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Defoliation alters spring growth flush characteristics and inhibits flowering in *Protea* cv. Carnival☆

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Abstract

Inflorescence initiation in *Protea* cv. Carnival (*P. compacta* R. Br. × *P. neriifolia* R. Br.) starts at spring budbreak, and production of involucral bracts occurs concurrently with spring flush elongation. The presence of mature leaves on an over-wintering shoot is essential for inflorescence initiation on the spring growth flush of 'Carnival' indicating that conditions prevailing during winter, whether environmental or intra-plant factors, are conducive to flowering.

Total defoliation applied 40 days before spring budbreak or earlier prevented flowering, and reduced the stem length and number of leaves on the spring growth flush. Later defoliation had a less marked effect on spring flush characteristics, and all shoots initiated flowers. Early defoliation prevented flowering either directly by a reduction in available carbohydrates or removal of photoperiod and temperature perceptive tissues, or indirectly by the resultant production of a weaker spring flush. Shoots are in the induced state and committed to flowering 6–7 weeks before inflorescence initiation begins. The induced state is retained for a period and then gradually lost.
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1. Introduction

Protea cv. Carnival (*P. compacta* R. Br. × *P. neriifolia* R. Br.) initiates flowers terminally on the spring growth flush when subtended by one or more previous flushes (Greenfield

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et al., 1994). The spring flush is preformed (Gerber et al., 2001). Production of leaf primordia for the spring flush starts during elongation of the preceding autumn flush and continues during winter, but is complete before spring budbreak. Growth of the spring flush, therefore, consists of elongation of preformed internodes, and differentiation and development of preformed leaf primordia. During elongation of the spring growth flush involucral bract primordia are formed. Shoots are, therefore, induced to produce flowers by the time of spring budbreak (Gerber et al., 2001). Inflorescence development occurs from mid-October and flowers are harvested from February to May in the southern hemisphere (Greenfield et al., 1994).

Defoliation or shading at critical times inhibits flower initiation in many plants. Shading of *Leucospermum* during summer, prior to the inductive phase, prevented flower initiation (Jacobs, 1983). In *Vaccinium ashei* (rabbiteye blueberry) (Lyrene, 1992) and *Solidago altissima* (goldenrod) (Meyer, 1998), defoliation caused a reduction in flower formation. The presence of mature leaves in mango was shown to be essential for flower induction which was suggested to involve a labile floral stimulus (Nunez-Elisea and Davenport, 1992).

Defoliation of shoots of Carnival at different times during winter and after spring budbreak was done to pinpoint the time when shoots became irreversibly induced to flower, to quantify the effect of defoliation on the characteristics of the spring flush subtending the inflorescence, and to elucidate the factors which play a role in the acquisition of the induced state.

2. Materials and methods

2.1. Plant material

Experiments were done on *Protea* cv. Carnival plants grown in a commercial plantation in the Stellenbosch district (latitude 33°15′S; longitude 19°07′E), South Africa. The climate is Mediterranean with an annual rainfall of 600–700 mm, falling mainly in winter. Summers are hot and dry. Plants were spaced 1 m in the row and 4 m between rows, clean cultivated, and were not irrigated or fertilised. Plants were managed and pruned for biennial bearing (Gerber et al., 1995).

2.2. Defoliation treatments

In mid-winter (early June) of 1997 shoots were tagged that were of similar size and consisted of three growth flushes, with the terminal flush being the autumn flush. Tagging shoots at the start of the experiment ensured that shoots used throughout the experiment had the same initial characteristics. Four-year-old plants were used, and spring budbreak occurred on 20 August 1997. Defoliation treatments were applied to individual shoots and were done on 3 June, 11 July, 29 July, 12 August, and 9 September 1997 (corresponding to 78, 40, 22 and 8 days before spring budbreak (DBSB), and the last date corresponding to 20 days after spring budbreak). The four degrees of severity of defoliation were: total defoliation, where all the leaves on the shoot were removed; severe partial defoliation,

where all the leaves were removed except those on the uppermost, autumn, flush; mild partial defoliation, where only the leaves on the uppermost, autumn, flush were removed; and no defoliation, or control, where all the leaves remained on the shoot. Leaves were cut-off with scissors at their point of inception.

With the onset of spring, vegetative growth continued on both defoliated and control shoots to produce a spring growth flush. On 11 February 1998, when flowers on control shoots were at the commercially harvestable stage, all shoots were picked and brought to the laboratory for analysis. The presence or absence of an inflorescence was recorded, the length of the spring flush measured and the number of leaves on the spring flush counted. Results are presented of the main contrast only, between total defoliation and no defoliation, or control, where the effect on flowering was distinct. The two severities of partial defoliation produced qualitative rather than quantitative responses to flowering (Gerber, 2000).

2.3. Statistical analysis

The experiment was set out as a randomised design with five single shoot replicates. Analysis of variance was performed, LSD values obtained, and orthogonal contrasts were fitted using the SAS programme (SAS Institute, 1990).

3. Results

3.1. Inflorescence initiation

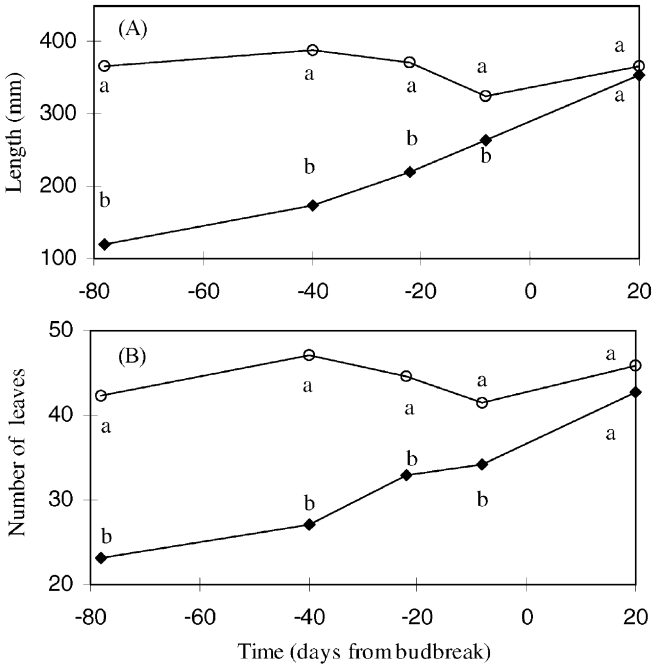
Total defoliation 40 DBSB or earlier in 1997 completely prevented inflorescence initiation (Table 1). Defoliation applied later than 40 DBSB had no effect on inflorescence initiation, and all shoots, whether defoliated or not, produced flowers.

3.2. Spring flush characteristics

The average length of the spring growth flush on non-defoliated shoots was 36.4 cm ($\pm$0.64) in 1997, with 45 ($\pm$0.9) leaves. On totally defoliated shoots the final length of the spring growth flush was greatly reduced when defoliation was applied before spring budbreak (Fig. 1A). When shoots were totally defoliated earlier than 40 DBSB in 1997 the

Table 1
Number out of five shoots which formed inflorescences after defoliation applied at different dates in 1997, compared with no defoliation, or control

Severity of defoliation	Date of defoliation (days from spring budbreak)				
	3 June (−78)	11 July (−40)	29 July (−22)	12 August (−8)	9 September (20)
Total	0/5	0/5	5/5	5/5	5/5
Control	5/5	5/5	5/5	5/5	5/5



ANOVA	A	B
Source	TRT*Time	TRT*Time
Significance	0.0001	0.0022

Contrasts	Linear	Quadratic	Linear	Quadratic
Total vs Control*Time	0.0001	0.0871	0.0001	0.5098

Fig. 1. Effect of time of defoliation of *Protea* cv. Carnival on spring flush characteristics, compared with non-defoliated shoots: (A) length of spring flush; (B) number of leaves on the spring flush. The time of defoliation is reported as the number of days from spring budbreak in 1997. Non-defoliated shoots are represented by open circles, and total defoliation by filled diamonds. Data represented are the average of five shoots per date, picked on 11 February 1998.

spring flush elongated to less than half the normal length. The effect of total defoliation on the length of the spring flush decreased linearly with time of defoliation, until shortly after spring budbreak when defoliation had no further effect.

Total defoliation in 1997 showed a linear trend with time in its effect on the number of leaves produced (Fig. 1B). The reduction was the greatest when shoots were defoliated early, and only when applied after spring budbreak did total defoliation no longer affect the number of leaves produced on the spring flush. The earliest time at which total defoliation was done (78 DBSB) reduced the number of leaves to almost half of the control value.

4. Discussion

Carnival initiates flowers terminally on the spring flush when subtended by one or more growth flushes, and rarely initiates flowers on flushes formed at other times of the year. When Carnival plants were pruned in late autumn, but early enough for a shoot growth flush to occur before winter, flowers were initiated on the spring flush formed following winter (Greenfield et al., 1994). A lack of pre-winter growth when plants were pruned later, at the start of winter, resulted in non-flowering. The presence of mature leaves are, therefore, essential for flower initiation, and these leaves must be retained on the shoot until 6–7 weeks before spring budbreak for the shoot to become induced for flower initiation to take place after spring budbreak. Conditions prevailing during winter, whether environmental or intra-plant factors, appear to be conducive to flowering.

Defoliation in Carnival only inhibited flower initiation when performed at, or earlier than 40 DBSB. We propose three possible reasons why early defoliation prevented flowering.

The relationship between assimilate availability and flowering has received much attention (Bernier, 1988). Reserve carbohydrates in permanent aerial parts of Carnival remain low throughout the year (Greenfield et al., 1995). New growth is afforded, therefore, by either provision of newly synthesised photosynthates or reserves in the current season's growth. Napier (1985) reported leaf sugar concentrations of 7% of dry mass in late winter in *Leucospermum* cv. Red Sunset, and studies on the dynamics of carbohydrate movement during the season indicate a similar pattern in protease (Hettasch, 1999). Total defoliation, therefore, removed not only the source of new photo-assimilates, but a potential reserve source as well, and this resulting decrease in available carbohydrates could be responsible for the lack of flowering in Carnival.

Alternatively, the lower carbohydrate status following early defoliation could have indirectly affected flowering, by resulting in the production of a weaker spring flush with fewer leaves. In many plants the relationship between meristem activity and floral differentiation has been investigated (Buttrose, 1970; Marcelis-van Acker, 1994; Verheij, 1996). In Carnival, the flowering spring flush had significantly more leaves than the non-flowering spring flush or other flushes (Gerber et al., 2001), although it is possible that a specific leaf number is not crucial to initiation. Rather, that a progressive increase in leaf number of successive growth flushes allows a quantitative response to inductive conditions, as seen in the grape, where the tendency to initiate a flower increased linearly with an increase in the number of preformed leaves (Buttrose, 1970).

Mature leaves must be present during winter for a Carnival shoot to initiate an inflorescence, indicating that photoperiod and/or low temperature may play a role in the acquisition of the induced state. Photoperiod does play a role in flowering of other members of Proteaceae (Malan and Jacobs, 1990; Malan and Brits, 1990), and the interaction of temperature and daylength has been investigated in *Banksia* (Rieger and Sedgley, 1996).

In conclusion, inflorescence initiation in Carnival is limited to a short period in spring, and plants flower in February–May. For inflorescence initiation to occur the presence of mature leaves is required on an over-wintering shoot of two or more growth flushes, and the leaves must remain on the shoot until about 40 DBSB to effect inflorescence initiation.

The low temperatures and short days of winter may be environmental inductive conditions for flowering, but the role of intra-plant factors which control the number of leaves and fate of the apical meristem (directly or indirectly) cannot be excluded. The induced state is gradually lost, since flowers can form on the first summer flush, but never on the second summer or autumn flushes.

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