Temperature and Irradiance Effects on Flowering of Two Species of *Leucocoryne*

J.L. Catley

*The Horticultural and Food Research Institute of New Zealand Ltd., Private Bag 11 030, Palmerston North, New Zealand*

**ABSTRACT.** The influences of temperature and irradiance on flowering of two species of *Leucocoryne* (*L. coquimbensis* F. Phil. and *L. ixioides* (Hook.) Lindl.) were examined in controlled environment growth rooms. 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. Inflorescence emergence data were recorded up to three times a week, measurements of floral development were made twice weekly and destructive harvests were carried out every 2 weeks. Both species of *Leucocoryne* flowered most quickly when grown at a mean temperature of 17.5 °C. *Leucocoryne coquimbensis* flowered first in all temperature regimes (means of 7.5, 12.5, or 17.5 °C), taking an average of 7.1, 5.1, or 4.5 months to flower, whereas plants of *L. ixioides* took 7.6, 5.4, or 4.7 months to flower. Although taking longer to flower, *L. ixioides* produced better quality flowers (taller scapes and more florets per inflorescence). Plants of *L. coquimbensis* grown in the two highest temperature regimes produced up to four inflorescences per bulb. As mean temperature decreased, the number of inflorescences produced by each bulb together with the number of florets in each inflorescence and the number of leaves produced before emergence of the inflorescence decreased. Decreases in these attributes were much greater with a 5 °C mean temperature drop from 12.5 °C, than a drop from 17.5 to 12.5 °C. At least half the florets in an inflorescence opened before the first floret began to senesce. The onset of senescence was delayed as mean temperature decreased. The highest irradiance level promoted development of further inflorescences of *L. ixioides* at all mean temperatures, and at a mean temperature of 17.5 °C for *L. coquimbensis*. Flower stem heights of *L. coquimbensis* increased as mean temperature increased and irradiance level decreased. An increase in irradiance level also promoted scape heights of *L. ixioides*, although maximum scape heights were attained at a mean temperature of 12.5 °C. Regardless of mean temperature or irradiance level, all cut stems were able to stand without support. These findings suggest days to flowering, inflorescence number and floral quality may be improved by growing these two species of *Leucocoryne* at mean temperatures greater than 17.5 °C, whereas mean temperatures below 12.5 °C will be detrimental to these floral attributes.

*Leucocoryne* is a geophytic genus from Chile comprised of 11 (Hoffman, 1989) or 12 species (Zoellner, 1972), belonging to the Alliaceae family (Dahlgren et al., 1985). Two of the species, *Leucocoryne coquimbensis* and *L. ixioides* are summer-dormant geophytes which have potential as cutflower crops. *L. coquimbensis* is endemic to the coast of central Chile from Coquimbo (hence its name) to Aconcagua (latitude 30 to 33°S) (Hoffman, 1989; Rundel, 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). Winter rains trigger growth followed by flowering in late spring and early summer (Bryan, 1989). Ohkawa et al. (1997) and van Leeuwen (1992) have shown *L. coquimbensis* requires a minimum of 4.5 months dry storage at an optimum temperature of 20 °C to break dormancy.

At the time of bulb lifting, differentiation of the first inflorescence and sometimes the second inflorescence has occurred (Ohkawa et al., 1998). During storage, floral organ development continues, the rate being dependent on temperature: 20 °C is considered the optimum (Ohkawa et al., 1998). After 9 months storage at 20 °C the scape begins to elongate, however after ≈11 months storage, abortion of the first inflorescence can begin and is universal in bulbs stored for at least 12 months (Kim et al., 1998a; Ohkawa et al., 1998). After planting, differentiation of secondary inflorescences continues and begins for tertiary inflorescences (Ohkawa et al., 1998).

The inflorescence of *Leucocoryne* is an umbel of 3-12 florets (Uphof, 1945). *Leucocoryne coquimbensis* has blue florets with white centers and prominent orange-yellow stamnodes and *L. ixioides* has white florets with cream stamnodes. Some species have an undesirable aroma when cut which can detract from the floral appeal (Lancaster et al., 2000). The manner in which a flower senesces may be important in determining a species’ usefulness as a cutflower or ornamental. McKenzie and Lovell (1992) describe three broad categories of flower senescence. One of these, into which *Leucocoryne* falls, is withering and persistence of the flowers and constituent floral parts. Other genera in this category include *Ipheion*, *Nothoscordum*, and *Triteleia*, genera closely related to *Leucocoryne*.

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 flowering, flower quality and crop scheduling. Previous studies of *Leucocoryne* by Kim et al. (1998a, 1998b), Ohkawa et al. (1998), Ohkawa et al. (1997), and van Leeuwen (1992) have examined either floral differentiation, bulb weight, storage temperatures or durations, and their effects on flowering. Elgar et al. (2003) also studied vase life. Therefore, until now there has been no attempt to define the effects of the environment on floral growth, or sub-
sequent quality, or to describe scape elongation and flowering. 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 these floral development studies are reported in this paper.

**Material and Methods**

**Plant material.** Bulbs of seedling populations of *L. coquimbensis* and *L. ixioides* were obtained from a commercial grower. Before receipt, the bulbs were stored dry between 20 and 25 °C for ≈28 weeks. Bulbs were prepared for planting immediately on arrival, by removing all secondary bulbs from the main bulb. Each main bulb weighed between 1.0 and 2.5 g. These bulbs were sorted by removing all secondary bulbs from the main bulb. Each treatment consisted of 36 pots, and each treatment was allocated to 1.5 trolleys. Trolley positions were reallocated as when the tips of the first floret tepal become translucent. Up to 11 destructive harvests were made during growth at intervals of up to 4 weeks. At each harvest, inflorescences from two randomly selected pots in each treatment (eight plants per treatment) were counted, separated, weighed, oven dried and reweighed.

Statistical analyses were carried out using Genstat 4.1 (Payne et al., 1993). Height and development stage data were analyzed using linear models. Generalized linear models with Poisson error distribution were used for the analysis of count data.

**RESULTS**

**Days to flowering.** Days from planting to spathe appearance and from planting to flowering increased with decreasing mean temperature (both *P < 0.001*) for both *Leucocoryne* species (Fig. 1A and B). Although there was no significant species difference in the number of days from planting to the appearance of the first spathe, there was in the number of days from planting to flower opening (both *P < 0.001*). Scapes appeared first in plants of *L. coquimbensis*, and they began flowering significantly earlier than those of *L. ixioides* at all temperatures (Fig. 1A and B). At mean temperatures of 7.5, 12.5, and 17.5 °C it took plants of *L. coquimbensis* 214, 153, and 137 d to flower from planting, in comparison to 228, 164, and 140 d for plants of *L. ixioides*. Spatha emergence of *L. coquimbensis* was more closely followed by scape emergence and flowering than that of *L. ixioides*. Irradiance level had no effect on the timing of any of these floral parameters.

The number of days from flowering of the first inflorescence to flowering of the second inflorescence was substantially shorter than the number of days from planting to flowering of the first inflorescence. *Leucocoryne coquimbensis* produced second inflorescences more quickly than *L. ixioides* at all mean temperatures. The number of days from flowering of the first inflorescence to flowering of the second inflorescence decreased as mean temperature increased (34, 16, and 13 d for *L. coquimbensis* and 44, 27, and 17 d for *L. ixioides*). No further data is available on the number of days it took for additional inflorescences to be produced.

**Floral attributes.** Final scape heights of both species were significantly affected by mean temperature and irradiance level.
was a small but significant effect on scape heights (Fig. 2A and B). There was also a significant increase in the number of inflorescences per bulb as irradiance level increased (3.2, 5.3, and 6.0 leaves for L. coquimbensis and 3.6, 5.5, and 6.8 leaves for L. ixioides) \( (P < 0.001) \) (Fig. 4). Irradiance level had no effect.

**FLOWERING DYNAMICS.** Floral development of the first inflorescence in both species of Leucocoryne proceeded in an orderly manner, although the timing (Figs. 5 and 6) and magnitude (Fig. 5) of these various phases was significantly affected by mean temperature, and sometimes irradiance (Fig. 6). Results of only the 710 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) irradiance level are presented in Fig. 5 for clarity, but results of the lowest irradiance level are described or depicted elsewhere in the text. Emergence of the scape (d, Fig. 5A and B), spathe (e, Fig. 5A and B), and umbel (f, Fig. 5A and B) proceeded in an orderly manner.

For both species the mean number of inflorescences per bulb increased as mean temperature increased (3.2, 5.3, and 6.0 leaves for L. coquimbensis and 3.6, 5.5, and 6.8 leaves for L. ixioides) \( (P < 0.001) \) (Fig. 4). Irradiance level had no effect.
**Discussion**

This study shows the timing, productivity and quality of *Leucocoryne* flowers were strongly influenced by temperature and...
to a small extent, irradiance level; and there are often several developmental processes occurring at any one time during flower growth and development. Although seedling populations were used in this study, they appear to be quite homogeneous in their responses to temperature and irradiance.

Flowering of the first inflorescence (Figs. 1 and 5) and the number of leaves that emerged before inflorescence emergence (Fig. 4) were affected by temperature, particularly as mean temperature decreased from 12.5 to 7.5 °C. The numbers of inflorescences each species produced (Fig. 3A and B) were also affected in the same manner, although these figures may be underestimated, as there was exceedingly slow growth at the lowest mean temperature of 7.5 °C, and very few plants of *L. ixioides* particularly, flowered by the time the experiment ended. Mean temperature had less effect on days to leaf emergence (a, Fig. 5) than days to first flowering (e, Fig. 5). Days to leaf emergence were similar at the two highest mean temperatures, but increased by approximately 20% as mean temperature decreased from 12.5 to 7.5 °C. In comparison, the number of days from planting to first flowering decreased by more than 50% at 17.5 °C for both species (Fig. 3A and B). Although *Leucocoryne* umbel shape was also variable in this study, it is not known if temperature and irradiance affect umbel symmetry.

Species differences were also present. Plants of *L. coquimbensis* flowered first, whereas plants of *L. ixioides* had more leaves at first flowering than *L. coquimbensis*, and plants of *L. ixioides* produced the best quality inflorescences containing more florets, on the tallest scapes.

No other studies appear to have been published on growth and flowering of *L. ixioides*, but there have been studies on *L. coquimbensis* and other closely related genera. Studies of *L. coquimbensis* by Okhawa et al. (1998b) found flowering took 100 d, which is considerably shorter than in the experiment reported here (145 d). Storage duration and temperature are similar in these two studies, but in the study of Okhawa et al. (1998), bulbs weighed more (3.0 ± 0.1 g), were stored cooler at 20 °C, and grown under longer daylengths (12.3 to 18.8 h). These different experimental variables may explain some of the disparities between these two studies as other studies on *Leucocoryne* and *Triteleia* have shown they can all affect flowering time. Work by Okhawa et al. (1997) showed mean storage temperatures above the optimum of 20 °C increased the number of days to flowering. Han et al. (1991) and Wilkins and Halsey (1985) found when *Triteleia laxa* was grown under a 16-h day in contrast to an 8-h day, flowering occurred 4 to 6 weeks earlier. Han (2001) also found days to flowering decreased as the weight of *T. laxa* corms increased, although Kim et al. (1998b) found no significant changes in flowering time as *L. coquimbensis* bulb weight increased over a narrow range of ±0.2 g above the critical bulb weight of 0.3 g. Other production figures from the current study were also compared with those of Okhawa et al. (1998). Plants in the current study produced less inflorescences (≈1.9 per bulb compared with ≈3.0), and less florets per inflorescence (≈5.8 compared with 8 to 8.6). Scape height in this current study was comparable (≈400 mm compared with 390 to 490 mm), which is consistent with the findings of Han et al. (1991), who found there was no correlation between scape heights of *T. laxa* and mother corm weights. In the current study, attached scapes continued to elongate after opening of the first floret (Fig. 5e–i). At mean temperatures of 17.5 °C this increase amounted to ≈60 mm for *L. coquimbensis*. This same growth, if not more, may have occurred if these stems had been cut, as Elgar et al. (2003) suggested there may be some growth in storage.

There are several possible reasons why flower quality and production levels in the current study differ with those of Okhawa et al. (1998). The current study shows the number of inflorescences and scape height are affected by irradiance level but Okhawa et al. (1998) did not specify irradiance levels or whether offsets were left on planted bulbs. Bulbs of *L. coquimbensis* used in the current experiment were more than the minimum critical flowering weight of 0.3 g for *L. coquimbensis* recommended by Kim et al. (1998b). Although critical bulb size is often required for flowering to occur in a range of bulb species (Le Nard and De Hertogh, 1993) this can vary with apical meristem size (Halsey, 1989), and environmental conditions during growth (Han, 2001; Hartsema, 1961). Han (2001) also found as the weight of mother corms of *T. laxa* increased, more inflorescences containing more florets were produced, although over a narrow weight range above the critical bulb weight of *L. coquimbensis*, Kim et al. (1998b) did not find this. There may also have been significant genetic differences in the provenances of *L. coquimbensis* used in each of these two experiments. Such ecological variation is confirmed by Kroon (1989) who found there was a great deal of variation between *Leucocoryne* populations in scape height, the number of inflorescences produced per bulb, and the number of florets per umbel.

The length of time florets on an individual inflorescence stay open before they start to senesce also affects ultimate flower stem quality. Although the inflorescences in this study were left on the plants, some comparisons with the control treatments of Elgar et al. (2003) can be made using those inflorescences grown at a mean temperature of 17.5 °C in this current study (2.5 °C lower than standard vase life temperature conditions). Unlike the findings of Elgar et al. (2003), all florets in an umbel opened in the current study. In the current study, vase life of both *Leucocoryne* species was 26 to 27 d at the highest PPF level of 710 μmol m⁻² s⁻¹ (Fig. 6). This is in contrast to the control treatments of Elgar et al. (2003) (9.1 to 9.6 d for *L. coquimbensis*, and 12 d for *L. ixioides*). Vase life should be longer in non-cut inflorescences, given other comparable opening conditions, therefore, these differences suggest there is potential to improve the vase life of cut inflorescences of *Leucocoryne*. In the current study, onset of senescence in relation to the completion of floret opening, differed with *Leucocoryne* species, but it is unclear if Elgar et al. (2003) found the same dynamics occurring. Senescence is a function of temperature (Wills et al., 1998), therefore it was not surprising in the current study to find that as mean temperature dropped, the dynamics of floret opening and senescence changed, and vase life increased.

In summary, both species of *Leucocoryne* flowered most quickly with good flower quality at the highest mean temperature of 17.5 °C used in this study. Although taking longer to flower, the population of *L. ixioides* produced better quality flowers. There were further improvements in inflorescence numbers of both species

---

J. Amer. Soc. Hort. Sci. 128(6):809–814. 2003.
when plants were flowered at a higher irradiance level, although scape heights decreased. An increase in mean temperature beyond 17.5 °C, may promote more inflorescences per bulb bearing more florets, and further reduce the time to flowering, although the scape height of *L. ixioides* may be compromised. A reduction in flowering time would undoubtedly add to the financial returns of this crop as a minimum of 4.5 months is a considerable period to have an unproductive crop in the ground.

This study also shows that production and quality levels of these two species decrease as mean growing temperature decreases. 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 so yields and quality may be affected. Greater crop protection to increase mean temperature may be another growing option, particularly if there is a considerable reduction in the time to flowering. Another option could be establishment of long-term storage protocols for leucocoryne, to allow production over the warmer, summer months. Dynamic studies of floret opening and storage protocols for leucocoryne, to allow production over the warmer, summer months. Dynamic studies of floret opening and

---

**Literature Cited**

Brooking, I.R. 1976. Soilless potting media for controlled-environment facilities. N.Z. J. Exp. Agr. 4:203–208.

Bryan, J.E. 1989. Bulbs. vol. II, I-Z. Timber Press, H.K.

Dahlgren, R.M.T., H.T. Clifford, and P.F. Yeo. 1985. The families of the monocotyledons: Structure, evolution, and taxonomy. Springer-Verlag, Berlin.

Elgar, H.J., T.A. Fulton, and E.F. Walton. 2003. Effect on harvest stage, storage an ethylene on vase life of *Leucocoryne*. Postharvest Biol. Technol. 27:213–217.

Halevy, A. 1989. Recent advances in control of flowering and growth habit of geophytes. Acta Hort. 266:35–42.

Han, S.S. 2001. Flowering of three species of *Brodiaea* in relation to bulb size. Scientia Hort. 91:349–355.

Han, S.S., A.H. Halevy, R.M. Sachs, and M. Reid. 1991. Flowering and corm yield of *Brodiaea* in response to temperature, photoperiod, corm size and planting depth. J. Amer. Soc. Hort. Sci. 116:19–22.

Hartsema, A.H. 1961. Recent advances in control of flowering and growth habit of geophytes. Acta Hort. 266:35–42.

Hoffman, A.E.J. 1989. Chilean monocotyledonous geophytes taxonomic considerations and their state of conservation. Herbetia 45:13–29.

Kim, H.H., K. Ohkawa, and E. Nitta. 1998a. Fall flowering of *Leucocoryne coquimbensis* F. Phil, after long-term bulb storage treatments.

Kim, H.H., K. Ohkawa, and E. Nitta. 1998b. Effects of bulb weight on the growth and flowering of *Leucocoryne coquimbensis* F. Phil. Acta Hort. 454:341–346.

Kroon, G.H. 1989. Evaluation of *Leucocoryne* als nieuwe snijbloem. Prophyta 43:15–16.

Lancaster, J.E., M.L. Shaw, and E.F. Walton. 2000. S-Alk(en)yl-L-cysteine sulfoxides, alliinase and aroma in *Leucocoryne*. Phytochemistry 55:127–130.

Le Nard, M. and A.A. De Hertogh. 1993. Bulb growth and development and flowering, p. 29–43. In: A.A. De Hertogh and M. Le Nard (eds.). The physiology of flower bulbs. Elsevier Sci. Publ. Co., Amsterdam, The Netherlands.

McCree, K.J. 1972. Test of current definitions of photosynthetically active radiation against leaf photosynthesis data. Agr. Meteorol. 10:443–453.

McKenzie, R.J. and P.H. Lovell. 1992. Flower senescence in monocotyledons: a taxonomic survey. N.Z. J. Crop Hort. 20:67–71.

Monteith, J.L. and M.H. Unsworth. 1990. Principles of environmental physics. p. 38. 2nd ed. Edward Arnold, London.

Ohkawa, K., H.H. Kim, E. Nitta, and Y. Fukazawa. 1998. Storage temperature and duration affect flower bud development, shoot emergence, and flowering of *Leucocoryne coquimbensis*. J. Amer. Soc. Hort Sci. 123:586–591.

Ohkawa, K., E. Nitta, Y. Fukazawa, and H.H. Kim. 1997. Effects of storage temperature and time on flower bud development, emergence and flowering of *Leucocoryne coquimbensis*. Acta Hort. 430:427 (abstr.).

Payne, R.W., P.W. Lane, P.G.N. Digby, S.A. Harding, P.K. Leech, G.W. Morgan, A.D. Todd, R. Thompson, G. Tunncliffe Wilson, S.J. Welham, and R.P. White. 1993. Genstat 5 reference manual. vol. release 3. Oxford Univ. Press, Oxford, U.K.

Rundel, P.W. 1981. The matorral zone of central Chile, p. 175–201. In: di Castri, F., D.W. Goodall, and R.L. Specht (eds.). Ecosystems of the world 11: Mediterranean-type shrublands. Elsevier Sci. Publ. Co., Amsterdam, The Netherlands.

SAS Institute. 1993. SAS/STAT user’s guide. version 6. 4th ed. SAS Inst., Cary, NC.

Uphof, J.C. 1945. *Leucocoryne* and related genera of South America. Herbertia 12:52–67.

van Leeuwen, P.J. 1992. Effects of storage temperature on bulb growth and flowering of *Leucocoryne* sp. 6th Intl. Symp. Flower Bulbs:156 (abstr.).

Wilkins, H.F. and A.H. Halevy. 1985. *Triteleia laxa*, p. 415–417. In: A.H. Halevy (ed.). CRC Handbook of flowering. vol IV. CRC Press, Boca raton, Fla.

Wills, R., B. McGlasson, D. Graham, and D. Joyce. 1998. Effects of temperature, p. 60–76. In: Postharvest. An introduction to the physiology & handling of fruit, vegetables & ornamentals. 4th ed. Hyde park Press, Adelaide, Australia.