Temperature and Irradiance Effects on Vegetative Growth of Two Species of *Leucocoryne*

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**Abstract.** The influences of temperature and irradiance on vegetative growth of two species of *Leucocoryne* (*Leucocoryne coquimbensis* F. Phil and *L. ixioides* (Hook.) Lindl.) were examined in controlled environment growth rooms. The growing environments had day/night temperatures of 10/5, 15/10, or 20/15 °C, providing mean temperatures of 7.5, 12.5, or 17.5 °C, and photosynthetic photon fluxes (PPF) of 497 or 710 µmol·m⁻²·s⁻¹. Leaf emergence data were recorded up to three times a week, and measurements of vegetative growth were made in the rooms twice weekly. Destructive harvests were carried out at intervals up to four weeks apart. Leaves of *L. ixioides* emerged first in all mean temperatures. As mean temperature decreased from 17.5 to 7.5 °C, the differences in first emergence dates became more apparent between species. Appearance of the second leaf of both species occurred in less than half the number of days the first leaf took to emerge. The time taken for further leaves to develop increased as temperature decreased, particularly for *L. ixioides* and at mean temperatures below 12.5 °C. Although leaves of *L. ixioides* emerged first, days to emergence of further leaves increased to lag behind production of *L. coquimbensis* leaves, particularly when mean temperatures dropped below 12.5 °C. Temperature also significantly affected growth of other plant parts. As mean temperature increased, maximum leaf, root and main bulb dry weights increased for both species, along with secondary bulb dry weights of *L. coquimbensis*. As irradiance increased, maximum leaf dry weights decreased and maximum bulb dry weights increased of both species, and maximum dropper dry weights of *L. coquimbensis* increased. *Leucocoryne coquimbensis* appears to have the greatest capacity to multiply vegetatively and this is enhanced by high mean temperatures. These results suggest that mean temperatures higher than those used in this study are required for sustained leaf emergence, particularly for *L. ixioides* although this species has the capacity to emerge at low temperatures. High mean temperatures are also likely to promote vegetative mass of all plant parts of both species, whereas higher irradiance levels than used in this study would enhance main bulb growth.

*Leucocoryne* is a geophytic genus from Chile comprised of 11 (Hoffman, 1989) or 12 species (Zoellner, 1972). Taxa classification has varied for this genus from Amaryllidaceae (Bryan, 1989) to Liliaceae (Willis, 1973), but Dahlgren et al., (1985) seem to provide the most thorough analysis of its taxa, placing it in the Alliaceae family. The genus *Nothoscordum*, is the closest relative of *Leucocoryne* (Crosa, 1988). Other related Chilean genera include *Ipheion*, *Tristagma*, *Zoellnerallium*, *Pabellonia*, and *Tritelia* (Hoffman, 1989).

Two species of *Leucocoryne*, *L. coquimbensis* and *L. ixioides*, have potential as cutflower crops. *Leucocoryne coquimbensis* is endemic to the coast of central Chile from Coquimbo (hence its name) to Aconcagua (latitude 30 to 33°S) (Hoffman, 1989; Run- del, 1981; Zoellner, 1972). *Leucocoryne ixioides* is found over a narrower latitude band (latitudes 32 to 34°S) with some overlap with *L. coquimbensis*. The habitats of *L. ixioides* are farther south and farther inland, in the slightly more elevated central provinces of the Cordillera de la Costa (Hoffman, 1989; Zoellner, 1972). Temperature patterns in central Chile are primarily a function of topography (Rundel, 1981). Coastal areas of central Chile show a gradual reduction in rainfall over the latitudes where *L. coquimbensis* is found, changing from a Mediterranean climate in the south to a desert climate in the north (Dallman, 1998; Rundel, 1981). Precipitation levels increase inland due to orographic lifting of air masses. In both areas winter frontal rains are the main source of precipitation with virtually all moisture falling over the period from April to September (Rundel, 1981). These rains trigger growth, followed by flowering in late spring and early summer (Bryan, 1989). A dormant period occurs during the hottest and driest part of the year. Ohkawa et al. (1997) and van Leeuwen (1992) have shown that *L. coquimbensis* requires a minimum of 4.5 months dry storage at an optimum temperature of 20 °C to break dormancy. Hoffman (1989) lists the conservation status of these two species as vulnerable.

In New Zealand, *Leucocoryne* is grown in plastic structures that provide rain protection, and where it flowers in spring. However, there is little knowledge of the effects of temperature and light on bulb development, vegetative growth and flowering. Previous studies on *Leucocoryne* by Kim et al. (1998a and 1998b), Ohkawa et al. (1998), Ohkawa et al. (1997) and van Leeuwen (1992) have examined either flower bud development, bulb weight, storage temperatures or durations, and their effects on flowering. Elgar et al. (2003) have studied vase life and Lancaster et al. (2000) have identified an undesirable aroma produced by some species of *Leucocoryne*. Therefore, until now there has been no attempt to define the effects of the environment on vegetative and floral growth, or to describe the sequence of plant development. As *Leucocoryne* has potential as a cutflower crop, such knowledge will benefit flower growers as it will aid scheduling decisions and potentially improve flower quality. The objectives of this study were to determine the influence of temperature and irradiance on plant growth and development of two species of *Leucocoryne* under controlled environment conditions. The results of the vegetative stages of plant growth are reported in this paper and those of the floral stages in a previous paper (Catley, 2003).

**Materials and Methods**

**Plant Material.** Bulbs of seedling populations of *Leucocoryne coquimbensis* and *L. ixioides* were obtained from a commercial...
grower. Before receipt, the bulbs were stored dry at 20 to 25 °C for ≥28 weeks. Bulbs were prepared for planting immediately on arrival by removing all secondary bulbs from the main bulb. Each bulb (defined as the main bulb in this study) weighed between 1.0 and 2.5 g. Main bulbs were sorted according to weight, then four main bulbs of similar weights (±0.1 g) were planted in 1.25 L pots, containing a 1:1 peat : pumice : gravel mixture (by volume) growing medium. The medium was amended with 3 g L⁻¹ 3-month Osmocote (14N–6.1P–11.6K), 6 g L⁻¹ 9-month Osmocote (18N–2.6P–10K), 3.3 g L⁻¹ Sierra Micromax (Grace Sierra, Heerlen, The Netherlands), 8 g L⁻¹ dolomite lime and 3.3 g L⁻¹ superphosphate (Ravensdown Fertilizer Co-op, Napier, New Zealand). During growth, a modified half-strength Hoagland's A nutrient solution was applied to excess twice daily (Brooking, 1976). Each treatment consisted of 36 pots, and each treatment was allocated to 1.5 trolleys. Trolley positions were reallocated within each room twice weekly to minimize positional effects. A completely randomized design was used for each irradiance and temperature combination.

ENVIRONMENTAL CONDITIONS. The pots were placed on trolleys in three controlled environment growth rooms at the New Zealand Controlled Environment Laboratory belonging to HortResearch in Palmerston North, in a range of growing regimes with day/night temperatures of 10/5, 15/10, or 20/15 °C, providing mean growing temperatures of 7.5, 12.5, or 17.5 °C respectively. Daily lighting in each room consisted of a 12-h light period of 710 µmol m⁻² s⁻¹ photosynthetic photon flux (PPF) at pot level. Vapor pressure deficits of 0.4/0.3 kPa (day/night) were maintained in these rooms. The changeover between day and night for temperature and vapor pressure deficit took 2 h, with the 12-h light period starting midway through this period.

The light levels in the main lighting period were provided by four 1-kW high pressure discharge lamps (Sylvania 'Metalarc') and four 1-kW tungsten halogen lamps. An additional irradiance level was achieved by fitting half the trolleys with neutral density filters (80% transmissivity) fitted midway through this period.

MEASUREMENTS AND DATA ANALYSIS. The time of first leaf emergence was determined by monitoring all plants up to three times a week. Ten randomly selected plants in each treatment were labelled shortly after planting. Emergence of all leaves in these plants was recorded, along with twice weekly measurements of leaf lengths. Up to 11 destructive harvests were made during growth at intervals of up to 4 weeks apart. At each harvest, plant parts (leaves, inflorescences, roots, droppers, and main and secondary bulbs) from two randomly selected pots in each treatment (eight plants per treatment) were separated, counted, oven dried and reweighed.

The destructive harvest data were analyzed as pot means using Genstat 4.1 (Payne et al., 1993). The data from the mean temperature regimes of 12.5 and 17.5 °C were analyzed separately because of different harvest dates. Analysis of variance was used for the weight data after square-root transformation (to obtain more uniform residuals). Generalized linear models with Poisson error distribution were used for the analysis of count data. Leaf data were analyzed using the GLM procedure in SAS with count variables being square-root transformed before analysis (SAS Institute, 1993).

Results

Leaf appearance: timing and pattern. Temperature significantly affected the days from planting to leaf emergence for both Leucocoryne species (P < 0.001), particularly as mean temperature dropped below 12.5 °C (Fig. 1). As mean temperature decreased, the number of days to emergence of the first leaf increased, particularly for L. coquimbensis. There was also a significant species difference (P < 0.001). In the regime with the highest mean temperature (17.5 °C), L. ixioides emerged faster (48 d) than L. coquimbensis (51 d). With a mean temperature reduction from 17.5 °C to 12.5 °C, L. ixioides took longest to emerge (50 d), whereas L. coquimbensis took 57 d. In the regime with the lowest mean temperature of 7.5 °C, L. ixioides took 58 d to emerge in comparison to 67 d for L. coquimbensis. The
number of days between emergence of the second, third, fourth and fifth leaves was also significantly affected by temperature ($P < 0.001$), particularly for *L. ixioides* (Fig. 1). Days to first leaf appearance and days from first leaf appearance to second leaf appearance also differed significantly. The second leaf of both species appeared in less than half the number of days it took for the first leaf to appear in the lowest mean temperature, and in about a quarter of the time in the two highest mean temperatures. After emergence of leaf two, the days taken for subsequent leaves to emerge were similar for *L. coquimbensis* regardless of mean temperature, but increased with leaf number and decreasing temperature for *L. ixioides*. Irradiance level had no statistical effect on leaf appearance.

Typical plots of leaf elongation for a single plant are presented in Fig. 2. The rate of leaf elongation was the greatest immediately after emergence. When a leaf blade had reached approximately half the maximum length of the longest (and first) leaf, a brief lag phase occurred. Definition of this lag phase was clearest in the first four emerged leaves of plants growing in the two highest temperature regimes and in the first two or three emerged leaves in the lowest temperature regime.

Leaf blade length decreased significantly as temperature decreased ($P < 0.0001$) and as leaf number increased ($P < 0.001$) (Fig. 3), but there was no significant difference between species, or between mean temperatures of 12.5 and 17.5 °C for *L. ixioides*. Significantly more leaves per bulb were produced by *L. ixioides* than *L. coquimbensis* ($P < 0.01$ for a mean of 7.5 °C; and $P < 0.001$ for mean temperatures of 12.5 and 17.5 °C), and as mean temperature increased ($P < 0.01$ for a mean of 7.5 °C; and $P < 0.001$ for mean temperatures of 12.5 and 17.5 °C). Irradiance level had no effect. Plants of *L. ixioides* had a mean maximum of 4.3, 6.3, or 10.3 photosynthesizing leaves when grown at a mean temperature of 7.5, 12.5, or 17.5 °C. In comparison, plants of *L. coquimbensis* had a maximum of 3.5, 5.3, or 9.2 photosynthesizing leaves.

**PLANT DEVELOPMENT.** Development of above- and below-ground plant structures of *Leucocoryne* occurred in the same order regardless of species although size varied with treatment and time (Fig. 4). Immediately after planting, main bulb mass decreased, but this soon rapidly reversed as leaves began to emerge and as root mass increased. This was closely followed by development of droppers and secondary bulbs, then later flower scapes. Droppers are stolon-like structures that often produce secondary bulbs at their tips (Rees, 1972) (Fig. 5).

Growing environments have significant effects on the ultimate dry weight (Fig. 6) and the number of vegetative parts of a *Leucocoryne* plant. There were signifi-
different harvest dates. When comparing all maximum dry weight and floral structures or from expanding plant parts such as the main bulb. There may also be different temperature optima for different organs.

Significant differences were observed between the two species in root and secondary bulb development. *Leucocoryne coquimbensis* produced significantly more dry root mass (*P* = 0.035 for a mean temperature of 7.5 °C and *P* = 0.001 for mean temperatures of 12.5 and 17.5 °C) (Fig. 6B and G), although *L. coquimbensis* produced heavier secondary bulbs in the regimes with mean temperatures of 12.5 and 17.5 °C (*P* = 0.002) (Fig. 6D and I).

No correlation was found between main bulb dry weight at planting time and the final harvested bulb dry weight (data not shown).

**Discussion**

To prosper in their natural growing environment *Leucocoryne* must make rapid growth at the onset of fall rains as the growing season is short. This study showed that *L. coquimbensis* and *L. ixioides* do indeed grow rapidly given favorable conditions.

It is critical for the first leaf to emerge as fast as possible, to enable assimilate production to begin. Until leaf emergence, energy used for growth depletes the reserves of the planted main bulb, as was evident by a decline in main bulb weight immediately after planting (Fig. 4). This study showed that for both species of *Leucocoryne*, high mean temperatures promoted leaf emergence (Fig. 1A and B), and along with low light levels, increased leaf dry matter accumulation (Fig. 6A and F).

Although the first and second leaves of *L. ixioides* appeared before the first and second leaves of *L. coquimbensis*, the rate of emergence of the following leaves of *L. ixioides* steadily declined as mean temperature decreased, particularly below 12.5 °C, to a point where the rate of leaf production became less than that of *L. coquimbensis*. In the time *L. coquimbensis* produced three leaves in the regime with a mean temperature of 7.5 °C, five and nearly six leaves had been produced in the regimes with means of 12.5 and 17.5 °C. In the same timeframe *L. ixioides* had not quite produced three leaves at the lowest mean temperature but had produced four or five leaves in the two highest temperature regimes. This reduction in leaf appearance rate of both species may be attributed to increasing competition for assimilates from newly developing plant parts such as secondary bulbs, roots and floral structures or from expanding plant parts such as the main bulb. There may also be different temperature optima for development of different organs.
No other studies appear to have been published on growth and development of *L. ixoides*. Ohkawa et al. (1998) found first leaf emergence of *L. coquimbensis* occurred much more quickly (7 or 15 d after 26 or 16 weeks storage at 20 °C, or 25 d after 16 weeks storage at 25 °C), than in this study (57 d), suggesting that the number of days to first leaf emergence increases as storage temperature increases, and as storage duration decreases. Therefore, these factors may account for some of the variation between the two studies. Another possible reason for leaf emergence variation may be attributed to provenance differences, as described by Kroon (1989).

This study also showed leaf elongation in both species of *Leucocoryne* follows a double sigmoid pattern (Fig. 2), something that has not been reported before. A well-defined lag phase normally occurred when the leaf blade had reached about half the potential height of the first (and longest) leaf blade. Onset of this lag stage appears to coincide with emergence of a new leaf and may be due to increasing localized assimilate competition. When this newly emerged leaf reached a similar length to the previous leaf blade, the older leaf resumed elongation, albeit, at a reduced rate, until a maximum length was attained. This time, resumption of leaf elongation was not impeded by emergence of any further leaves indicating again that competition for assimilates may be quite localized. As more leaves were produced, ultimate leaf blade length declined (Figs. 2 and 3) along with the rate of leaf elongation, to a stage where there was no second sigmoid growth curve. At this stage, competition for assimilates may have increased dramatically as major development of other plant parts was occurring.

A study on leaf elongation in the closely related species, *Triteleia laxa* (Hane et al., 1994) does not show a clear double sigmoid pattern or a well-defined lag phase, although a decline in leaf expansion just below half the maximum leaf height can be seen. It is worthy to note this is at the point in the curve where the standard error bar is the largest, indicating there is a greater variation in their data here than at other times during leaf expansion. Han et al. (1994) pooled their leaf elongation data and took measurements a month apart. In combination, these methods may have masked a lag phase. It would be worthwhile to see if *T. laxa* does indeed have the same pattern of leaf elongation as *Leucocoryne*.

A good balance between leaf, bulb and root growth, and an understanding of the environmental factors promoting growth of these plant organs are important for a potential new cutflower crop such as *Leucocoryne* as they sustain good flowering and propagation rates. This study found temperature had the greatest effect on leaf, root and main bulb dry mass, and irradiance had the greatest effect on leaf, main bulb and dropper dry weights. An increase in mean temperature increased both the rate of leaf emergence and leaf blade length for both species of *Leucocoryne*, although *L. ixoides* produced more but shorter leaves than *L. coquimbensis*. As leaf dry weight is the product of the number of leaves produced and their ultimate size, there was no leaf dry weight difference between species. These two species of *Leucocoryne* were studied because of their cutflower potential. Leaves are absent on the flower stem, therefore leaf length or number, per se, are not important floral quality parameters. Leaves are important though, for their potential capacity to provide assimilates for good flower production; or if selections are to be considered for pot plant potential.

As with many bulbs there is a minimum required size for good quality flower production (Le Nard and De Hertogh, 1993), therefore good bulb growth—in terms of the main and secondary bulbs—is to be encouraged. This study shows high temperatures promote weight gains of main and secondary bulbs; and high irradiance levels promote main bulb weights. These weight gains may be tempered by main bulb planting weight as Kim et al. (1998a) found as bulb weight increases, the rate of bulb enlargement decreases. It can therefore be postulated that high mean growing temperatures would increase maximum dry weights of all vegetative plant parts of both species, and high irradiance levels would promote maximum main bulb and dropper weights. It should be pointed out that the nature of this experiment was such that plants growing in the regime with a mean temperature of 7.5 °C developed more slowly than those grown in the other two temperature regimes so did not reach the same level of development by the time the study was terminated. Therefore, the data shown from the regime with a mean temperature of 7.5 °C may be underestimated particularly for dry weight data and numbers of secondary bulbs and droppers. It should also be noted that although seedling populations were used in this study, they appear to be quite homogeneous in their responses.

*Leucocoryne* form secondary bulbs at two sites: directly from axillary buds in the parent bulb, and on the end of droppers. In *Leucocoryne*, a dropper is a stolon-like structure with a meristematic tip that extends well below the parent bulb (Fig. 5). Kim et al. (1998a) has also reported the presence of these structures in their study of *Leucocoryne*, as has Rees (1972) when reporting on tulips. Dropper development appears to be an adaptive feature to overcome long hot and arid summers, similar to summer conditions that occur in Chile.

There appears to be a difference in the vegetative reproductive capacity of the two species of *Leucocoryne* studied. *Leucocoryne coquimbensis* has the greatest potential to multiply vegetatively via secondary bulbs, and high temperatures enhance this capacity.

In summary, this study suggests that the optimum mean temperature for emergence of *L. ixoides* is between 12.5 and 17.5 °C, although mean temperatures for emergence of later leaves may benefit from temperatures equal to or greater than 17.5 °C. Optimum temperatures for first leaf emergence for *L. coquimbensis* appear to be slightly higher than those used in this study. Defining these optimum temperatures is important so that conditions can be provided to ensure that leaves emerge as quickly as possible so rapid development of other vegetative organs can proceed without delay. Once leaves began to appear, higher mean temperatures than those used in this study are also likely to promote vegetative mass of all plant parts of both species of *Leucocoryne*. Higher irradiance levels than those used in this study may be of benefit to main bulb weight gains. This may rule out growing this crop under plastic in all but the warmest areas in New Zealand, as planting normally occurs in early winter. Under these conditions during early growth, irradiance levels would be lower than the lowest irradiance level used in this study. Good dry matter gains may be possible if more protected cultivation was provided, or if long-term storage protocols could be established for *Leucocoryne*, so crops could be grown in the shoulder periods of the summer months. Catley (2003) gave similar temperature recommendations to optimize floral quality and minimize flowering times of *Leucocoryne*.

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