Effect of Photoperiod and Shoot Decapitation on Flowering of *Leucospermum* 'Red Sunset'

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Abstract. Incandescent light night break (NB) and day continuation (DC) prevented flower formation in *Leucospermum* R.Br. cv. Red Sunset. Natural short days (NSD) during winter were inductive for flowering of intact shoots until 28 Aug. (Southern Hemisphere), but only until 24 July for decapitated shoots. Vegetative axillary buds released from correlative inhibition by shoot decapitation were less responsive to inductive short days (SD) than distal axillary buds on intact shoots. At least 42 inductive SD cycles were required for normal flowering after cessation of shoot growth. The effective length of the NB depended on the length of the NSD of winter. A 2-hr NB prevented flowering in vegetative buds released from correlative inhibition by shoot decapitation on 3 Mar., but was inadequate for axillary buds on shoots decapitated on 1 May. When the NB was begun during winter and discontinued before natural day (ND) lengths became too long in spring, the flowering time was delayed.

Vegetative and reproductive growth of *Leucospermum* cv. Red Sunset (Proteaceae) follow a seasonal sequence. Plants grow vegetatively during late spring and summer (November to March, Southern Hemisphere) and individual shoots have strong apical dominance. Reproductive development commences in autumn (April) after shoot extension growth has terminated, inflores-

cence development occurs during winter (May to September), and the flowers open in early spring (September to October). The inflorescence is a capitulum arising from an axillary bud distally situated on a shoot (Jacobs, 1985). Dormant axillary buds on actively growing shoots can be forced to break dormancy by decapitation of the terminal growing point. If decapitation occurs after shoot growth has ceased (in December to February), shoots grow from the upper axillary buds, indicating that the axillary buds have not yet been induced to flower (Jacobs, 1983).

The developing inflorescence correlatively inhibits other axillary buds from developing. The degree of inhibition depends on bud position on the shoot. The first six to 10 axillary buds

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basipetal to the developing inflorescence are only partly inhibited, develop to a size of ≈ 5 mm in diameter, and are referred to as secondary flower buds (Jacobs, 1985). Buds basipetal to these are completely inhibited and do not develop. These inhibited buds do not flower and give rise to the new cycle of shoot growth in the spring after flower harvest (Jacobs, 1983; Jacobs et al., 1984). Removal of the correlative inhibition of these vegetative buds by decapitation of the upper 5 cm of the apical shoot during April to May results in the development of an inflorescence from the uppermost axillary bud (Jacobs, 1985). Shoot decapitation during June results in fewer axillary buds forming an inflorescence and all axillary buds develop vegetatively when shoot decapitation is delayed until July to August (Jacobs, 1985). This behavior led Jacobs (1983) to conclude that photoperiod does not control flower initiation because flower initiation did not occur during long days (LD) between December and March, and the capacity of axillary buds to flower is lost during SD from July and August.

Here we report on the SD requirement for flower initiation in *Leucospermum* and explain the apparent anomaly in the loss in responsiveness of axillary buds to inductive SD after shoot decapitation during July and August.

Materials and Methods

Plant material. Plants of 'Red Sunset' *Leucospermum*, a natural hybrid probably of *L. cordifolium* (Salisb. ex Knight) Fourcade and *L. lineare* R.BR., from a commercial plantation were used in this research. These plants were 9 years old and had previously been propagated from the same clone. They were grown under natural climatic conditions near Stellenbosch, Cape Province, South Africa ($33^{\circ} 54'S$). The plants were spaced 1 m apart with 3-m rows, clean-cultivated, and were not irrigated or fertilized. The mean annual rainfall for the area is 600 to 700

mm and occurs mainly during winter. The longest day (22 Dec.) is 14.25 hr and the shortest day (21 June) is 9.53 hr.

Day continuation during winter. Natural day lengths were extended from 1800 to 0800 HR by means of two 100-W incandescent light bulbs with reflectors suspended 1 m apart, 30 cm above each plant. The light intensity was $30 \mu\text{mol} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$, 60 cm from the light source. The day continuation (DC) treatments began on 1 Mar. and were discontinued on 1 May, 29 May, 26 June, 24 July, 21 Aug., 18 Sept., 16 Oct., or 13 Nov. Two plants were used for each treatment. Suitable partitions separated plants in each treatment. Upon discontinuation of the respective DC treatments, 24 shoots in each group were marked and 12 of these were decapitated by removing the terminal 5 cm of each shoot. In the case of the treatment group in which the DC was discontinued on 1 May, 72 additional shoots were selected and 12 were decapitated on each of the following dates: 29 May, 26 June, 24 July, 21 Aug., 19 Sept., or 16 Oct. The number of shoots in each treatment group that formed an inflorescence, and the date on which inflorescences on nondecapitated shoots reached anthesis (75% of styles reflexed), were recorded.

Number of short-day cycles to flowering. Two 'Red Sunset' plants were subjected to six DC incandescent light treatments from 1800 to 0800 HR as described above. The DC treatments began on 1 Mar., were discontinued on 1 May, 15 May, 29 May, 12 June, and 26 June or continued until 10 July, when DC treatment was reintroduced to all treatments. Consequently, plants in the six treatments were exposed to 72, 56, 42, 28, 14, or 0 natural short days (NSD). In each treatment, 24 shoots (12 shoots/plant) were marked on 10 July and 12 shoots were decapitated. On 15 Nov. the number of shoots that flowered and the number of florets/inflorescence were determined.

Some 15 distal axillary buds on nondecapitated shoots were

Fig. 1. Influence of photoperiod and shoot decapitation on flowering of *Leucospermum* cv. Red Sunset. (line a) Plants were grown under day continuation (DC) from 1 Mar. until the dates indicated on the x-axis; thereafter under natural short days (NSD) of winter. Incandescent lights were on from 1800 to 0800 HR. (line b) Plants were grown as above, but shoots were decapitated and DC was discontinued on dates indicated on x-axis. (line c) Plants were grown under DC treatment until 1 May, thereafter under natural day length. Shoots were decapitated on dates indicated on x-axis.

Table 1. Number of natural short days (NSD) of winter required for flowering and the influence of shoot decapitation on flowering and flower quality of *Leucospermum* cv. Red Sunset plants.

Date of NSD treatments ^z	No. NSD cycles (days)	Flowering shoots (%)		No. florets/inflorescence ^y ± SE
		Intact	Following decapitation ^x	
DC ^w	0	0	0	---
26 June–10 July	14	0	0	---
12 June–10 July	28	0	0	---
12 May–10 July	42	67	0	170 ± 12.4
15 May–10 July	56	92	0	167 ± 6.9
1 May–10 July	72	92	0	173 ± 8.4

^zBefore and after NSD treatment, plants were under day continuation (DC) treatment, i.e., under incandescent lights from 1800 to 0800 HR.

^yDetermined on 15 Nov. Values based on 12 intact shoots/treatment.

^xDecapitated on 10 July.

^wDC treatment from 1 Mar. to 15 Nov.

Table 2. Flowering response of *Leucospermum* cv. Red Sunset to length of incandescent night break (NB) and natural day length at shoot decapitation.

Time (HR) of NB ^z	Length of NB (hr)	Flowering of decapitated shoots (%) ^y		
		Date decapitated		
		3 Mar.	2 Apr.	1 May
Control ^x	0	100	100	100
0030–0130	1	67	100	100
2400–0200	2	0	50	100
2300–0300	4	0	25	25
2200–0400	6	0	0	0
2100–0500	8	0	0	0

^zIncandescent lights from 1 Mar. to 30 Sept.

^yDetermined on 30 Sept. Values based on 12 decapitated shoots/treatment.

^xPlants were under natural short days of winter without NB treatment.

Table 3. The date of flower and days to flower from discontinuation of day continuation (DC)^z treatment until anthesis of *Leucospermum* cv. Red Sunset

Date of discontinuation of DC treatment ^y	Date of flower	Days to flower
1 May	1 Oct.	153
29 May	30 Oct.	154
26 June	26 Nov.	153
24 July	10 Dec.	136
21 Aug.	30 Dec.	131
18 Sept.	20 Jan.	124

^zIncandescent lights on from 1800 to 0800 HR.

^yHad commenced on 1 Mar.

collected every 2 weeks after 10 July from each group of plants. These axillary buds were used to follow the morphological changes taking place in the bud by scanning electron microscopy (SEM). After the bracts had been removed, buds were ethanol-dehydrated, critical-point-dried (Nell and Rasmussen, 1979), and sputter-coated with gold at 8 mA for 5 min in a Giko IB-2 ioncoater. These buds were viewed on an ISI 100 ASA Scanning Electron Microscope at an accelerating voltage of 25 kV. Micrographs were taken with a Konica FS-1 camera (55-mm lens) using Ilford HP5 (400 ASA) film.

Length of night break. Two 'Red Sunset' plants per treatment were subjected to night break (NB) treatments of various lengths from 1 Mar. to 30 Sept., when the experiment ended. NB treatments were for 1, 2, 4, 6, or 8 hr and began at 0030, 2400, 2300, 2200, or 2100 HR, respectively. Plants grown under NSD of winter with no NB served as control. On 3 Mar., 2 Apr., and 1 May, 12 shoots (six shoots/plant) in each treatment were decapitated as described. The percentage decapitated shoots that flowered was recorded on 30 Sept.

Results and Discussion

Effect of photoperiod and shoot decapitation on flowering.

Plants grown under incandescent DC throughout the winter failed to flower (Fig. 1). When DC was discontinued between 1 May and 21 Aug., nondecapitated shoots flowered. Plants under NSD of winter between these dates flowered. When DC was discontinued after 21 Aug., a rapid decrease in the flowering percentage of nondecapitated shoots occurred, indicating that the photoperiod after the date was too long for floral induction. Consequently, nondecapitated 'Red Sunset' plants had an absolute SD requirement for flower induction and initiation.

Decapitation of shoots on the date that DC was discontinued resulted in axillary buds forming inflorescences, but only when decapitation was performed on 24 July or earlier; when it was delayed, the percentage of shoots that flowered rapidly decreased. Axillary buds that were released from correlative inhibition by decapitation may have responded to wound ethylene (Napier and Jacobs, 1989). This response may have been responsible for the formation of shoots from axillary buds when the terminals were removed and the DC treatments discontinued on 18 Sept. Nondecapitated shoots gave rise to shoots when DC was discontinued on 16 Oct. only. We estimate that the day length should be shorter than 12 hr for flower induction and initiation of axillary buds on shoots, whether decapitated or not.

Shoots on plants grown under NSD conditions flowered when decapitation was performed up to 29 May (Fig. 1). When plants were decapitated at later dates, fewer flowering shoots formed. The gradual decrease in shoots forming an inflorescence during the NSD of winter caused Jacobs (1983) to conclude that photoperiod was apparently not involved. The plant responses observed during the present study show that this is clearly not the case (Fig. 1).

The early decrease in the capacity of decapitated shoots to form an inflorescence under inductive NSD possibly is related to physiological changes in the plant. Apparently, the responsiveness of inhibited axillary buds to inductive NSD decreased as the reproductive development of the distally situated axillary in florescence progresses during winter.

Number of inductive short-day cycles to flower. The minimum number of inductive SD cycles required for flowering of intact shoots was 42 (Table 1). After 42 cycles, 67% of shoots flowered, and this percentage was increased to 92% after 56 cycles. After 14 inductive SD, the dome of the apical meristem in the axillary bud was still conical (Fig. 2A). After 28 inductive SD, the apical meristem still grew (Fig. 2B) and finally became flat (Fig. 2C). After 70 days of DC, the meristem returned to the original conical shape that was associated with the vegetative condition (Fig. 2D). Apical meristem observed after 42 inductive SD were enlarged and, when these plants were returned to DC (Fig. 2E), the meristem continued reproductive development and florets were visible after 28 days of DC (Fig. 2F).

When shoots were decapitated on 10 July and placed under DC, axillary buds elongated. Correlatively inhibited axillary buds

Fig. 2. Development of the inflorescence of *Leucospermum* cv. Red Sunset (SEM, bars = 100 μ m). (A) The apical meristem remained conical after 14 inductive short-day (SD) cycles. (B) After 28 SD cycles, the apical meristem increased in diameter but remained conical. (C) After 28 SD cycles followed by day continuation (DC) treatment for 46 days, the apical meristem increased in diameter from 300 to 550 μ m and finally became flat. (D) After 28 SD cycles followed by 70 DC treatments, the apical meristem returned to its original conical shape as (A). (E) After 42 SD cycles, the apical meristem was still conical and bract primordia were forming. (F) After 42 SD cycles followed by 28 DC treatments, the floret primordia were initiated in the axils of the bracts. a = Apical meristem; b = bract; f = floret.

are thus not responsive to inductive SD conditions (Table 1). The number of florets/inflorescence did not increase when the number of inductive SD cycles were increased above 42 (Table 1).

Length of NB to prevent flowering. The length of a NB required to prevent flowering depends on the ND length (Table 2). A 1-hr NB in the middle of the natural dark period was partially effective in preventing flowering when axillary buds

were released from correlative inhibition by decapitation of the shoot on 3 Mar. However, this 1-hr NB was ineffective when shoots were decapitated in April or May, when the photoperiod was shorter. A 2-hr NB completely inhibited flowering when shoots were decapitated on 3 Mar., but was ineffective when shoots were decapitated on 1 May, when a 6-hr NB was required to prevent flowering (Table 2).

Delay in flowering time. Flowering dates of nondecapitated shoots were delayed by a delay in the onset of inductive SD cycles by DC treatment (Table 3). Plants flowered on 1 Oct. when DC was discontinued on 1 May, whereas flowering occurred on 20 Jan. when DC was discontinued on 18 Sept., some 114 days after 1 Oct. The number of days (153) from the start of inductive SD cycles to anthesis was similar irrespective of commencement between 1 May or 26 June. A progressive decrease in the number of days to anthesis occurred when DC was discontinued following 26 June (Table 3). The reduction in the time of flowering from induction to anthesis was possibly related to more rapid inflorescence development during high tem-

peratures of summer, similar to earlier findings (Jacobs and Honeyborne, 1979).

Extending the marketing season of *Leucospermum* through daylength control of flowering appears feasible.

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