

Post-fire Flowering Patterns in *Blandfordia nobilis* (Liliaceae)

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Abstract

Blandfordia nobilis Smith (Liliaceae) is a small herbaceous monocotyledon that resprouts from a rhizomatous corm after fire. The complex pattern of flowering shown in the five years following a fire in January 1987 was investigated for five populations near Sydney. This pattern was then related to concurrent changes in soil chemistry.

Most (60%) plants flowered in the first post-fire flowering season (November–January), but this dropped to fewer than 20% of the plants flowering by the third or fourth season. Most plants flowered only once, but almost all plants did flower. Consequently, 35% of the flowering events were by plants that flowered only within the first year. Flowering in the first season produced more flowers per plant in that season, and was also correlated with increased chance that a plant would flower again. Repeat flowering produced fewer flowers per plant in the subsequent seasons, but multiple flowering did increase the total number of flowers produced per plant. This form of pulse flowering and short secondary juvenile period after fire seems to be typical of resprouting monocotyledons in Australia, but is much less common among resprouting dicotyledons.

The pulse of flowering appears to be closely associated with changes in the soil chemistry during the post-fire period. Many of the soil attributes measured show either a characteristic decrease or increase during the 3–4 years following the fire, with a subsequent reversal in the trend. The plants thus flower prolifically during these changing soil conditions, but almost cease flowering when these changes are reversed, thereby taking advantage of soil conditions that are not available throughout most of the inter-fire period.

Introduction

Two general types of regeneration by plants after fire are usually recognised: death of all adult plants during the fire followed by regeneration solely from seeds (obligate seed regenerators); and regeneration from protected dormant vegetative buds on adult plants that survive the fire (vegetative resprouters) (Gill 1981). For those species that resprout after fire, the length of the secondary juvenile period (the time each plant takes to return to sexual reproduction after the fire) is of importance, since repeated inter-fire intervals that are shorter than this period will prevent the establishment of new individuals. The evolutionary development of the resprouting strategy is often considered to be a response to frequent fires (e.g. Keeley and Zedler 1978), and therefore the secondary juvenile period of these species is predicted to be very short. However, there are few quantitative data on the post-fire behaviour of resprouting species in Australia, and most of the available data are for dicotyledons (e.g. Pyke 1983; Auld 1986; Delfs *et al.* 1987; Zammit and Westoby 1987; Bradstock and Myerscough 1988). Among monocotyledons, only a few members of the Xanthorrhoeaceae (e.g. Gill and Ingwersen 1976; Lamont and Downes 1979) and Haemodoraceae (Lamont and Runciman 1993) have received detailed attention to date.

Fire also influences soil properties, including the chemistry, structure and hydrology (Humphreys and Craig 1981). In particular, the distribution and availability of mineral

nutrients are affected by inputs of heat and ash during and immediately after the fire (Raison 1979; Walker *et al.* 1986). The soil properties are then further modified by the changed activities of soil micro-organisms (Warcup 1981; Theodorou and Bowen 1982). These changes may also be expected to affect the regeneration responses of the plant species, in conjunction with the direct effects of fire intensity and duration on plant survival, germination and flowering.

The aim of this study was to investigate the spatial and temporal patterns of post-fire flowering and morphology in *Blandfordia nobilis* Smith (Liliaceae) over a 5 year period, and to relate these patterns to concurrent changes in soil chemistry. *Blandfordia nobilis* is a tufted herbaceous perennial monocotyledon endemic to the central coastal region of New South Wales (Porter *et al.* 1992). Plants are common in the wet sedgeland and heaths of the Sydney region, with the summer flowering period (Zimmerman and Pyke 1988a, 1988b) giving them the common name of Christmas Bells. Adult plants are usually able to survive fire, regenerating from a rhizomatous corm. Vegetative regeneration is rapid after a fire, and plants are easily located in the immediate post-fire environment. However, they are often hard to find at other times, individuals apparently becoming suppressed during the latter part of each inter-fire interval.

Materials and Methods

Five study sites were located in Garigal National Park (33°15'55" S, 150°42'30" E), about 12 km north of Sydney. The area was burnt by a fire in January 1987, with Sites 1–4 established in November 1987 (the beginning of the first potential post-fire flowering season) and Site 5 in November 1988. Sites were examined during the flowering seasons at the end of 1987–1991 inclusive.

Garigal N.P. incorporates heath and scrub on the exposed ridges and plateaus, woodland on the higher slopes and more sheltered ridges and plateaus, and open-forest on the lower slopes and gullies (Pople 1985). It is a natural watershed, with the south-facing slopes and gullies providing the wettest habitats. *Blandfordia nobilis* usually occurs on the higher sheltered slopes with an abundance of moisture. The soils are typical of those derived from Hawkesbury Sandstone, being shallow and sandy with low nutrient levels.

The five study sites were chosen to represent the range of habitats occupied by *B. nobilis* within Garigal N.P., and each contained a disjunct population of plants. All plants in each population were permanently marked with a metal tag (Sites 1–5 had 43, 52, 61, 44 and 136 plants respectively), and each plant was examined each year for its total number of flowers, average corolla length (mm), and length of the flowering stem (cm). Most plants produced only one flowering stem per season, but occasionally two were formed.

At the same time, duplicate 2 kg soil samples were collected from each site each year from the top 20 cm of the profile (excluding the A₀ horizon). They were analysed (within 4 weeks of collection) by Sydney Environmental and Soil Laboratory Pty Ltd for: pH (in 1:2 soil:water); parts per million (ppm) of exchangeable Na, K, Ca and Mg, plus their sum (TEC); ppm of total available P, Fe, NH₄, and SO₄; %meq of cation exchange capacity (CEC); and Al as % of the CEC.

Site 4 was followed only in 1987–1988 as it became overgrown during the study and the flowering pattern could not be followed thereafter. Site 5 was not examined in 1987. For the soil characteristics, NH₄ and SO₄ concentrations were not recorded in 1991.

There is potentially a huge range of flowering patterns that could be tested. Therefore, we used multivariate pattern analysis to detect general trends in the data (i.e. trends that are repeated among several of the data variables), followed by a series of univariate statistical analyses to examine these general patterns in more detail. The plant and soil data for each site in each year were analysed by canonical correspondence analysis (ter Braak 1988). This is a constrained ordination technique based on correspondence analysis that, in a joint analysis of both data sets, assesses the degree to which the plant data set and the soil data set show co-variation (ter Braak and Prentice 1988). That is, it seeks patterns among the sites and years that occur in both data sets, while ignoring patterns that are unique to either one of the data sets alone. This is thus a direct gradient analysis technique analogous to canonical correlation analysis but which avoids many of the mathematical constraints inherent in that technique (ter Braak and Prentice 1988), as these are unrealistic for most biological data sets.

Individual plant or soil characteristics that were highlighted by this multivariate analysis were then compared using analysis of variance (Wilkinson 1989), *G*-tests (Sokal and Rohlf 1981), or a generalised repeated-measures analysis for categorical data (SAS Institute 1988).

Results

The canonical correspondence analysis produces two inter-related ordination diagrams, one for each of the two data sets. The similarities among the sites and years are indicated by the spatial relationship of the points—points near each other show more similarity among themselves (based on the plant and soil characteristics) than they do to points further away. The patterns of variation in the flowering or soil characteristics are indicated by the direction and length of the arrows—the direction of each arrow indicates the direction of maximum change in that characteristic among the sites and years, and the relative lengths of the arrows indicate the relative strength of the change. For each of these diagrams, the two axes shown display 96.9% of the variation shared in common between the plant and soil data sets. In turn, these two axes from the canonical correspondence analysis account for 64.3% of the variation shown by the first two axes of the equivalent correspondence analysis of the plant data set alone. This implies that nearly two-thirds of the variation among sites and years shown by the plant data set is shared with the soil data set.

The first ordination diagram from the canonical correspondence analysis indicates that Sites 1–4 were very similar in their flowering behaviour, and Site 5 differed from the others only in having more plants present in the population (Fig. 1). However, there were large differences in flowering between the sampling years, with a trend in flowering behaviour from 1987 to 1990 and 1991 (Fig. 1). This trend is formed mainly by a decrease in the proportion of the plants that are flowering, but is also formed by a smaller decrease in the number of flowers per plant (Fig. 1). The stem and corolla lengths did not change between years.

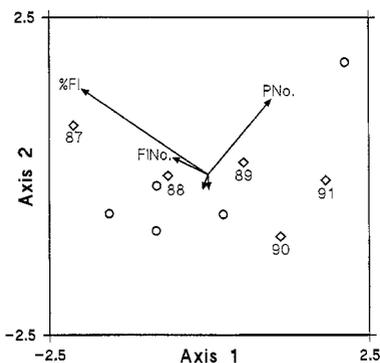


Fig. 1. Projection of the *B. nobilis* sites onto axes representing the first two axes of the biplot from the canonical correspondence analysis of the flower and soil data. The multivariate similarities among the sites and years are indicated by the spatial relationship of the symbols, while the pattern of variation in the flowering characteristics are indicated by the direction and length of the arrows. Only the centroids of the five sites (○) and the five years (◇) are shown; the numbers represent the year of sampling, and Site 5 is in the top right-hand corner of the diagram. PNo.: number of plants per site; %Fl: percentage of plants flowering; FNo.: number of flowers per plant. The arrows for stem length and corolla length are not labelled.

Generalised Wald statistics from repeated-measures contingency analyses (i.e. an analogue of repeated measures ANOVA based on a categorical data model) indicate that the change in frequency of flowering plants between years is significant at all of the sites (Site 1: $W = 38.65$, $P < 0.001$; Site 2: $W = 47.56$, $P < 0.001$; Site 3: $W = 396.77$, $P < 0.001$; Site 4: $W = 15.68$, $P < 0.001$; Site 5: $W = 78.11$, $P < 0.001$), decreasing from 50–70% of the plants in the first year after the fire to less than 20% later on (Fig. 2). Some sites (e.g. 3, 4, 5) reached a constant low level of flowering in their third flowering season while other sites (e.g. 1, 2) reached it in their fourth year (Fig. 2).

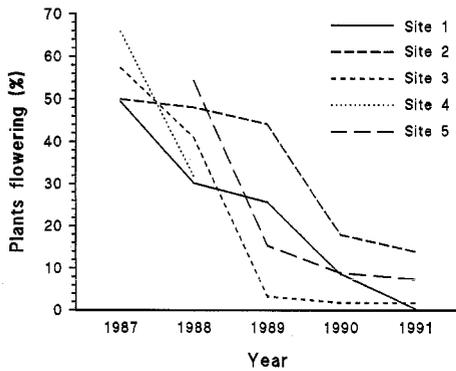


Fig. 2. Percentage of plants flowering each year at each of the five *B. nobilis* study sites.

Analyses of the flowering behaviour of individual plants through time were done only for the 155 plants at Sites 1, 2 and 3. A goodness-of-fit *G*-test indicates that the number of seasons in which each of these plants flowered does not follow the binomial expectation for a constant probability of flowering (probability of flowering = 0.25, i.e. 195 actual flowering events out of a possible 780; $G = 35.67$, $P < 0.001$). The probability of flowering thus changed for the plants during successive seasons, with a greater than expected probability of flowering at least once. Only 18 plants did not flower at all, while nearly two-thirds of the plants flowered only once during the study (Table 1). The plants approximately followed the binomial expectation for two or more seasons, with no plant flowering in all five years.

For those 137 plants that flowered, a goodness-of-fit *G*-test indicates that the number of plants flowering for the first time in each year was unequal ($G = 177.54$, $P < 0.001$), with over half of the plants flowering in the first season after the fire (1987) and none flowering for the first time in 1991 (Table 1). Of those 40 plants that flowered more than once, 43% did not flower in consecutive years, 38% flowered in two consecutive years, 15% flowered in three consecutive years, and 5% flowered in four consecutive years.

Table 1. Number of *B. nobilis* plants flowering at Sites 1, 2 and 3 (out of 155 plants) during the period 1987 to 1991 inclusive

Number of flowering seasons	Year of first flowering						Overall percentage of plants
	1987	1988	1989	1990	1991	Not flowering	
0	–	–	–	–	–	18	12
1	50	36	7	4	0	–	63
2	17	8	1	0	–	–	17
3	7	3	0	–	–	–	6
4	4	0	–	–	–	–	3
5	0	–	–	–	–	–	0
Overall percentage of plants	57	34	6	3	0	–	100

The number of flowers per flowering plant at all sites in all years varied from 1 to 21. A goodness-of-fit *G*-test indicates that the frequency distribution of flower number per plant does not follow the Poisson expectation (mean number of flowers per plant = 6.73;

$G = 75.61, P < 0.001$). The number of flowers per plant is thus not randomly distributed around the mean, with more plants than expected producing few (1–3) or many (11–21) flowers, and fewer than expected producing intermediate (7–10) numbers.

For those 137 plants that flowered at Sites 1, 2 and 3, two-factor (site, year of first flowering) analyses of variance indicate that the total number of flowers produced over the 5 years by plants first flowering in 1987 was significantly greater than for those plants first flowering in later years ($F = 6.79, P < 0.001$) (Fig. 3a). This was partly because the average number of flowers per plant in their first flowering season was significantly greater for those plants flowering for the first time in 1987 ($F = 6.772, P < 0.001$) (Fig. 3a), while the average number of flowers per flowering plant did not differ between seasons ($F = 2.07, P = 0.080$) (Fig. 3a). The difference was, however, also because those plants flowering for the first time in 1987 tended to also flower in subsequent years (see below).

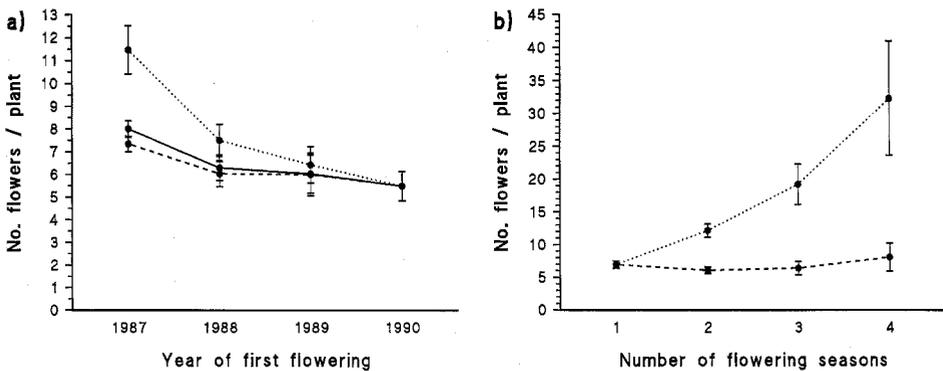


Fig. 3. Total number of flowers (summed across all flowering seasons) per *B. nobilis* plant (dotted line), average number of flowers (averaged across only those seasons in which flowering occurred) per flowering plant (dashed line) and average number of flowers per plant in their first flowering season (solid line) for plants (a) in differing years of first flowering, and (b) with differing numbers of flowering seasons. Based only on the 137 flowering plants at Sites 1, 2 and 3. Each point is the mean \pm standard error.

Two-factor (site, number of flowering seasons) analyses of variance indicate that the total number of flowers produced over the 5 years was significantly greater for those plants that flowered more often ($F = 58.22, P < 0.001$) (Fig. 3b), while the average number of flowers per flowering plant in any one season did not differ between groups ($F = 0.42, P = 0.738$) (Fig. 3b). A contingency G -test indicates that it was those plants flowering for the first time in 1987 that tended to flower more than once whereas plants first flowering in later years did not ($G = 4.03, P < 0.05$) (36% versus 20% of the relevant plants; Table 1). Flowering in the first year following the fire thus enhanced a plant's reproductive potential by an increased number of flowers in the first year and/or by an increased number of later flowering seasons.

A three-factor (plant, whether first or second of two sequential flowering seasons, whether seasons consecutive or not, time*consecutive interaction) analysis of variance indicates that a plant produced more flowers in its first flowering season than it did in its immediately subsequent flowering (time: $F = 12.86, P = 0.001$), and that this was not affected by whether the flowering seasons were consecutive or not (consecutive: $F = 0.05, P = 0.820$; time*consecutive: $F = 2.63, P = 0.110$) (Table 2). Consequently, it is the first of any pair of flowering seasons that contributes most to a plant's reproductive potential.

Table 2. Number of flowers per flowering *B. nobilis* plant in successive flowering seasons

Numbers are mean (standard error); numbers with similar letters are not significantly different as indicated by analysis of variance (based on the 137 flowering plants at Sites 1, 2 and 3)

Flowering season	Time	
	First season	Next season
Seasons consecutive	7.40 (0.69) a	6.52 (0.70) b
Seasons not consecutive	7.33 (0.80) a	5.00 (0.60) b

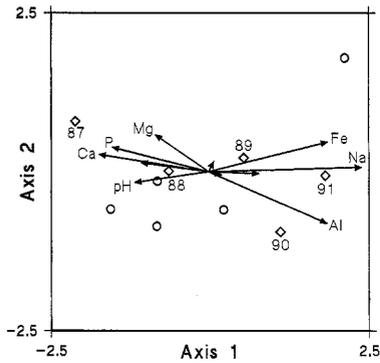


Fig. 4. Projection of the *B. nobilis* sites onto axes representing the first two axes of the biplot from the canonical correspondence analysis of the flower and soil data. The multivariate similarities among the sites and years are indicated by the spatial relationship of the symbols, while the pattern of variation of the soil characteristics are indicated by the direction and length of the arrows. Only the centroids of the five sites (\circ) and the five years (\diamond) are shown; the numbers represent the year of sampling. The arrows for K concentration, Ca/Mg ratio, cation exchange capacity, and total of exchangeable cations are not labelled.

Table 3. Results of two-factor analyses of variance of soil chemical characteristics between the five study sites over the five sampling years

Soil characteristic	Analysis of variance <i>F</i> (<i>P</i>)	
	Site	Year
pH in water	5.57 (0.011)	5.65 (0.010)
Na (ppm)	1.88 (0.185)	5.89 (0.009)
K (ppm)	5.47 (0.011)	1.53 (0.260)
Ca (ppm)	16.69 (<0.001)	5.37 (0.012)
Mg (ppm)	0.83 (0.535)	1.79 (0.200)
Ca/Mg	0.50 (0.735)	0.38 (0.819)
P (ppm)	0.99 (0.452)	4.38 (0.023)
Fe (ppm)	4.16 (0.027)	4.92 (0.016)
NH ₄ (ppm)	3.70 (0.048)	8.36 (0.006)
SO ₄ (ppm)	4.14 (0.036)	220.85 (<0.001)
Al (% of CEC)	6.00 (0.008)	102.98 (<0.001)
CEC (meq/100g)	11.57 (0.001)	11.24 (0.001)
TEC (meq/100g)	1.88 (0.184)	6.16 (0.007)

The second ordination diagram from the canonical correspondence analysis indicates that the trend in flowering behaviour from 1987 to 1990 and 1991 was associated with changes in many of the soil chemical characteristics (Fig. 4), with decreases in pH and in Ca, Mg and P concentrations, and increases in Al, Fe and Na concentrations.

Two-factor (year, site) analyses of variance indicate that several of these characteristics showed significant differences between the sample years (Table 3). Three basic trends are discernible (Fig. 5):- a decrease for 3-4 years, followed by an increase (pH; Ca, P and SO₄ concentrations; total exchangeable cations); an increase for 3-4 years, followed by a decrease (Al and Fe concentrations; cation exchange capacity); and a general increase (Na and NH₄ concentrations). These changes in soil chemistry are thus associated with the changes in flowering behaviour of the *B. nobilis* plants. The decrease in the number of flowering plants parallels the temporal changes in soil characteristics for the first 3-4 years; but after this time, the changes in soil chemistry are not associated with further changes in flowering behaviour.

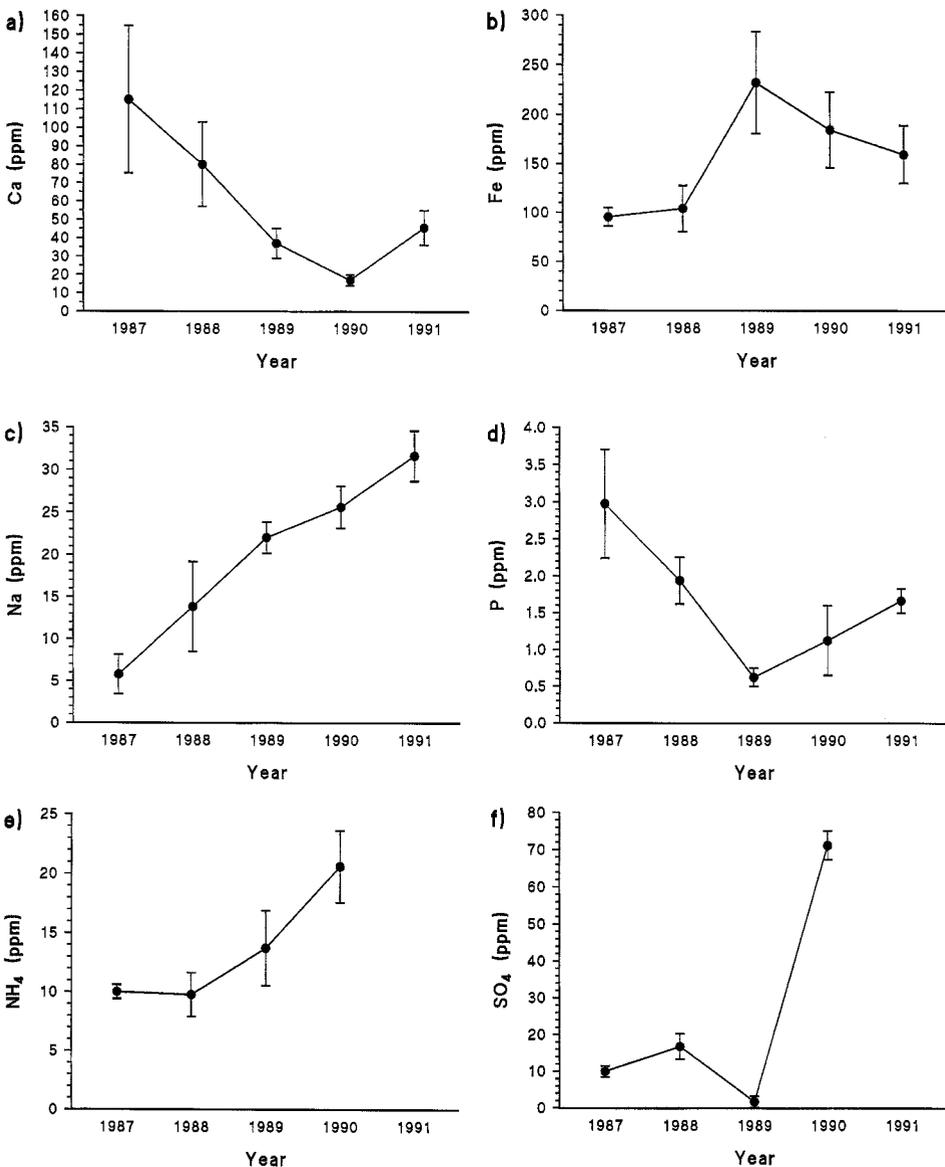


Fig. 5

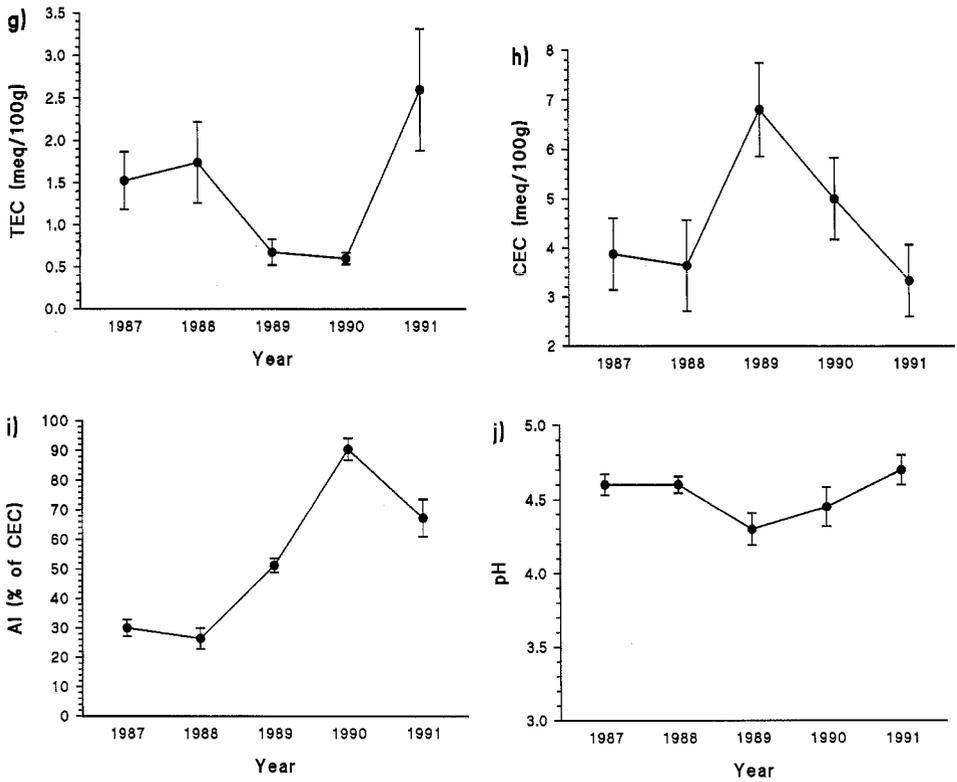


Fig. 5. Annual changes in those soil characteristics showing statistically significant differences between years at the five *B. nobilis* study sites. Each point is the mean \pm standard error.

Discussion

B. nobilis plants follow a complex pattern of flowering in the 5 years following a fire, but this pattern is consistent between spatially separated populations. Most plants flower in the first available flowering season after the fire, with the proportion of flowering plants dropping to fewer than 20% by the third or fourth season. Most plants flower only once after the fire, but almost all plants that resprout after fire do flower. Consequently, 35% of the total flowering was by plants that flowered only in 1987. Flowering in the first available post-fire season produces more flowers per plant in that season, and also increases the chance that a plant will flower again. Repeat flowering produces fewer flowers per plant in the subsequent seasons, but multiple flowering does significantly increase the total number of flowers produced per plant.

Zimmerman and Pyke (1988a), in their study of *B. nobilis* at Barren Grounds Nature Reserve south of Sydney, found that only 12–13% of the tagged plants at their two sites that flowered at the end of 1984 flowered again in 1985, which compares with the average of 18% of our plants that flowered in any two consecutive years. This suggests that our results may be generally applicable throughout the species' range. Furthermore, Zimmerman and Pyke (1988b) found that the floral nectar was less abundant but more viscous during the late 1984 flowering season compared to that of 1986, suggesting that there may also be temporal patterns in other aspects of floral behaviour that are important for successful reproduction.

Our results indicate that *B. nobilis* has an extremely short secondary juvenile period, and that the plants do most of their flowering in the first flowering season (November–January) following a summer or autumn fire. Plants burnt in winter or spring will probably not flower until the second summer. This same rapid pulse of flowering in the immediate post-fire period has previously been recorded for arborescent resprouting monocotyledons such as *Xanthorrhoea*, *Kingia* and *Dasypogon* (Specht *et al.* 1958; Gill and Ingwersen 1976; Baird 1977, 1984; Lamont and Downes 1979; van der Moezel *et al.* 1987), and for herbaceous resprouting monocotyledons such as geophytic orchids, including species of *Burnettia*, *Caladenia*, *Diuris*, *Glossodia*, *Lyperanthus* and *Prasophyllum* (Baird 1977, 1984; Barnett 1984; Bates 1984), geophytic lilies such as *Burchardia umbellata* (Baird 1977), the geophytic *Haemodorum paniculatum* and *H. spicatum* (Baird 1977), and rhizomatous herbs such as *Macropidia fuliginosa* and *Anigozanthos pulcherrimus* (Lamont and Runciman 1993). It has also been reported for orchids and lilies in South Africa (e.g. Martin 1966; Levyns 1966) and California (e.g. Stone 1951).

This strategy, however, is known in only a few resprouting dicotyledons, such as the shrubby *Angophora hispida* (Myrtaceae) in eastern Australia (Auld 1986) and *Stirlingia latifolia* (Proteaceae) in western Australia (Baird 1984), and the herbaceous *Stylidium carnosum* (Stylidiaceae) and *Eryngium pinnatifida* (Apiaceae) in western Australia (Baird 1977). However, some coastal sage shrubs in California (Keeley and Keeley 1984) and garrigue shrubs in France (Trabaud and de Chanterac 1985) also display this pulse flowering habit. Most resprouting Australian dicotyledons take longer to flower, usually not flowering until 2–3 years after a fire (Baird 1977, 1984; van der Moezel *et al.* 1987), although some species, such as *Banksia oblongifolia* (Zammit and Westoby 1987), *Lambertia formosa* (Pyke 1983) and *Telopea speciosissima* (Pyke 1983, 1987) in eastern Australia and *Isotropis cuneifolia*, *Pimelea sulphurea* and *Verticordia grandis* (van der Moezel *et al.* 1987) in western Australia, appear to reach a peak 2–3 years after fire and then decline to a variable low level.

Pulse flowering also has significant implications for the recruitment of new individuals into the *B. nobilis* populations. If most of the reproduction occurs in one (and only one) post-fire season, then it is likely that most of the seedling establishment also occurs during a restricted period (since the fruits are not retained on the adult plants), unless there is some mechanism of long-term seed dormancy. This means that most of the seedlings will be an even-aged cohort. Thus, surviving new recruits will either all be killed by the next fire or will all mature into reproductive adults, and there will be minimal recruitment between fires.

The pulse of flowering in *B. nobilis* appears to be closely associated with changes in the chemistry of the soil during the post-fire period. Many of the soil attributes measured show either a characteristic decrease or increase during the 3–4 years following the fire, with a subsequent reversal in the trend. The *B. nobilis* plants thus flower prolifically during these changing soil conditions, but almost cease flowering when these changes are reversed. The *B. nobilis* plants may thus be taking advantage of soil conditions that are not available throughout most of the inter-fire period, although there are no pre-fire soil data to verify this.

Most soil characteristics are reported to show rapid changes in the immediate post-fire period but to return to pre-fire levels within 1–2 years in many different areas of Australia (e.g. Specht *et al.* 1958; Siddiqi *et al.* 1976; Theodorou and Bowen 1982; Grove *et al.* 1986; Tomkins *et al.* 1991). Similarly, the microbiology of the soils usually returns to the pre-fire conditions within 2 years (e.g. Theodorou and Bowen 1982). Therefore, pulse flowering by any species in the first 12 months after a fire will generally be associated with changed soil conditions, while flowering at 2–3 years is unlikely to be. It is apparently only the more herbaceous plants that are immediately capable of taking advantage of this situation, both in terms of their own physiological needs for flowering and in terms of early post-fire recruitment of seedlings. However, the later flowering of the woody shrubs may be reliant on nutrient intakes during the first 1–2 years, with the nutrients directed either into necessary vegetative

growth prior to flowering or into physiological activities directly preparatory for flowering. Clearly, there is a need for manipulative experiments to test these behavioural hypotheses.

Our data indicate that the soil conditions at our study sites continued to change for 3–4 years following the fire. This continuous change after a fire appears not to have been reported before, as most studies have been of a shorter duration. However, the frequency of sampling in our study was not adequate to pick up the shorter-term changes previously reported, and would also not pick up seasonal fluctuations in any of the characteristics measured (cf. Tomkins *et al.* 1991).

The association of the behaviour of the *B. nobilis* plants with changed soil conditions may also explain the way in which the plants become vegetatively suppressed during the inter-fire intervals, in that their vegetative growth may also be tied to suitable soil conditions existing during the immediate post-fire period. However, neither of the two reproductive morphological characteristics measured showed any pattern with time since fire, nor with the soil chemical characteristics recorded.

The work reported here could be improved in a number of ways. Firstly, the establishment of explicit control samples is needed to confirm that the flowering behaviour reported here is actually a fire-induced response. The ideal arrangement would be a symmetrical repeated measures analysis of a spatially and temporally replicated BACI (Before–After, Control–Impact) design (see, for example, Green 1993), which involves sampling the plants before the fire as well as afterwards, and comparing this to plants in comparable control populations that are not burnt. Unfortunately, the major practical difficulty with this design is that locating *B. nobilis* plants in areas that have been unburnt for more than 1–2 years is almost impossible (as it is for many other herbaceous species in the Sydney region). This means that any such plants that were located would probably not represent a random sample of the available plants. Clearly, the only realistic solution is to locate plants immediately after a fire, and then to follow their fate until after the next fire (whenever that may be), thus providing data both before and after the second fire; this is a long-term project for anyone who contemplates it.

Secondly, the behaviour of the plants after replicate fires (especially in a wider geographical area) needs to be sampled in order to conclusively demonstrate the generality of the responses observed.

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