

## Research Article

# Size-Dependent Flowering in relation to Grazing in a Short-Lived Monocarpic Perennial

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In short-lived monocarpic perennials flowering probability depends on size and relative growth. Reproducing at a smaller size results in a higher prereproductive survival and shorter generation time but also may lead to lower fecundity. Conversely, reproducing at a larger size allows greater fecundity but leads to higher mortality during the prolonged vegetative period. Herbivory may influence the above described relationships via alterations in size at reproduction and survival. Here we use field data to explore in detail the reproduction of the short-lived monocarpic perennial *C. vulgare* under seasonal grazing. Vegetative plants were marked in paddocks with and without winter grazing, and their size, growth, and flowering status were recorded during a growing season in a field grazing experiment. Grazing increased both survival of vegetative plants and flowering probability, but it did not affect flowering size. The increase in flowering probability is a result of differential plant growth and size and may be related to greater resource availability, including light (necessary for flowering induction in *C. vulgare*) in grazed paddocks.

## 1. Introduction

Biennial plants have been characterised as plants that grow vegetatively in their first growing season, flower in the next, and die after flowering. However, in the field, most of them behave as short-lived monocarpic perennials [1–3]. In these species, flowering probability depends on size and relative growth just before bolting rather than on age [2, 4]. In relation to this trait, the concepts of “flowering size,” “size at flowering,” and “threshold size for flowering” have been used equivalently. The threshold size for flowering is equal to or above the physiological minimum size to produce one seed, and it is referred to as an internal plant setting that can be reflected by plant size at flowering [5].

Optimisation models for flowering have shown that the threshold size is probably the result of the interplay between size-dependent growth, which in turn determines the increase in seed production and size-dependent survival [1, 5, 6]. The optimal reproductive size is determined through the trade-off between survival and fecundity affected by the critical size of reproduction. Reproducing at a smaller size results in a higher prereproductive survival and shorter

generation time but also may lead to lower fecundity. Conversely, reproducing at a larger size allows greater fecundity but leads to higher mortality during the prolonged vegetative period [7].

In real populations, factors like pollination success and herbivory may influence the above described relationships via alterations in size at reproduction and survival. A larger critical size at flowering can be favoured by an increase in fecundity through increasingly successful pollination in larger individuals [8]. On the contrary, smaller vegetative and reproductive sizes can be favoured in grazed plants, since the probability of being consumed in palatable species increases with plant size [9]. However, for unpalatable plants like *Cirsium vulgare* [10] paddock grazing may be beneficial by reducing competition from other, palatable species [11].

*Cirsium vulgare* (Savi) Ten. is a monocarpic perennial native of Europe [12] that has size-dependent survival and flowering rates [2, 13]. Previous demographic studies have shown higher population growth of *C. vulgare* under grazing and altered plant size-dependent survival [3, 13]. Here we used field data to test the hypothesis that grazing may alter the trade-off between size-dependent survival and

size-dependent flowering probabilities. To this, we studied in detail the reproductive behaviour of *C. vulgare* plants under seasonal grazing, focusing on the influence of plant size and growth on survival and flowering probabilities.

## 2. Methods

**2.1. Study Plant and Field Experiment.** *C. vulgare* is described as a monocarpic perennial in North Europe [2] but annual genotypes were found in populations from Southern Europe [14]. *C. vulgare* has size requirements for flowering (by photoinduction) but not for vernalization [2]. Seedling emergence is gap-dependent [3, 13, 15]. *C. vulgare* does not accumulate a persistent seed bank in the soil [16]. The abundance of *C. vulgare* tends to increase with grazing intensity [17].

The seasonal grazing experiment was set up at Little Wittenham Nature Reserve in Oxfordshire, England, in 1986. As winter grazing showed greater effects on *C. vulgare* demography compared with spring and summer grazing [3], we chose the winter grazed paddocks for this study. The experiment was fully factorial with two randomized blocks assigned over 16 ( $2 \times 8$ ) 50 m  $\times$  50 m paddocks. In total, there were eight paddocks with winter grazing and eight paddocks without winter grazing (hereafter referred to as WG+ and WG–, resp.). Winter grazing ran from 1 November to 21 March. More detailed site and experiment descriptions are given in Bullock et al. [3].

**2.2. Field Measurements.** To obtain data on rosette size-dependent growth and flowering, 384 and 184 rosettes  $\geq 5$  cm in grazed (WG+) paddocks and nongrazed (WG–) paddocks, respectively, were marked and their size was measured as the broadest diameter to the nearest centimetre on 14 February 1998. The number of *C. vulgare* rosettes (conspecific neighbourhood) within an area of 30 cm radius around the focal individual was recorded. Measurements of rosette size were repeated on the first days of May (the date known to be immediately preceding bolting, Gillman et al. [13]). Rosette size in spring before bolting is the best flowering predictor measure for species with size-dependency related to photoinduction, because the final decision concerning whether or not a rosette flower is made in spring rather than in the previous autumn/winter [2]. Rosette diameter at flowering stage, the number of flowerheads produced per plant, and the number of seeds per flowerhead were recorded in 25 plants for WG+ and 17 plants for WG– in July–August of 1998. The number of seeds predated before dispersal by the moth *Eucosma cana* was also recorded in each flowerhead.

The abundance of *C. vulgare* was censused in April. In each paddock, all the rosettes in seven evenly spaced 3 m wide transects were counted. In this and all the censuses described below the 10 m strip around the perimeter of each paddock was avoided to reduce edge effects.

**2.3. Growth of Vegetative Rosettes.** Relative growth rates ( $g$ ) of rosette diameter were calculated for the period of February 1998–May 1998, following Kachi and Hirose [1] equation:

$$g = (\ln x_{t+1} - \ln x_t), \quad (1)$$

where  $x$  is the rosette diameter in time  $t$  and  $t + 1$ , with  $t$  being February 1998 and  $t + 1$  being May 1998.

**2.4. Survivorship of Vegetative Rosettes.** Survival of vegetative rosettes ( $p_v$ ) is a function of plant size and survival, expressed as a logistic regression equation:

$$p_v = \frac{e^{(\mu + \alpha x + \beta g)}}{1 + e^{(\mu + \alpha x + \beta g)}}, \quad (2)$$

where  $x$  is plant size (in cm) and  $g$  is recent growth (relative increase in size, in the period between February 1998 and May 1998). The parameter  $\mu$  is called the “intercept” and parameters  $\alpha$  and  $\beta$  are called the “regression coefficients.” Each of the regression coefficients describes the size of the contribution of that risk factor. A positive regression coefficient means that the explanatory variable increases the probability of the outcome, while a negative regression coefficient means that the variable decreases the probability of that outcome. The parameters  $\mu$ ,  $\alpha$ , and  $\beta$  are estimated by maximisation of the likelihood function  $L(\mu, \alpha, \beta)$ , yielding  $L_{\max}$ . Differences among fitted curves for  $k$  groups can be tested by calculating the  $\ln(L_{\max})$  for both the pooled data and the groups separately, with the test statistic  $\Lambda$ , which compares the goodness-of-fit for the pooled data with that of the separate groups.  $\Lambda$  follows approximately a  $\chi^2$  distribution with  $2k - 2$  degrees of freedom [2, 18]. To visualize the data set on which a curve is based, we calculated the observed probability of survival (fraction of plants that survived) for subsamples of plants in each size and growth classes.

Plant size used in this analysis was the broadest rosette diameter (cm) measured in February 1998. Survival was considered for the period of February–July/August 1998.

**2.5. Flowering.** Flowering probability ( $p_f$ ) is a function of plant size, recent growth, and number of nearest *C. vulgare* rosettes, expressed as a logistic equation [2, 18]:

$$p_f = \frac{e^{(\mu + \alpha x + \beta g + \gamma n)}}{1 + e^{(\mu + \alpha x + \beta g + \gamma n)}}, \quad (3)$$

where  $p_f$  is the flowering probability,  $x$  is plant size before bolting (the broadest rosette diameter in May 1998, in cm),  $g$  is recent growth (as defined above), and  $n$  is the number of *C. vulgare* rosettes within an area of 30 cm radius around the focal individual. Parameter values for each function and differences among fitted curves were calculated as above (survivorship of vegetative rosettes). To visualize the data set on which a curve is based, we calculated the observed probability of flowering (fraction of plants that flowered) for subsamples of plants in each size and growth classes.

Flowering plant status was recorded in July/August.

**2.6. Seed Production.** The relationship between flowerhead production ( $f$ ) and rosette size ( $x$ ) has been described as allometric,  $f = ax^c$ ; that is, the relative increase of the

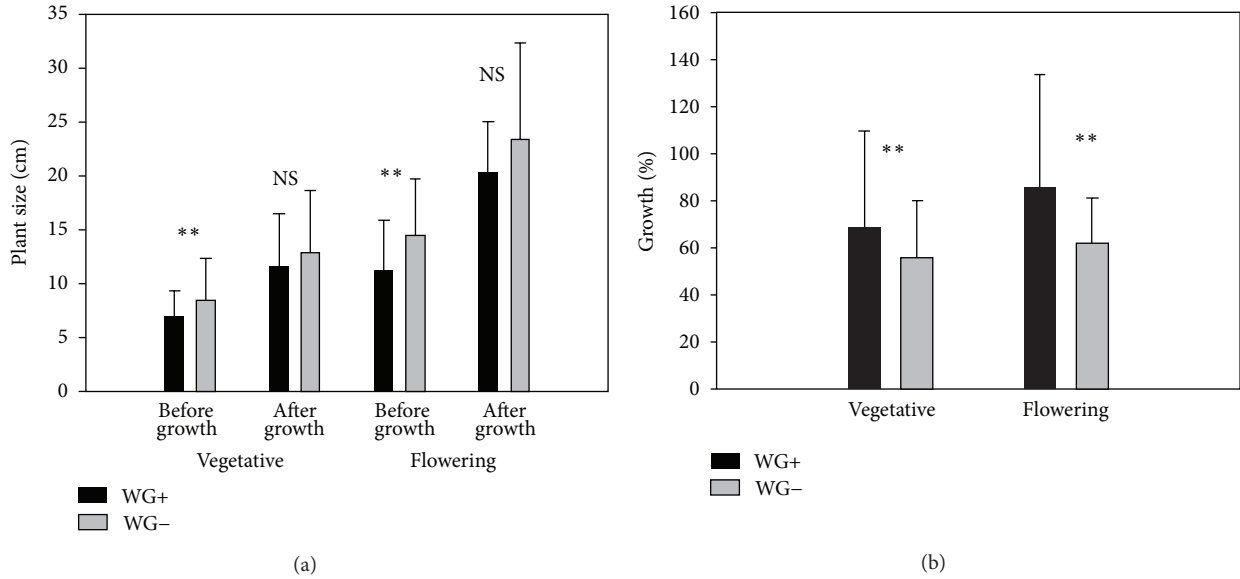


FIGURE 1: (a) Rosette size (the broadest diameter in cm) at vegetative and flowering stage before (before growth) and after (after growth) the growth period. (b) Percentage of growth for plants that remained vegetative or flowered after the sampling period in both grazing treatments. Values are means with s.d. bars. Different letters indicate significant differences between grazing treatments (paired comparisons, *t*-test,  $P < 0.01$ ). WG+ and WG-: paddocks with and without winter grazing.

reproductive output is proportional to the relative increase of the vegetative size [19, 20]. This relationship is analysed as

$$\ln(f) = \ln(a) + c \ln(x). \quad (4)$$

All statistical analyses were performed using SPSS software (Inc., Chicago, IL, V. 8.0).

*t*-tests were used to perform paired comparisons.

### 3. Results

**3.1. Growth and Survivorship of Vegetative Rosettes.** Initial plant sizes of plants that either remained vegetative or subsequently flowered were significantly smaller in paddocks with grazing than in paddocks without grazing, comparing sizes within the same vegetative or flowering plant status. However, after the growth period rosette sizes between grazing treatments were not statistically different (Figure 1(a)). Growth was significantly higher in WG+ than in WG- paddocks, comparing either vegetative or subsequently flowering plants (Figure 1(b)). However, when comparing growth between vegetative and flowering plants within the same grazing treatment, WG+ flowering plants showed higher growth than vegetative plants (*t*-test,  $P < 0.016$ ) while growth of WG- vegetative and flowering plants did not differ (*t*-test,  $P > 0.71$ ).

The number of plants was  $180.5 \pm 26.3$  in WG+ and  $48.4 \pm 12.2$  WG- (mean and s.d. for eight paddocks in each treatment). Survivorship of vegetative plants was higher in WG+ (74.62%) than in WG- (33.74%) paddocks.

The relationship between plant size and survival probability differed significantly between grazing treatments (Table 1).

TABLE 1: Results of the logistic regression using maximum likelihood estimates for the relationship between plant size, plant growth, and survival probability. WG+ = paddocks with winter grazing; WG- = paddocks without winter grazing.  $\mu$  = intercept;  $\alpha$  and  $\beta$  = regression coefficients of size and growth, respectively.

Parameter	Maximum likelihood estimates	S.E.	<i>P</i> values
WG+			
$\mu$	-1.618	1.019	0.111
$\alpha$	0.410	0.161	0.011
$\beta$	0.118	0.085	0.168
WG-			
$\mu$	1.970	0.689	0.003
$\alpha$	0.454	0.117	0.000
$\beta$	-0.606	0.120	0.000
WG+ WG- comparison			
Test statistic ( $\Lambda$ )	30.745		
<i>P</i> value	0.005		

The probability of survival increased with plant size in WG+ paddocks, while growth had a minor effect. In WG- paddocks also plant size positively influenced plant survival, while plant growth had a comparable although negative effect on it.

The observed and estimated survival probabilities for size and growth classes agreed fairly well (Table 2). Both observed and predicted survival probabilities diminish with growth in small- and medium-size classes in WG- paddocks (Table 2).

TABLE 2: Observed survival probability for different size and growth classes in both grazing treatments. In parenthesis there is the predicted probability (maximum likelihood estimate). Size: the broadest rosette diameter (cm) in February 1998. Growth: relative increase in size, in the period between February 1998 and May 1998. “—” indicates that no plant within the respective size and growth range was observed.

(a)			
Winter grazing +			
Growth (%)	Size (cm)		
	5–10	11–20	21–30
0–50	0.78 (1.00)	1.00 (1.00)	1.00 (1.00)
51–100	0.87 (1.00)	1.00 (1.00)	—
101–200	1.00 (1.00)	1.00 (1.00)	1.00 (1.00)
201–400	1.00 (1.00)	1.00 (1.00)	1.00 (1.00)
(b)			
Winter grazing –			
Growth (%)	Size (cm)		
	5–10	11–20	21–30
0–50	0.99 (1.00)	1.00 (1.00)	—
51–100	0.64 (0.94)	0.96 (1.00)	1.00 (1.00)
101–200	0.00 (0.00)	0.37 (0.45)	1.00 (1.00)
201–330	—	0.17 (0.00)	—

3.2. *Flowering Probability.* Flowering was increased in grazed paddocks. Of the total marked plants, 29.35% flowered in WG+ and 16.4% in WG– paddocks. The minimum size immediately before bolting of a rosette that flowered afterwards was 10 cm in WG+ and 12 cm in WG– paddocks. However, sizes of rosettes that subsequently flowered were not statistically different between grazing treatments (Figure 1(a)).

The relationship between plant size measured before bolting, plant growth, and flowering probability differed significantly between grazing treatments (Table 3). The probability of flowering increased with plant size, plant growth, and the number of conspecific neighbours in WG+ paddocks. In contrast, plant size had a low effect, growth had a more appreciable effect, and conspecific neighbourhood had no effect (or even a small negative effect) on flowering probability in WG– paddocks. The estimates from the logistic regression described fairly well the observed flowering probabilities of different size and growth classes. Plants increased their flowering probability with growth even in the small-size class in WG+ paddocks. Higher percentage of growth in WG– paddocks did not increase the flowering probability in the smaller plants.

However, when analysing the ratio of the flowering probabilities for the small- (5–10 cm) and medium-size (11–20 cm) plants without taking growth into account, the ratio for WG+ was 0.04 (0.028 and 0.73 for small- and medium-size plants, resp.), and the ratio for WG– was the same, 0.04 (0.016 and 0.42 for small- and medium-size plants, resp.) (Table 4). Thus, the proportions of small- and medium-size plants that flowered in each grazing treatment were equal.

TABLE 3: Results of the logistic regression using maximum likelihood estimates for the relationship between plant size, plant growth, number of neighbours in an area of 30 cm radius, and flowering probability. WG+ = paddocks with winter grazing; WG– = paddocks without winter grazing.  $\mu$  = intercept;  $\alpha$ ,  $\beta$ , and  $\gamma$  = regression coefficients of size, growth, and number of neighbours, respectively.

Parameter	Maximum likelihood estimates	S.E.	P values
WG+			
$\mu$	–5.117	0.791	0.000
$\alpha$	0.405	0.092	0.000
$\beta$	0.152	0.060	0.011
$\gamma$	0.395	0.129	0.001
WG–			
$\mu$	–4.418	0.759	0.000
$\alpha$	0.187	0.079	0.016
$\beta$	0.317	0.118	0.008
$\gamma$	–0.031	0.291	0.914
WG+ WG– comparison			
Test statistic ( $\Lambda$ )	8.758		
P value	0.005		

TABLE 4: Observed flowering probability for different size and growth classes in both grazing treatments. In parenthesis there is the predicted probability (maximum likelihood estimate). Size: the broadest rosette diameter (cm) in May 1998, before bolting. Growth: relative increase in size, in the period between February 1998 and May 1998. “—” indicates that no plant within the respective size and growth range was observed.

(a)			
Winter grazing +			
Growth (%)	Size (cm)		
	5–10	11–20	21–33
0–50	0.13 (0.06)	0.80 (0.40)	1.00 (1.00)
51–100	0.40 (0.19)	0.91 (1.00)	—
101–200	0.54 (0.67)	1.00 (1.00)	1.00 (1.00)
201–400	1.00 (1.00)	—	1.00 (1.00)
(b)			
Winter grazing –			
Growth (%)	Size (cm)		
	5–10	11–20	21–33
0–50	0.05 (0.00)	0.56 (0.00)	—
51–100	0.32 (0.00)	0.79 (0.68)	0.95 (1.00)
101–200	—	1.00 (1.00)	0.98 (1.00)
201–330	—	1.00 (1.00)	—

3.3. *Seed Production.* There was an allometric relationship between plant size (rosette diameter) and number of flowerheads produced per plant, described as follows.

$$\ln N \text{ flowerheads} = 3.082 \ln \text{Diameter} - 8.737 \quad (r = 0.79, P < 0.001, P \text{ constant} < 0.001, n = 25) \text{ for WG+};$$

$\ln N$  flowerheads = 4.052  $\ln$  Diameter – 12.007 ( $r = 0.89$ ,  $P < 0.001$ ,  $P$  constant  $< 0.001$ ,  $n = 17$ ) for WG–.

The slope was significantly higher in WG– than in WG+ paddocks ( $t$ -test,  $P < 0.001$ ); that is, increasing size is reflected in a higher number of flowerheads per plant in paddocks without grazing treatment. However, the number of flowerheads per plant was not statistically different between grazing treatments ( $21.5 \pm 16.88$  in WG+ paddocks and  $19.811 \pm 15.89$  in WG– paddocks, mean  $\pm$  s.d.) ( $t$ -test,  $P > 0.05$ ). The average production of undamaged, viable seeds per flowerhead was not statistically different between grazing treatments ( $117.16 \pm 47.94$  in WG+ and  $97.53 \pm 14.64$  in WG–,  $t$ -test  $P > 0.05$ ). The percentage of seeds predated before dispersal was 57 and 64 for WG+ and WG–, respectively.

#### 4. Discussion

It has been postulated that, in short-lived monocarpic perennial species like *C. vulgare*, flowering probability increases with size and relative growth just before bolting [2, 4, 21]. General results from this study agree with this postulate. However, when we explored the effects of grazing in detail we found differential responses in flowering behaviour and relevant traits like size-dependent survival and growth.

Winter grazing increased both survival of vegetative plants and flowering probability. Survival of vegetative plants was positively influenced by plant size in paddocks with and without winter grazing, but it was negatively affected by recent growth in paddocks without winter grazing. Increasing growth has been associated with an increase in plant survival in monocarpic perennial plants [2, 18]. However, it has been postulated that fast growth may be negative for survival of smaller individuals, since allocation to growth, presumably at the expense of storage and resistance, leads to higher mortality by an increase in competition [22]. In the grazed paddocks, however, competition by resources may be lower than in ungrazed paddocks. It is well known that grazing increases resources for plants, like nutrients and light [23]. In the experimental plots, soil nitrogen content was greater [15] and the percentage of canopy cover was lower allowing for greater light availability [3] in the grazed paddocks compared with the ungrazed ones. Forcella and Wood [11] effectively found that sheep grazing reduced interspecific competition from neighbouring plants and increased *C. vulgare* seedling survival. Thus, fast growth of plants of small and medium size in winter grazed paddocks would not lead to an increase in mortality. Higher vegetative survival of plants under grazing, especially of smaller ones, has also been found in a previous study on *C. vulgare* conducted in the same experimental plots [3].

Although both plant size and recent growth increased flowering probability, size had a greater effect in winter grazed paddocks while growth had a higher effect in paddocks without winter grazing. Plants in paddocks without winter grazing probably experience more competition from nonconsumed palatable species and, thus, once they have survived the critical small sizes, growing fast to escape competition may signify a greater contribution to flowering than size

itself. DiTomaso et al. [24], in a shadowing experiment, found that decreasing the availability of light to yellow starthistle (*Centaurea solstitialis*) plants caused a reduction in root productivity, although aboveground biomass and seedhead numbers for yellow starthistle did not differ between shadow treatments. Although in our field experiment the root size of *C. vulgare* plants was not measured, there is the possibility that increased competition in paddocks without winter grazing, even if it could result in a decreasing of root storage, would not be influencing growing and flowering the next season.

Conspecific neighbourhood also was positively related with flowering probability in winter grazed paddocks, while it had no effect in paddocks without winter grazing. The positive effect of conspecific neighbourhood may be in fact a surrogate effect of the greater resource availability in grazed paddocks already mentioned, reflected in turn in an increased flowering probability. Light availability is an especially important environmental factor for *C. vulgare*, since it has flowering dependent on photoinduction [2]. Thus, the presence of other *C. vulgare* plants does not necessarily increase competition for a particular plant, since resources are presumably nonlimiting in these grazed paddocks. Conspecific neighbourhood did not also show effects on *Cirsium vulgare* flowering in undisturbed old fields in Canada [25].

In this study, although a higher survival of smaller- and medium-sized plants was found in grazed paddocks, no effect on reduction of flowering size was detected. Although at the beginning of the growing season plant size was significantly lower in paddocks with winter grazing, after the growing period (immediately before bolting) both vegetative and flowering plant size was similar between grazing treatments. Thus, although observed frequencies of flowering plants showed higher flowering probabilities for smaller plants in winter grazed paddocks, this did not result in a smaller final size of flowering plants in these paddocks, due to the effects of a greater growth compared with ungrazed paddocks. Moreover, the positive effect of plant size in flowering probability was more marked in winter grazed paddocks. In the previous grazing field experiment conducted in populations of *C. vulgare* mentioned above [3], although winter grazing increased survival of smaller plants, still there was a minimum rosette size threshold for flowering above which flowering probability increased with size.

The number of flowerheads increased allometrically with plant size, and this effect was more marked in paddocks without winter grazing. Reproductive output always increases with plant size in monocarpic species [22]. However, winter grazing did not affect the number of flowerheads produced per plant. Thus, no compensation effect was found for any possible damage to floral bud already formed by the final part of the winter grazing season. Compensatory production of extra floral buds is a common response of short-lived monocarpic plants to injuries caused by disturbance or grazing [26]. A similar number of flowerheads in grazing treatments was also reported by Bullock et al. [3], in the previously cited study, although these authors reported a decrease in the final number of flowerheads per plant in winter grazing treatments as a consequence of an increase

in flowering of smaller plants that in turn produced fewer flowerheads. As pointed out above, this study did not show a decrease of size of flowering plants with winter grazing treatment. As also the number of seeds per flowerhead did not differ between grazing treatments and predispersal seed predation was low and similar in both grazing treatments, no effect of winter grazing on net reproductive output other than increasing the number of flowering plants was detected in this study.

## 5. Conclusions

In conclusion, this work showed that in the *C. vulgare* populations studied during the 1998 growing season winter grazing increased the flowering probability although it did not affect flowering size. This increase in flowering probability is a result of differential plant growth and size and may be related to greater resource availability, including light (necessary for flowering induction in *C. vulgare*) in winter grazed paddocks. Positive effects of grazing in populations of *C. vulgare* may then be more related to greater availability of microsites for germination and greater resources availability which in turn increases survival of vegetative plants and flowering probability than with more specific reproductive effects.

## Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

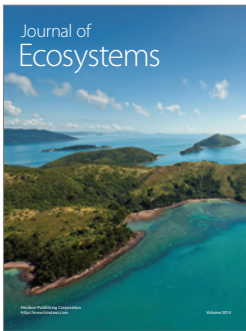
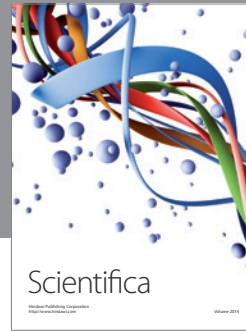
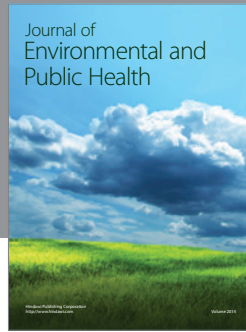
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