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Flowering control in *Watsonia*: Effects of corm size, temperature, photoperiod and irradiance

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ABSTRACT

The role of corm size, light and temperature in flowering of *Watsonia* species was evaluated to facilitate their commercial production. In addition to exhibiting desirable ornamental attributes, the species selected represented the major climatic regions in South Africa. A day/night temperature regime of 12/7 °C released vegetative dormancy in all species and thereafter elicited vernalization in *Watsonia pillansii* – highlighting an obligate cold requirement for this species. Flowering of *Watsonia borbonica* and *Watsonia tabularis* was not enhanced by additional chilling, but rather by long (16 h) or day-neutral (12 h) photoperiods. Microscopic examination of the shoot apical meristem revealed that extension of the 2nd leaf was a critical stage developmentally, and signified the anatomical transition to flowering. Late-development temperatures to a maximum of 25 °C ensured healthy vegetative growth and supported the maturation of the inflorescence and the opening of floret buds. Irradiance did not affect flower induction, but a minimum light intensity of 150 μmol m^{-2} s^{-1} proved essential in sustaining the energetic demands of the competitive growth and reproductive processes. Excessively high irradiance (950 μmol m^{-2} s^{-1}) impacted negatively on attractiveness through increased bud blasting. Flowering success was not correlated to corm mass, but rather to the environment under which the corm was stored, or the conditions under which the plant was grown. Understanding the phenology of these species *in situ* and the link between flowering and season provide a useful tool for predicting the artificial requirements necessary to elicit optimal flowering under industry conditions.

1. Introduction

Flowering is a complex series of events controlled by endogenous processes and exogenous environmental cues, with both light and temperature playing crucial roles in flower induction, initiation and maturation (Bernier, 1988; Halevy, 1990). However, exactly how flowering is impacted by light and/or temperature varies greatly among species (Adams et al., 1998). Further, the shoot apical meristem (SAM) of juvenile plants is unresponsive to factors that promote flowering (Levy and Dean, 1998). This juvenility is followed by an adult phase during which the SAM becomes competent to flower under inductive conditions. The timing and nature of attaining competency are species specific and are also impacted on by the environmental conditions under which a plant is grown.

Exposure of competent individuals to cool temperatures promotes flowering in many perennial/biannual species. In some cases cool temperatures promote flower induction (~ vernalization), whereas in other instances they allow for the resumption of growth once development has been arrested (~ dormancy release). Successful flowering can also be conditional on cool temperatures being followed by long days, high temperatures, or both (Bernier et al., 1981). The duration of cold treatment (1–16 weeks) and the temperature required for vernalization (2–18 °C) or dormancy release (2–10 °C) varies greatly within and between genera (Robertson et al., 1996) and reflect *in situ* environmental parameters. For example, seasonal thermoperiodicity is a major factor controlling growth, development and the induction and release of dormancy in many geophytes (Hartsema, 1961; Halevy, 1990). Consequently, temperature control can play a role in the production of high quality bulb/corms intended for export and for flower production during reproductive forcing (Du Toit et al., 2002).

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Abnormalities such as individual flower bud atrophy (blasting) and inflorescence abortion (blindness) are common phenomena in plants forced under sub-optimal temperature regimes (Shillo and Halevy, 1976c; Roh, 2005).

Another major environmental factor regulating flowering is photoperiod (Thomas and Vince-Prue, 1997). The induction requirement can be facultative or obligate for either short (SDs) or long days (LDs), or non-existent (day neutral, DN). Similarly, bud maturation can be impacted by photoperiod; but this requirement often differs from those day-lengths necessary for flower induction.

Failure to flower, reduced percent flowering and decreased flowering uniformity can also stem from small bulb/corm size (Roh, 2005), with minimum critical propagule size and weight varying between species (De Hertogh and Le Nard, 1993; Han, 2001). This has important industry ramifications, because relatively larger propagules sell for higher prices if they have the potential to flower, or to produce plants bearing more flowers (Wang and Breen, 1984).

Watsonia is a genus in the Iridaceae containing 52 geophytic species that is closely allied to industry-significant *Gladiolus*, *Freesia*, *Sparaxis*, *Ixia*, and *Crocus*. *Watsonia* plants typically produce attractive flowers with potential as cut flower or landscape crops. Recent work has established micropropagation protocols for some promising species Ascough et al. (2007a,b) and Thompson et al. (2005, 2010) induced dwarf phenotypes suitable for pot cultivation. However, the environmental requirements for flower and/or corm production remain undetermined. This study aimed to (1) determine the temperature at which corm dormancy is released, (2) determine the minimum corm size required for successful flowering, (3) evaluate the influence of temperature on plant development and flowering, (4) determine the critical photoperiod required for optimal flowering, and (5) investigate the impact of irradiance on the flowering of selected *Watsonia* species.

2. Materials and methods

2.1. Cultivation

Corms of *Watsonia angusta* Ker Gawl., *Watsonia borbonica* (Pourr.) Goldblatt, *Watsonia pillansii* L. Bolus and *Watsonia tabularis* J.W. Mathews & L. Bolus were sourced from local commercial growers (Cape Seed and Bulb, Stellenbosch; Nurseriwilde, Mooi River; Val-Lea Vista Nursery, Hayfields). The species represent the climatic zones prevalent in South Africa, with *W. borbonica* and *W. tabularis* experiencing winter (April–September) rainfall maxima only; and *W. angusta* and *W. pillansii* occurring in winter, year-long and summer (October–March) rainfall regions. The study was conducted at the University of KwaZulu-Natal in Pietermaritzburg, South Africa (altitude 762 m; 29°37′S:30°24′E).

Throughout 'control' or untreated plants were maintained in a greenhouse or a 25% shade house, with conditions as follows: average day/night temperatures in the greenhouse (regulated by fans, evaporative cooling and heaters to within a 25–15 °C max:min range) were 23/14 °C with an average midday maximum irradiance of 450 μmol m^{-2} s^{-1} and natural photoperiodic conditions (average ambient photoperiod = 11 h). The day/night temperatures and photoperiods experienced in the shade house were ambient (24/7 °C) for the period April–October, with an average midday maximum irradiance of 950 μmol m^{-2} s^{-1}. Temperature data were recorded using Hobo® data loggers (CW Price & Co, Midrand, South Africa), with measurements at 05:00 and 12:30 taken as 'minimum' and 'maximum', respectively. Photosynthetically active radiation (PAR) was measured using point and line quantum sensors (Apogee instrument, Inc., Logan, Utah).

All corms were planted in 12 cm diameter pots containing a sterile loam, compost and sand mix (3:1:1, v/v/v) and maintained in the shade house until treatment was initiated; usually when 1–2 leaves had emerged. Plants were irrigated weekly with a hydroponic nutrient solution (Chemicult®, Kompel, South Africa; 20 g in 10 l water, consisting of macro (6.5% N, 2.7% P, 13.0% K, 7% Ca, 2.2% Mg and 7.5% S) and micro elements (0.15% Fe, 0.024% Mn, 0.024% B, 0.005% Zn, 0.002% Cu and 0.001% Mo)), unless specified otherwise.

Since no two corms were identical, each plant was considered an experimental unit, with a minimum of 10 replicates per treatment except for the dormancy release experiment (Experiment I), where $n = 20$. Data on leaf length (measured along the leaf axis) and number, vertical inflorescence height, days to flowering (from planting to opening of the 1st floret bud), flowering percent and flower number per plant were recorded after each treatment for each experiment. To further gauge marketability, plants were subjectively assessed for sturdiness, flower presentation, physical abnormalities and chlorosis, and an aesthetically pleasing height:spread ratio (Deneke and Keever, 1992). In addition, greater plant quality was associated with increased perpendicular height from the soil level to the point of emergence of the new leaf from within the leaf sheath.

3. Experimental

3.1. I – termination of dormancy and the effect of corm size

Corms of *W. borbonica*, *W. pillansii* and *W. tabularis* were cleaned of loose soil, dried and graded according to size (≤10 g, 11–20 g, 21–40 g, 41–60 g) before being stored in paper bags at 4 °C, 10 °C or at ambient temperature (~20 °C). Corms of *W. angusta* were less than 10 g and were categorized as follows: ≤3 g, 4–5 g, 6–7 g and 8–10 g. Corms were observed weekly for morphological changes, with dormancy considered 'released' when contractile roots and the leaf sheath were emergent. Microscopic observations of sacrificed SAMs were made weekly to determine the nature of the transition from the juvenile to the competent stage.

3.2. II – flowering induction

After corms of *W. angusta*, *W. borbonica*, *W. pillansii* and *W. tabularis* had extended 1–3 leaves, they were transferred to temperature-controlled Conviron® growth cabinets (Controlled Environments Ltd., Winnipeg, Canada), set to 12/7 °C (day/night temperature) with a 16 h photoperiod and an irradiance of 150 μmol m^{-2} s^{-1} (provided by cool white fluorescent tubes (110 W, GE Healthcare, Philips, USA; 75% total wattage) and incandescent globes (100 W, Philips, USA; 25% total wattage). The red/far-red ratio of the artificial lighting was 0.68 μmol m^{-2} s^{-1}, measured using a quantum radiation sensor (Model SKP 200; Skye Instruments Ltd., Llandrindod Wells, Powys, UK). After 12 weeks, plants were returned to the shade house. At the end of the season (~ nine months) corms were harvested and data on flowering responses were recorded. Further, the number of cormels produced and their fresh masses were recorded.

In addition, corms of *W. borbonica*, *W. angusta* and *W. tabularis* were used in a reciprocal experiment to establish (i) the developmental stage (1–2 or >3 leaves extended) at which plants were sensitive to low temperature, and (ii) the duration of cold treatment required to induce flowering. This was conducted over 12 weeks in two growth chambers maintained at either 12/7 °C or 21/18 °C. Irradiance was constant at 150 μmol m^{-2} s^{-1} with a 16 h photoperiod. After six weeks plants from the 12/7 °C chamber were transferred to the 21/18 °C chamber, and vice versa. After a further six weeks, plants were returned to the greenhouse. Two 'control groups' of plants were grown at either temperature regime for the duration of the study.