Leaf Mass Partitioning as a Determinant of Dry Matter Accumulation in *Zantedeschia*

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ABSTRACT. Dry matter accumulation and partitioning in plants of *Zantedeschia* Spreng. 'Best Gold' *aff. Z. pentlandii* (Wats.) Wittm. (syn. *Richardia pentlandii* Wats.) were quantified under a range of temperature and photosynthetic photon flux (PPF) regimes using plant growth analysis. The relative rate of dry matter accumulation [relative growth rate (RGR_M), $g\cdot g^{-1}\cdot d^{-1}$] was highly correlated with the partitioning of the daily increment of dry matter into leaf tissue [leaf matter partitioning (LMP), $g\cdot d^{-1}$ per $g\cdot d^{-1}$]. In contrast, a poor correlation existed between RGR_M and net assimilation rate (NAR, $g\cdot m^{-2}\cdot d^{-1}$). Maximum values of RGR_M increased linearly with increasing temperature (from 13 to 28 °C), with a base temperature of 2.1 ± 2.7 °C. The optimum temperature for growth was PPF dependent with maximum total plant dry mass occurring under high PPF (694 $\mu mol\cdot m^{-2}\cdot s^{-1}$) at 25 °C. However, as the plant responded to PPF by altering LMP, final total plant dry mass was actually greater under the low PPF regime (348 $\mu mol\cdot m^{-2}\cdot s^{-1}$) at temperatures <22 °C. The optimum temperature for dry matter accumulation was close to the average daily air temperature during the growing season for the natural habitat of the parent species. Similarly, the greater dry matter accumulation under the combination of either low PPF and cooler temperatures or high PPF and warmer temperatures was paralleled by the diversity of PPF habitats in the natural open grassland and forest margin the parent species occupies. It is therefore suggested that *Zantedeschia* 'Best Gold' is well adapted to optimize growth under these environmental conditions.

Zantedeschia K. Spreng. is a relatively new horticultural crop with an expanding international market for cut flowers and tubers. The growth response of this genus to environmental factors such as temperature and photosynthetic photon flux (PPF) has not been described. To optimize commercial production it is essential to characterize the effects of the relatively large diurnal and seasonal variation of temperature and PPF on growth. Such information will provide the basic foundation needed to develop crop management strategies, crop growth models, and future breeding strategies.

Traditional plant growth analysis, where relative growth rate (RGR) (Table 1) is presented as the product of leaf area ratio (LAR) and net assimilation rate (NAR), provides an empirical description of growth and development (Warren Wilson et al., 1986; West et al., 1920). Hunt (1982) summarized this simple but fundamental concept with "the growth rate of the plant depends simultaneously upon the efficiency of its leaves as producers of new material and upon the leafiness of the plant itself." This initially empirical description has elements of a basic mechanistic model, as the importance of the various components can be assessed.

While early growth analysis research endeavored to illustrate a causal relationship between plant growth and NAR, poor correlations often occurred (Poorter, 1990). This has primarily been attributed to a strong negative correlation between NAR and LAR (Konings, 1990; Poorter, 1990). In contrast, strong correlations between RGR and the various components of LAR have been reported for many species.

For many species grown under a range of environments, the strong correlation between RGR and LAR has been expressed in terms of relative leaf area expansion rate (RLAER) as well as the instantaneous ratio in the rates of change with time of leaf area and total plant dry mass {leaf area partitioning (LAP), Eq. [1]} (Jackson, 1963; Potter and Jones, 1977). The value of LAP as a component of growth analysis is that it takes into account differences in RGR and RLAER when they occur.

$$LAP = (\delta A/\delta t)/(\delta M/\delta t) \qquad [1]$$

Increased cultivation temperatures have been associated with increased partitioning of dry matter toward leaf growth and, therefore, increasing LAR and LAP (Farrar, 1988). However increased PPF is associated typically with increased dry matter accumulation but reduced LAR and LAP (Konings, 1990; Poorter, 1990). In addition, increased temperature and PPF have been associated with increased NAR.

In many species natural distribution is influenced by temperature minima during the growing season or annual period (Korner and Larcher, 1988; Woodward, 1988). Climatological data of the sites of origin of *Zantedeschia* could also provide some indication of the possible temperature tolerance range and, therefore, those temperatures worthy of investigation (Funnell, 1993a). Similarly, the natural habitat of *Zantedeschia* species in open grassland and forest margins (Letty, 1973) might indicate an ability to tolerate shade.

The objective of this study was to use plant growth analysis to understand how growth of *Zantedeschia* 'Best Gold' responds to

variable temperature and PPF during development, and, in so doing, determine horticulturally relevant environmental parameters and management strategies.

Materials and Methods

CULTURAL. Nonendodormant tubers of *Zantedeschia* Spreng. 'Best Gold' were lifted from the field (Palmerston North, New Zealand; 40° 20′S) immediately before two plantings—one in early August 1988 and the other in late July 1989. On both occasions tubers were graded for evenness of size ($\approx$1 cm in diameter, 0.4 g dry mass) and for the presence of a single dominant bud. Tubers were planted in 60-mL cell trays containing a 50 peat : 30 pumice (v/v) growing medium containing 3 kg·m^{-3} dolomite lime. Plants were subsequently grown for 18 d on a heated (20 °C) closed mist bench under greenhouse conditions (minimum air temperature 15 °C, ventilation at 24 °C). Uniform emerged plants were selected (protective sheath leaves 1 cm in length), potted into 1.2-L pots containing the same growing medium, and transferred to treatment environments. The treatments were imposed using controlled environment (CE) facilities in the National Climate Laboratory at the Horticulture and Food Research Institute of New Zealand Ltd. at Palmerston North. Plants were randomly allocated to one of twelve temperature–PPF treatment combinations, with two of the twelve combinations being common to both plantings. Each treatment comprised 96 plants. 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. An open plant canopy was maintained by regularly sampling individual plants and repositioning them, which eliminated interplant shading.

ENVIRONMENTAL. The day/night (daily mean) temperature treatments were 16/10 (13), 22/10 (16), 22/16 (19), 28/16 (22), 28/22 (25) and 28/28 (28) ± 0.5 °C. In all treatments, day/night vapor pressure deficit was maintained at 1.0/0.4 kPa. Photoperiod was 12 h, and day/night and night/day temperature and vapor pressure changeovers were each 2 h, with the lights switching off and on at the midpoint of each respective changeover.

Lighting was provided by four 1000-W high-pressure multivapor-lamps (Sylvania Metalarc) and four 1000-W Philips quartz halogen lamps, separated from the plant growth room by a plate glass and water thermal barrier (Warrington et al., 1978). The PPF at pot surface height was 694 ± 20 µmol·m^{-2}·s^{-1} (high PPF). Within the same CE 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 were rotated 180° about their own axis to minimize any influence of environmental gradients.

EXPERIMENTAL. To monitor growth, 6 or 12 plants were destructively harvested from the time of planting in cell trays until growth rate declined. Once in the CE rooms, harvests occurred at the appearance of each successive leaf. This was taken to be when a minimum of 75% expansion of that leaf had occurred on 90% of plants within a treatment. Once increases in tuber dry mass were detected, sampling occurred more frequently, until the rate of total plant dry mass accumulation declined.

At each harvest, the area of exposed leaves (i.e., leaf blades not enveloped by subtending petioles) was measured using a leaf area meter (model 3100, LI-COR). All measurements were carried out within 4 h of removal from treatment. Plants were then vacuum dried to constant mass at 0.3 kPa and 40 °C and dry mass was taken of exposed leaves, shoot (i.e., petioles of exposed leaves, together with apex, nonexposed leaves, and sheath leaves), petioles of senescing exposed leaves, senescing exposed leaf blades, tuber, and roots.

Within each temperature–PPF treatment combination, plants were arranged in a completely randomized design. To evaluate partially the variation due to time and between CE room effects, two temperature–PPF combinations (22/16 °C high PPF and 22/16 °C low PPF) were used in different CE rooms at the two planting times. Comparison of values for RGR$_M$ during exponential growth did not detect differences between planting times (data not presented) and mean values were used for subsequent analysis.

Log$_e$ transformed total plant dry mass data, total plant leaf area, and leaf dry mass data, collected subsequent to placement in the CE rooms, were fitted either to the Gompertz function, Eq. [2], or its logarithmic form, Eqs. [3] and [4] (Causton and Venus, 1981), using the nonlinear regression parameter estimation procedure of the Statistical Analysis System (SAS Institute, Cary, N.C.). A constant was added to all transformed data to eliminate negative values from the fitting process.

Table 1. List of variables, parameters, and abbreviations.

Symbol	Description	Unit
A	Total plant leaf area	cm^2
α	Asymptotic potential growth of parameter under investigation	
β	A measure of the starting size of the parameter under investigation	
δ	Mathematical notation for an interval	
e	The base of natural logarithms	
κ	Rate constant of parameter as a function of size	per day
L	Total plant leaf mass	g
t	Time	days
T	Mean temperature	°C
M	Total plant dry mass	g
LAP	Leaf area partitioning	cm^2·d^{-1}/g·d^{-1}
LAR	Leaf area ratio	m^2·g^{-1}
LMP	Leaf mass partitioning	g·d^{-1}/g·d^{-1}
NAR	Net assimilation rate	g·m^{-2}·d^{-1}
RGR	Relative growth rate	g·g^{-1}·d^{-1}
RLAER	Relative leaf area expansion rate	cm^2·cm^{-2}·d^{-1}
RLMR	Relative leaf mass increase rate	g·g^{-1}·d^{-1}

*,**,***Significant F value at P = 0.05, 0.01, or 0.001, respectively

$$\mathrm{Log}_e M = \alpha_M e^{(-e^{(\beta_M - \kappa_M t)})} \qquad [2]$$
$$\mathrm{Log}_e A = \alpha_A - e^{(\beta_A - \kappa_A t)} \qquad [3]$$
$$\mathrm{Log}_e L = \alpha_L - e^{(\beta_L - \kappa_L t)} \qquad [4]$$

Total plant relative growth rate (RGR_M), as a function of time, was calculated using the first differential of Eq. [2], i.e., Eq. [5] (Causton and Venus, 1981).

$$RGR_M = \alpha_M \kappa_M e^{(\beta_M - \kappa_M t)} e^{(-e^{(\beta_M - \kappa_M t)})} \qquad [5]$$

Similarly, RLAER and relative leaf mass increase rate (RLMR), as functions of time, were calculated using the first differentials of Eqs. [3] and [4], i.e., Eqs. [6] and [7], respectively (Causton and Venus, 1981).

$$RLAER = \kappa_A e^{(\beta_A - \kappa_A t)} \qquad [6]$$
$$RLMR = \kappa_L e^{(\beta_L - \kappa_L t)} \qquad [7]$$

NAR, as defined by West et al. (1920), was calculated using derived formulae and data from Eqs. [2], [3], and [5], i.e., Eq. [8].

$$NAR = (RGR_{M(t)} W_{(t)})/A_{(t)} \qquad [8]$$

LAP (Eq. [1]) and LMP (Eq. [9]), as defined by Jackson (1963), were calculated using derived formulae and data from Eqs. [2] to [7], i.e., Eqs. [10] and [11], respectively.

$$LMP = (\delta L/\delta t)/(\delta M/\delta t) \qquad [9]$$
$$LAP = (RLAER_{(t)} A_{(t)})/(RGR_{M(t)} M_{(t)}) \qquad [10]$$
$$LMP = (RLMR_{(t)} L_{(t)})/(RGR_{M(t)} M_{(t)}) \qquad [11]$$

The value of t used in the calculation of NAR, LAP, and LMP was the time (days from planting) at the midpoint of exponential total plant dry mass accumulation, i.e., maximal RGR_M.

All effects on dry mass were expressed on the basis of the daily mean temperature. For each PPF regime the relationship between RGR_M and temperature was established by regression analysis using the REG procedure of SAS. Comparisons for homogeneity of the derived slopes and intercepts between PPF treatments were conducted as outlined by Zar (1984).

Results

OVERVIEW AND DETERMINATION OF BASE TEMPERATURE. Under all treatments total plant dry mass, leaf area, and leaf mass followed sigmoidal patterns of growth, adequately described by a family of Gompertz or logarithmic Gompertz functions (Fig. 1). During the first 18 d total plant dry mass declined. This period coincided with root establishment, and development of the shoot to ≈1 cm in length, but with no leaf lamina exposed. At the time of the first harvest after placement within the treatments, total plant dry mass had either stabilized or begun to increase. This period coincided with the first leaf attaining ≥75% of its complete expansion.

During the initial stages of growth, RGR_M was greater with higher temperature and under higher PPF ($P < 0.001$) (Fig. 2). However, after RGR_M was maximal, RGR_M values were greater under the lower PPF regime. At maximal RGR_M a positive linear relationship between RGR_M and temperature existed under high ($P \leq 0.001$) and low ($P \leq 0.001$) PPF regimes (Fig. 3). There was no difference in slope between PPF regimes ($P > 0.05$), but RGR_M was consistently greater under the higher PPF regime, as indicated by differences between intercept values ($P \leq 0.05$). Hence, a doubling of the temperature from 13 to 26 °C resulted in an approximate doubling in the value of RGR_M, regardless of PPF regime. The linear response of maximum RGR_M to temperature allowed extrapolation of the linear regression to predict a base temperature for
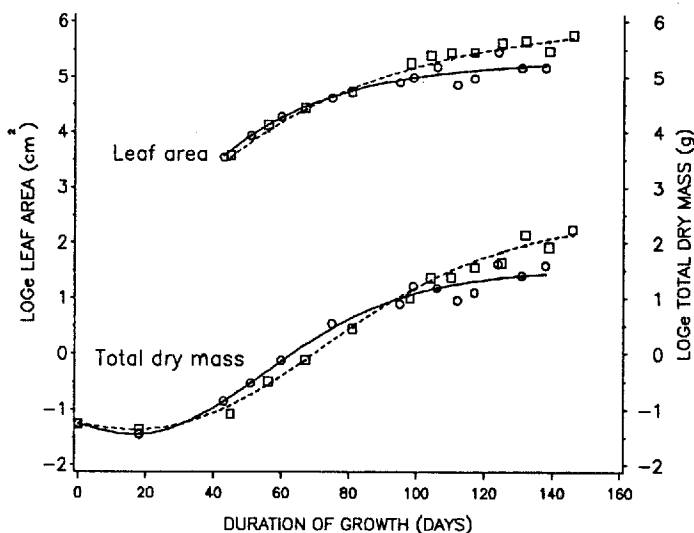

Fig. 1. Examples of fitted functions for leaf area and total plant dry mass with time, for plants of Zantedeschia 'Best Gold' grown at 16 °C under high (○) and low (□) PPF regimes. Mean square error values for fitting the functions for all treatment environments varied between 0.05 and 0.83.
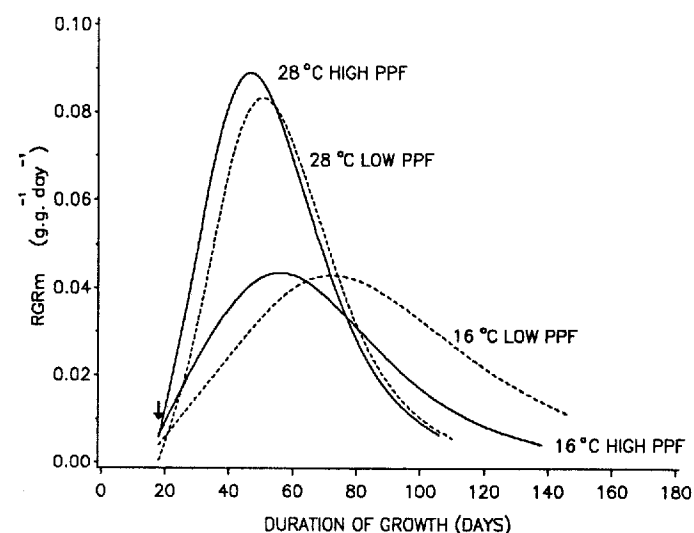

Fig. 2. Examples of relative growth rate (RGR_M) as a function of time, for Zantedeschia 'Best Gold' indicates day of transfer to treatment environments.
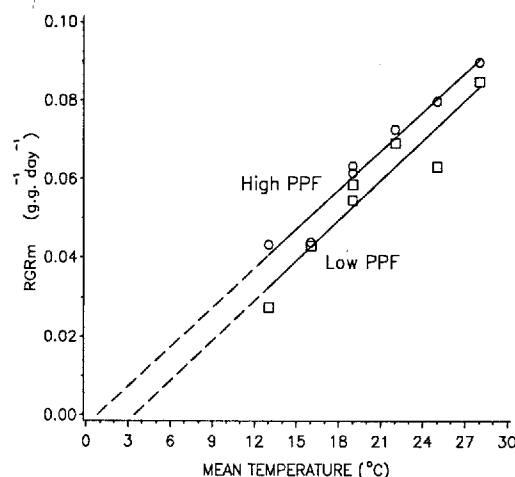

Fig. 3. Maximum value of RGR_M as a function of temperature, for plants of Zantedeschia 'Best Gold' grown under high (○) and low (□) PPF regimes. Fitted equation for high PPF is $RGR_M = 0.0033 \times T - 0.003$, $r^2 = 0.96^{**}$ and for low PPF is $RGR_M = 0.0034 \times T - 0.01$, $r^2 = 0.90^{**}$.

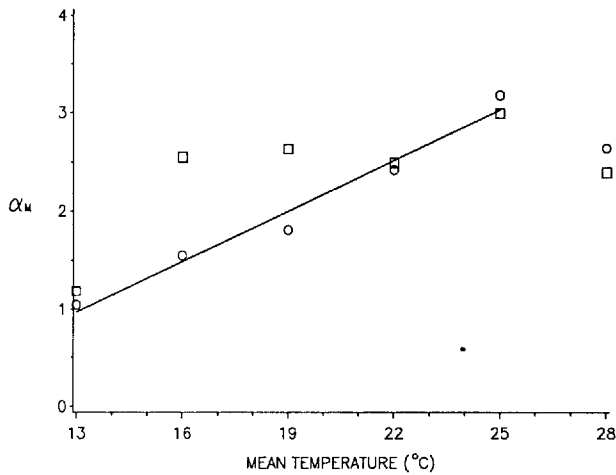Fig. 4. Log$_e$ maximum total plant dry mass (α_M) as a function of mean temperature, for *Zantedeschia* 'Best Gold' grown under high (○) and low (□) PPF regimes. Fitted line for high PPF regime was $\alpha_M = 0.17 \times T - 1.2$, $r^2 = 0.97^{***}$.

growth (Arnold, 1959) of 0.8 ± 4 °C under the high PPF regime and 3.4 ± 4.2 °C under the low PPF regime. Pooling the data from both PPF regimes resulted in an estimated base temperature for total plant growth of 2.1 ± 2.7 °C.

MAXIMUM TOTAL PLANT DRY MASS. Apart from maximum total plant dry mass (α_M), actual values of the fitted parameters are available from Funnell (1993a). Values of α_M were highly dependent on treatment. Under the high PPF regime, α_M increased linearly with increasing temperature (T) to 25 °C ($P \leq 0.001$). However, in contrast, under the low PPF regime α_M was not influenced by temperatures >13 °C. Above 13 °C, under the low PPF regime, α_M averaged 2.61 ± 0.13 (i.e., 13.64 g), while at 13 °C α_M was 1.19 ± 0.13 (i.e., 3.28 g), i.e., depressed by 76% on the basis of a back-transformed data comparison.

This interaction between temperature and PPF on the maximum total plant dry mass, resulted in greater values of α_M under the lower PPF regime at temperatures <22 °C. At temperatures >19 °C, maximum total plant dry mass was either not influenced by PPF (e.g., 22 °C) or was greater under the high PPF regime. Maximum α_M occurred at 25 °C, being 3.18 ± 0.07 (i.e., 24.0 g) under the high and 2.99 ± 0.12 (i.e., 19.9 g) under the low PPF regime. The value of α_M decreased at temperatures above this under both PPF regimes (Fig. 4).

MAXIMUM LEAF AREA AND DRY MASS. Maximum leaf area, i.e., α_A of the fitted Gompertz curves, of plants grown under the high PPF regime, increased linearly with increasing temperature (T) to 25 °C ($P \leq 0.05$, Eq. 12). As with total plant dry mass, values of α_A under low PPF were not influenced by temperatures above 13 °C ($P > 0.10$). Above 13 °C, under the low PPF regime, α_A averaged 5.98 ± 0.06 (i.e., 395.4 cm^2), while at 13 C α_A was 4.87 ± 0.88 (i.e., 130.3 cm^2), i.e., depressed by 67% on the basis of a back-transformed data comparison.

$$\alpha_A = 0.11T + 3.5, (r^2 = 0.97^{**})$$ [12]

Maximum leaf dry mass (α_L) responded similarly to α_A, with maximum leaf dry mass increasing linearly with temperature (T) through 25 °C, under high PPF ($P \leq 0.01$, Eq. 12). Under low PPF, temperatures >13 °C did not influence α_L ($P > 0.10$), averaging 0.73 ± 0.07 (2.08 g). At 13 °C, α_L was -0.77 ± 0.27 (i.e., 0.46 g), i.e., depressed by 78% on the basis of a back-transformed data comparison.

$$\alpha_L = 0.14T + 2.3, (r^2 = 0.94^{**})$$ [13]

The greatest values of α_A, i.e., 6.22 ± 0.06 (502.7 cm^2), and α_L, i.e., 1.23 ± 0.08 (3.42 g), were attained at 25 °C. Maximum leaf area and leaf dry mass were reduced at 28 °C.

Treatment differences in the development of leaf area and dry mass occurred throughout the period of study. When RGR$_M$ was maximum, total plant leaf area was greater under low PPF than under high PPF, at temperatures 19 °C and lower, whereas at temperatures >19 °C, leaf area was greater under the high PPF regime (Table 2).

RELATIONSHIPS BETWEEN DERIVED PARAMETERS. During the exponential phase of total plant dry mass accumulation, a positive linear relationship existed between RGR$_M$ and RLAER (Fig. 5A) and RLMR (Eq. [14]), regardless of PPF regime and temperature ($P > 0.0001$).

$$RGR_M = 0.75RLMR, (r^2 = 0.92^{***})$$ [14]

In contrast, no relationship between RGR$_M$ and NAR was detected for the entire data set, nor for separate PPF regimes ($P > 0.10$, Fig. 5B). While NAR was typically greater under the higher PPF regime ($P \leq 0.01$), no influence of temperature occurred ($P > 0.10$).

Positive, linear relationships existed between RGR$_M$ and LAP under both PPF regimes (Fig. 5C), with the slope of the line describing the relationship being greater under the higher PPF ($P > 0.05$). In contrast, a single, positive, linear relationship existed between RGR$_M$ and LMP regardless of PPF regime and temperature (Fig. 5D).

Discussion

The strong correlation between rate of leaf expansion and RGR$_M$ during the exponential phase in *Zantedeschia* (Fig. 5A) has been illustrated with a number of plant species, grown under a range of environments (Patterson et al., 1978; Potter and Jones, 1977). However extrapolation of this relationship infers that when RLAER is 0 cm$^2 \cdot$cm$^{-2} \cdot$d^{-1} a RGR$_M$ of 0.015 ± 0.005 g$\cdot$g$^{-1} \cdot$d^{-1} would be expected. RLAER can not be considered the sole cause of growth. While a strong correlation between RGR$_M$ and LAP was shown to exist for plants of *Zantedeschia* grown at a range of temperatures, the magnitude of the relationship was more than doubled when plants were grown under high compared with low PPF conditions (Fig. 5C). In contrast a single, positive, linear correlation between RGR$_M$ and LMP was determined for *Zantedeschia* under the wide range of temperature and PPF conditions examined (Fig. 5D).

In developing the potentially more causal relationship between RGR$_M$ and LAP, Potter and Jones (1977) used data derived from a number of species grown over a range of temperatures without variation in PPF regime. If the current experiment had used only one PPF regime the same conclusion would have been reached as that of Potter and Jones (1977). It is therefore evident that in contrast to LMP, LAP may be limited in its application in inferring a linear relationship with RGR$_M$ to situations where a single PPF regime is used. This theory is further strengthened when the equation presented in Fig. 5D is extrapolated to where a zero value

Table 2. Leaf area (cm^2) at maximal RGR$_M$ of Zantedeschia 'Best Gold' grown at a range of daily mean temperatures and high and low PPF regimes.

	Leaf area (cm^2) at temperatures (°C) indicated					
PPF	13	16	19	22	25	28
High	33.3	70.1	82.5	73.9	99.9	87.4
Low	38.8	77.1	97.6	65.5	71.1	77.7

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of LMP would result in a zero RGR_M. We conclude that as a component of growth analysis, LMP is able to take into account differences in RGR_M, RLMR and RLAER when they occur. Since PPF levels are not constant in the natural environment (i.e., daily, seasonal and latitudinal changes), we suggest that LMP will provide a more robust determinant of growth of *Zantedeschia* than LAP when subsequent crop growth models are developed.

The improved ability to predict RGR_M in *Zantedeschia* via a single relationship using LMP rather than two independent relationships using LAP, was a result of LMP accounting for differences in specific leaf mass. Changes in daily quantum integral account for differences in specific leaf mass of a number of plant species (Warrington and Norton, 1991). In addition, differences in specific leaf mass have accounted for variation in LAP in perennial ryegrass (*Lolium perenne* L.) and maize (*Zea mays* L.) (Hunt and Halligan, 1981; Tollenaar, 1989).

The poor correlation between NAR and RGR_M in *Zantedeschia* (Fig. 5B) occurs with other species (Lambers and Poorter, 1992; Poorter, 1990). However, examples of increased RGR_M as a result of increased NAR have been determined in some studies, especially when the growing environment influences photosynthesis more directly (Jensen, 1981). Hence the response of photosyn-

thetic rate in *Zantedeschia* to variable temperature and PPF, and its influence on plant growth, must be determined if comprehensive crop growth models are to be developed.

Variation exists among species in the presence and strength of correlations between growth (e.g., RGR_M) and LMP and/or LAP (Patterson et al., 1978; Potter and Jones, 1977; Sage and Pearcy, 1987). Species vary in the mechanisms by which they acclimate to their growing environment. Shade-tolerant species and ecotypes often exhibit an ability to acclimate to alteration in PPF through an enhanced alteration of the leaf area ratio and, thereby, LMP and LAP (Bjorkman, 1981). In contrast, sun species and ecotypes frequently possess a greater capacity to alter NAR under conditions of increased PPF. The strong correlation between LMP, LAP and RGR_M, and no correlation between NAR and RGR_M, supports the conclusion that *Zantedeschia* 'Best Gold' exhibits the phenotypic plasticity of a shade-tolerant species.

In terms of Hunt's (1982) simple description of growth, differences in *Zantedeschia* plant dry mass during the exponential phase of total plant dry mass accumulation, appear to be primarily attributable to changes in leafiness of plants. Increasing temperature resulted in increased leaf development; at maximum RGR_M leaf areas at intermediate temperatures were greater under the
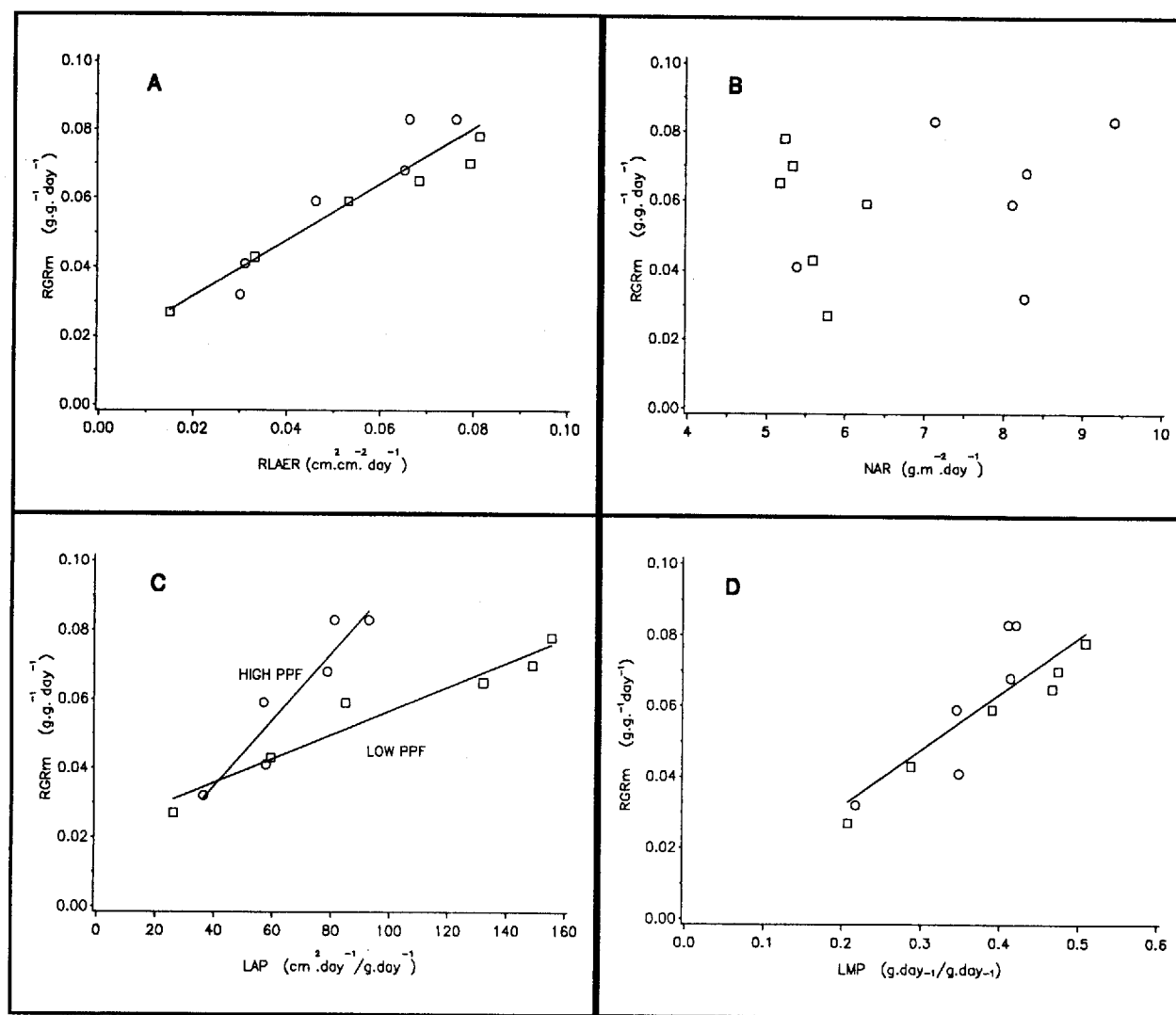
Fig 5. RGR_M as a function of RLAER (**A**), NAR (**B**), LAP (**C**), and LMP (**D**), for *Zantedeschia* 'Best Gold' grown under high (O) and low (□) PPF regimes and six mean temperatures. Fitted equation for **A** is $RGR_M = 0.82 \times RLAER + 0.015$, $r^2 = 0.88^{***}$. Fitted equation for **C** under high PPF is $RGR_M = 0.0008 \times LAP + 0.003$, $r^2 = 0.72^{**}$ and under low PPF is $RGR_M = 0.0003 \times LAP + 0.023$, $r^2 = 0.93$, ***. Fitted equation for **D** is $RGR_M = 0.156 \times LMP$, $r^2 = 0.98^{***}$.

lower PPF (Table 2). This increased leaf development, under low PPF, was able to maintain RGR_M at rates similar to those achieved under high PPF by compensating almost fully for any probable reduction in NAR (Fig. 3). Similarly, at intermediate temperatures maximum total plant dry mass was greater under the lower PPF (Fig. 4), resulting from greater leaf area development under the lower PPF regime.

The response of dry matter accumulation to PPF regime varied with temperature. Differences in total plant dry mass between PPF regimes were greatest at intermediate temperatures, with little or no difference being evident at extreme temperatures. This response is equally explained by variation in LAP and LMP (Fig. 5 C and D). Therefore Zantedeschia is best able to acclimate to and compensate for changes in PPF, via alteration in LAP and LMP, at temperatures of 13 to 28 °C. A temperature of 28 °C initially stimulated very rapid growth (Fig. 3) but resulted in decreased maximum total plant dry mass compared with that attained at 25 °C (Fig. 4). Values of the causally related RGR_M, LAP, and LMP, were similarly depressed at 28 °C relative to those at 25 °C, supporting the theory that leafiness of the plant is a dominant determinant of plant growth (Hunt, 1982).

The pooled predicted base temperature for growth of 2.1 ± 2.7 °C is within the range of 2 and 5 °C predicted for germination of many plant species used as winter crops such as wheat (*Triticum aestivum* L.) and turnips (*Brassica rapa* L.) (Angus et al., 1981). In contrast, warm-season crops originating from warm–temperate and subtropical climes, such as cotton (*Gossypium hirsutum* L.), sorghum (*Sorghum bicolor* (L.) Moench.), rice (*Oryza sativa* L.), and maize, have base temperatures of 8 to 10 °C. Just how accurate such estimations of base temperature are is open to debate, as base temperatures change with development (Porter and Delecolle, 1988). The low base temperature for *Zantedeschia* was somewhat surprising in that climatological data for sites of natural habitat indicate a warm–temperate climate for this crop (Funnell, 1993a). Natural distribution of perennial species is critically dependent on the temperature minima during the growing season and/or annual period (Korner and Larcher, 1988; Woodward, 1988). The discrepancy between the predicted base temperature of 2.1 °C and minimum soil temperatures reaching 8.1 °C in its natural habitat (Funnell, 1993a) may be due to other environmental and physiological factors. Rainfall is minimal during winter and winter dormancy does occur in summer flowering *Zantedeschia* (Corr and Widmer, 1988; Funnell, 1993a). These factors which prevent growth of *Zantedeschia* during winter in the natural habitat may affect the selection pressure for base temperature. Growth and development of recently planted *Zantedeschia* tubers is restricted at temperatures $<7 \pm 3$ °C (Funnell, 1993b). An alternative explanation for the low predicted base temperature is that plants with developed leaf area are able to continue photosynthesis at low temperatures that would normally restrict assimilate use for continued growth of new tissue (Acock et al., 1990).

The values of RGR_M do not clarify the shade response type for *Zantedeschia*. A maximum RGR_M value of 0.08 $g \cdot g^{-1} \cdot d^{-1}$ at 25 °C and high PPF (Fig. 3) is well within the range of 0.03 to 0.4 $g \cdot g^{-1} \cdot d^{-1}$ reported for other plant species (Lambers and Poorter, 1992), but is between typical values for sun species (e.g., 0.1 to 0.4 $g \cdot g^{-1} \cdot d^{-1}$) on the one hand and shade species (e.g., 0.02 to 0.04 $g \cdot g^{-1} \cdot d^{-1}$) on the other (Warren Wilson, 1972). This perhaps reflects the phenotypic plasticity of this species.

The response of RGR_M to temperature was consistent with that of other C_3 crop species (Grace, 1988) where RGR_M increased by 7%/°C (Fig. 3). The linear relationship between RGR_M and temperature (Fig. 3) also identifies the horticulturally relevant base

temperature $(2.1 \pm 2.7$ °C), linear range of temperature response (2.1 to 28 °C), and mean temperature for maximum growth (i.e., 25 °C). These values can form the basis for any future crop growth models, and indicate to horticulturists the need to maintain a daily average temperature of 25 °C during cultivation to maximize growth. As air temperatures in protected environments can exceed 25 °C for prolonged periods during summer, effective cooling systems will need to be used if growth is not to be detrimentally affected. Alternatively, selecting a cultivation site that naturally provides a mean temperature near 25 °C may provide an alterative strategy to maximize growth.

Temperatures used in the current study included those frequently encountered throughout the growing season by producers of *Zantedeschia*, under protected and nonprotected cultivation. Similarly, the two PPF regimes used equated to a daily integral PPF received under peak, unshaded, midsummer (high PPF), and winter (low PPF) conditions. Total plant dry matter accumulation of *Zantedeschia* was found to be highly adaptive to PPF regime due to its ability to alter the partitioning of dry matter to leaf development. Hence an important horticultural management consequence is that, irrespective of environmental conditions, establishment and maintenance of an effective leaf area will be critical if growth is to be maximized.

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