - 18 \]  

Over the entire period of leaf expansion, a strong partial correlation existed between Pn 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 Pn and PPF was \( r = 0.72 \) and, Pn and DTEMP was \( r = 0.66 \). Beta coefficients for the prediction of Pn 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 Pn.

\[ P_n = 0.06 \times \text{PLA} + 0.013 \times \text{PPF} + 0.55 \times \text{DTEMP} - 14 \]  

**Pn as a function of duration from commencement of daily lighting.** Pn increased rapidly during the first hour of lighting (Fig. 2). Subsequent variation in Pn was minor for the remaining period of stable temperature, vapor pressure deficit, and PPF conditions. Over this period of stable environment, values of Pn averaged 10.5 ± 0.7, 9.1 ± 0.3, and 5.3 ± 0.5 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) at days of 28, 22, and 16 °C, respectively. Across the duration of stable environment, Pn declined linearly (\( P \leq 0.05 \)) and ~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 \( \mu \text{mol m}^{-2} \text{s}^{-1} \).

**PPF as a function of Pn.** Under all treatments, the increasing value of Pn with increasing PPF was described by a family of Tanh functions on a basis of both leaf area (Fig. 3A and B) and leaf area.
Further, rates of $P_n$ were consistently higher for leaves grown under 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 dry weight basis than on a unit leaf area basis (Fig. 3).

At all temperatures, light-saturated photosynthetic rate ($P_{\text{max}}$) 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, $P_{\text{max}}$ 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 $P_{\text{max}}$ per unit leaf area were minimal, indicating a relatively flat response to temperature. When expressed on a leaf dry weight basis, $P_{\text{max}}$ increased following a linear trend with increasing temperature under both $PPF$ regimes ($P \leq 0.001$, Fig. 4B). This response of $P_{\text{max}}$ 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% $P_{\text{max}}$) was estimated from the modelled data to occur between 600 and 700 $\mu$mol m$^{-2}$ s$^{-1}$ (Table 1). For plants grown under high $PPF$, light saturation was achieved between an estimated $PPF$ of 1100 and 1300 $\mu$mol m$^{-2}$ s$^{-1}$.

When expressed on the basis of both unit leaf area and unit leaf dry weight, apparent quantum yield ($\alpha$) 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 $\alpha$ 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, $\alpha$ 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 temperature and $\alpha$ was very pronounced, while under the low $PPF$ regime, 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 ($0.5 \pm 0.1$ $\mu$mol m$^{-2}$ s$^{-1}$) was only marginally greater than the accuracy of measurement of the equipment ($\pm 0.3$ $\mu$mol m$^{-2}$ 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
Values of Pn were in the low to intermediate range (Bjorkman, in comparison with other plant species (non-Araceae) these values were similar to those reported for other members of the Araceae (Schaffer and O'Hair, 1987). However, in comparison with other plant species (non-Araceae) these values of Pn were in the low to intermediate range (Bjorkman, 1981; Connor and Sadras, 1992).

The synchrony of changes in Pn 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 (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 Pn 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 Pn, 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 Pn values were primarily a function of growing environment. Furthermore, changes in Pn during the daily period of lighting were small enough to be within the margin for measurement error (0.7 µmol·m⁻²·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 Pn in leaves of Zantedeschia 'Best Gold' with photoperiod during this early stage of crop establishment.

Rates of Pn 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 Pn values measured at the PPF under which they were grown originally (i.e., Pnmax) reaching an average 85% of the light-saturated rate (i.e., Pmax). 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 µmol·m⁻²·s⁻¹ during growth of plants at 28 °C, resulted in a 70% increase in light-saturated Pn 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 Pn ≤ 25% (Prioul and Bourdu, 1973).

Irrespective of temperature, when grown under low PPF, light saturation of photosynthesis was reached between 600 and 700 µmol·m⁻²·s⁻¹. In contrast, for plants grown under high PPF, light saturation was achieved between an estimated 1100 and 1300µmol·m⁻²·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 Pn values than those grown under full sunlight (Schaffer and O’Hair, 1987). Given that PPF on a clear summer day frequently exceeds 1200 µmol·m⁻²·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)
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) | PPF | Leaf area (µmol·m⁻²·s⁻¹) | Leaf DW (µmol·m⁻²·s⁻¹) | PPF at compensation point° | Leaf area (µmol·m⁻²·s⁻¹) | Leaf DW (µmol·m⁻²·s⁻¹) | PPF saturation range° | Leaf area (µmol·m⁻²·s⁻¹) | Leaf DW (µmol·m⁻²·s⁻¹) |
|--------------|-----|--------------------------|-------------------------|---------------------------|--------------------------|-------------------------|-----------------------|-------------------------|-------------------------|
| 16 High      | 1300| 700                      | 600                     | 1200–1400                 | 700                      | 600                     | 1200–1400             | 700                     | 600                     |
| 16 Low       | 800 | 700                      | 600                     | 1200–1400                 | 700                      | 600                     | 1200–1400             | 700                     | 600                     |
| 22 High      | 1300| 700                      | 600                     | 1200–1400                 | 700                      | 600                     | 1200–1400             | 700                     | 600                     |
| 22 Low       | 800 | 700                      | 600                     | 1200–1400                 | 700                      | 600                     | 1200–1400             | 700                     | 600                     |
| 28 High      | 1300| 700                      | 600                     | 1200–1400                 | 700                      | 600                     | 1200–1400             | 700                     | 600                     |
| 28 Low       | 800 | 700                      | 600                     | 1200–1400                 | 700                      | 600                     | 1200–1400             | 700                     | 600                     |

°Gas exchange at a PPF of 0 µmol·m⁻²·s⁻¹.
°°PPF at which gas exchange rate was 0 µmol·m⁻²·s⁻¹.
°°°PPF at which Pₐ ranged between 90% and 100% of Pₘₐₓ.

allows for a high rate of CO₂ 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 CO₂/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 C₃ 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 Pₐ 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 (Lettly, 1973). These habitats would have either full sun or partial shade, and would result in an incident PPF as high as 1200 µmol·m⁻²·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, Pₐ 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 Pₘₐₓ, 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 Pₐ. 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 (m²·kg⁻¹) | PPF | High | Low |
|--------------|--------------|-----|------|-----|
| 16 High      | 26.4°        | 29.6|      |     |
| 16 Low       | 25.5         | 35.0|      |     |
| 22 High      | 27.9         | 37.2|      |     |
| 22 Low       | 13.3         | 17.8|      |     |
| LSDₐ₀      | 1.3          |     |      |     |

**Significance of F
Temperature (T) **
PPF **
T × PPF **

°Mean separation between any two values by lsd, P = 0.05 (n = 6).
**Significant at P ≤ 0.01.

Literature Cited

Bai, Y. and J.F. Kelly. 1999. A study of photosynthetic activities of eight asparagus genotypes under field conditions. J. Amer. Soc. Hortic. Sci. 124:61–66.

Bennett, K.J., H.G. McPherson, and J.J. Warrington. 1982. Effect of pretreatment temperature on response of photosynthesis rate in maize to current temperature. Austral. J. Plant Physiol. 9:773–781.

Bjorkman, O. 1981. Responses to different quantum flux densities, p. 57–107. In: O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler (eds.). Encyclopaedia of plant physiology. New series vol. 12A. Physiological plant ecology. Springer Verlag, Berlin.

Bjorkman, O. and B. Demmig. 1987. Photon yield of O₂ evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. Planta 170:489–504.
Brooking, I.R. 1976. Soilless potting media for controlled-environment facilities. N.Z. J. Expt. Agr. 4:203–208.
Caulfield, F. and J.A. Bunce. 1988. Comparative responses of photosynthesis to growth temperature in soybean (Glycine max L. Merrill) cultivars. Can. J. Plant Sci. 68:419–425.
Connor, D.J. and V.O. Sadas. 1992. Physiology of yield expression in sunflower. Field Crops Res. 30:333–389.
Ehleringer, J. and R.W. Pearcy. 1983. Variation in quantum yield for CO2 uptake in C3 and C4 plants. Plant Physiol. 73:555–559.
Fahl, J. I., M.L.C. Carelli, J. Vega, and A.C. Magalhaes. 1994. Nitrogen and irradiance levels affecting net photosynthesis and growth of young coffee plants (Coffea arabica L.). J. Hort. Sci. 69:161–169.
Funnell, K.A. 1993. *Zantedeschia*, p. 683–739. In: A.A. De Hertogh and M. Le Nard (eds.). The physiology of flower bulbs. Elsevier Scientific Publishers, Amsterdam, The Netherlands.
Funnell, K.A., I.J. Warrington, E.W. Hewett, and J. Plummer, 1998. Leaf mass partitioning as a determinant of dry matter accumulation in *Zantedeschia*. J. Amer. Soc. Hort. Sci. 123:973–979.
Giaquinta, R. 1978. Source and sink leaf metabolism in relation to phloem translocation. Carbon partitioning and enzymology. Plant Physiol. 61:380–385.
Ho, L.C., R.G. Hurd, L.J. Ludwing, A.F. Shaw, J.H.M. Thornley, and A.C. Withers. 1984. Changes in photosynthesis, carbon budget and mineral content during the growth of the first leaf of cucumber. Ann. Bot. 54:87–101.
Pallas, J.E. 1973. Diurnal changes in transpiration and daily photosynthetic rate of several crop plants. Crop Sci. 13:82–88.
Sato, T., M. Kawai, and T. Fukuyama. 1978. Studies on matter production of taro plant (Colocasia esculenta Schott). I. Changes with growth in photosynthetic rate of single leaf. Jpn. J. Crop Sci. 47:425–430.
Schenker, B. and S.K. O’Hair. 1987 Net CO2 assimilation of taro and cocoyam as affected by shading and leaf age. Photosyn. Res. 11:245–251.
Union of South Africa Department of Transport. 1954. *Climate of South Africa*. Part 1—Climate statistics. Climatology Branch, Weather Bureau. Govt. Printer, Pretoria.
Valenzuela, H.R., S.K. O’Hair, and B. Schaffer. 1991. Developmental light and net gas exchange of cocoyam (Xanthosoma sagittifolium). J. Amer. Soc. Hort. Sci. 116:372–375.
van Iersel, M.W. and O.M. Lindstrom. 1999. Temperature response of whole-plant CO2 exchange rates of three magnolia cultivars. J. Amer. Soc. Hort. Sci. 124:277–282.
Warrington, I.J., M. Peet, D.T. Patterson, J. Bunce, R.M. Haslemore, and H. Hellmers. 1977. Growth and physiological responses of soybean under various thermoperiods. Austral. J. Plant Physiol. 4:371–380.
Zelitch, I. 1971. Dark respiration and photorespiration, p. 127–171. In: I. Zelitch (ed.). *Photosynthesis, photorespiration, and plant productivity*. Academic Press, New York.