



Extreme variation in the reproductive phenology of the weed *Ruellia nudiflora*

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Summary

Temporal variation in morphological and life-history traits is directly linked to phenotypic plasticity in perennial plants. Phenotypic plasticity in reproductive phenology determines colonisation ability and population persistence in invasive weeds. We describe the reproductive phenology of *Ruellia nudiflora* (a cleistogamous weed) and assess the plasticity of its response to between-year environmental variation in two contrasting light environments. We recorded the flower and fruit production of focal plants under two experimental levels of light intensity (open vs. shaded) over two years. Our results suggest that light differentially affects the phenology of reproductive structures, but not between-year variation. Specifically, individual production of chasmogamous structures (flowers and fruit) ended earlier under shaded conditions than in the open, whilst production of cleistogamous fruits was not

affected. At the population level, there was between-year variation in the phenology of chasmogamous structures, which were bimodal and unimodal in the first and second year respectively. At the individual level, we found very low repeatability, suggesting high levels of phenotypic plasticity. Temporal variation in rainfall did not explain phenological variation. Although shade did not affect between-year variation, it produced a briefer period of production of chasmogamous structures. This effect of shade may have some consequences for the genetic background of *R. nudiflora*'s progeny, because only chasmogamous flowers can be out-crossed, and this therefore might be an important factor to consider when designing management strategies.

Keywords: cleistogamy, fruit phenology, invasive plants, mixed mating system, phenotypic plasticity, repeatability, Yucatan.

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Introduction

The reproductive phenology of invasive plants has long been a subject of interest for weed researchers (Young *et al.*, 1970; reviewed by Ghersa & Holt, 1995). The phenology of reproductive structures largely determines potential mate availability (Augspurger, 1981), utilisation of seasonally available resources (Galen &

Staton, 1991) and the impact of some biotic interactions such as pollination and predispersal seed predation on sexual reproduction (Elzinga *et al.*, 2007). Variation in the timing of flowering has been observed in several native and invasive plant species (e.g. Primack, 1980; Botto & Coluccio, 2007; Munguía-Rosas *et al.*, 2012). This variation is typically correlated with plant reproductive success and therefore has an

important selective value (Munguía-Rosas *et al.*, 2011). Variable reproductive phenology can have a positive effect on plant population persistence, especially under highly unpredictable environmental conditions (Primmack, 1980; Bishop & Schemske, 1998; Wolkovich & Cleland, 2011). Also, the ability of invasive plants to rapidly adjust their reproductive schedule to novel environments is crucial because, during the colonisation process, reproduction can be seriously compromised if the conditions for reproduction are not suitable in the new environment (Barrett & Husband, 1990; Griffith & Watson, 2006; Godoy *et al.*, 2009). Previous studies have shown that observed environmentally induced latitudinal variation in the reproductive phenology of some invasive plants may facilitate the expansion of their distribution range (e.g. Kollmann & Bañuelos, 2004). Other researchers have identified a positive correlation between early flowering and local plant abundance, and between reproductive season length and the geographical distribution range, implying a strong link between reproductive phenology and invasiveness (Lloret *et al.*, 2005; Hulme, 2011).

It is known that the reproductive phenology of some alien plants species may exhibit a rapid and genetically based adaptive response to novel environments following their introduction (Atlan *et al.*, 2009; Keller *et al.*, 2009). On the other hand, there are studies suggesting that phenotypic plasticity may be a more important facilitator of colonisation than genetic adaptation in some invasive plant species (Richards *et al.*, 2006; Richardson & Pyšek, 2006; Barrett *et al.*, 2008). Whether genetically based or a plastic response, the point is that in unpredictable environments, elevated phenotypic variance in traits closely associated with fitness, such as phenology, can be seen as a bet-hedging strategy if the variation reduces the inter-generational variation in mean fitness and increases long-term fitness (Simons & Johnston, 1997).

Characterising the phenology variation of invasive plants may improve our understanding of their invasiveness, habitat requirements and their interaction with the biotic and abiotic environment (Andrew & Ustin, 2009). Invasive weed management must take phenological variation into account, because phenology influences the effectiveness of both monitoring and control (Ghersa & Holt, 1995; Young *et al.*, 1998; Andrew & Ustin, 2008). Most field research on variation in the reproductive phenology of invasive plants has focused on spatial variation (e.g. Kollmann & Bañuelos, 2004; Andrew & Ustin, 2009; Molina-Montenegro & Naya, 2012) and less attention has been paid to temporal variation (e.g. Seghieri & Simier, 2002). In contrast to spatial variation (where plastic and genetically based variations are confounded), temporal variation in

phenology is directly linked to phenotypic plasticity, which has great relevance for population persistence in invaded habitats (Wolkovich & Cleland, 2011). Although phenotypic plasticity has several advantages for invasive plants, it also known that plasticity is costly to plant fitness (Dewitt *et al.*, 1998; Auld *et al.*, 2007). Some research has addressed the role of internal constraints on phenotypic plasticity (reviewed by Auld *et al.*, 2007), but far less attention has been paid to how external ecological factors limit phenotypic plasticity (Valladares *et al.*, 2007). Phenotypic plasticity occurs within an ecological context where plants are exposed to a variety of environmental factors; thus, plants under stressful conditions may be limited in their plastic response to other environmental factors. To our knowledge, there has been no study of the ecological limits of plasticity in invasive weeds.

Ruellia nudiflora (Engelm. & A. Gray) Urb. is a perennial weed native to Texas (Turner, 1991), which currently has a widespread distribution in Mexico, Central America and the Caribbean (Long, 1977; Daniel, 1997; Campos-Ríos & Chiang, 2006). In the Yucatan Peninsula and some other regions of Mesoamerica, *R. nudiflora* is becoming increasingly problematic, because it produces large, dense mono-specific patches along roadsides, in urban gardens and, to a lesser extent, in agricultural fields and disturbed forest (MA Munguía-Rosas, unpubl. obs.). *Ruellia nudiflora* is a cleistogamous species, meaning that individual plants produce both chasmogamous (open and potentially cross-pollinated; hereafter CH) and cleistogamous (closed, obligately self-pollinated; hereafter CL) flowers (dimorphic cleistogamy *sensu* Culley & Klooster, 2007). Cleistogamous plants are typically plastic in their production of floral types; that is, these plants usually produce more CH flowers under optimal conditions and more CL flowers under suboptimal conditions (Campbell *et al.*, 1983; Culley & Klooster, 2007). As the reproductive system of several invasive plant species (Campbell *et al.*, 1983; Meyer & Lavergne, 2004; Cheplick, 2005, 2006), it has been suggested that cleistogamy may improve their colonising ability (Cheplick, 2005, 2006). Thus, cleistogamy is expected to be highly advantageous for invasive plants because it both maintains fitness in suboptimal environments via CL flowers and opportunistically maximises fitness under favourable conditions via CH flowers.

In this study, we describe the reproductive phenology (i.e. phenology of CH and CL flowers and fruit) of *R. nudiflora* under two experimental levels of light availability (ambient light vs. a reduction of 50%) over 2 years. These experimental light conditions simulate two contrasting habitats where *R. nudiflora* occurs: open spaces and the understory of disturbed forest

(Munguía-Rosas *et al.*, 2012). We are particularly interested in the influence of the light environment on between-year phenotypic variation in reproductive phenology. As shaded habitats are considered suboptimal for *R. nudiflora* (Cervera & Parra-Tabla, 2009; Munguía-Rosas *et al.*, 2012), we expect shading to act as an ecological constraint on between-year phenotypic variation in the phenology of *R. nudiflora*, that is, we expect lower between-year variability under shaded conditions. To address between-year variation at the individual level, we used repeatability (defined as the total variation that is reproducible among repeated measures of the same plant; Nakagawa & Schielzeth, 2010). We predict lower repeatability under shaded conditions than in open spaces. The 2 years of study were different in terms of rainfall (16% difference); therefore, we also assessed whether rainfall influences phenological variation in the study species.

Materials and methods

Study area and plant species

The study site is in the locality of Molas, municipality of Merida in north-central Yucatan, Mexico (20°49'51" N, 89°36'44" W, 10 m a.s.l.). The climate at this site is warm subhumid with summer rains. Mean annual rainfall is 850 mm, and temperature is 26.2°C (Chico-Ponce & León, 1999). Vegetation is a heavily disturbed tropical dry forest mixed with crop lands (mainly citrus). The prevalent mosaic of disturbed natural vegetation and anthropogenic habitats (crop lands and rural towns) produces a wide variety of light environments for *R. nudiflora*, with the extremes represented by open spaces and the understory of disturbed forest (c. 50% less light relative to open spaces). The landscape configuration of the study area is typical of many other areas in lowland Mesoamerica colonised by *R. nudiflora* (MA Munguía-Rosas, unpubl. obs.). The 2 years of the study (2010 & 2011), the plants received contrasting rainfall, with about 16% less rain in 2011 (723 mm) than in 2010 (862 mm).

Ruellia nudiflora (Acanthaceae) is a non-native perennial herb with an extended distribution in Mexico and other countries in Central America (Campos-Ríos & Chiang, 2006). *Ruellia nudiflora* was probably introduced by humans as an ornamental species, as occurred with other exotic Acanthaceae species in the region (Meyer & Lavergne, 2004). *Ruellia nudiflora* is becoming one of the most common weed species in urban gardens, agricultural fields and disturbed forest in the Yucatan Peninsula and many other regions in Mesoamerica. Under field conditions, *R. nudiflora* reproduces by seed; the fruit are capsules and seeds are

dispersed ballistically (Standley *et al.*, 1974). This weed species has a dimorphic cleistogamous reproductive system (*sensu* Culley & Klooster, 2007): CL flowers are reduced in size, corollas do not open, and they are obligately self-pollinated, whilst CH flowers are larger, do open and can be out-crossed (Abdala-Roberts *et al.*, 2009). Although CH flowers are self-compatible, self-pollinated CH flowers have a far lower probability of setting fruit than out-crossed flowers (Abdala-Roberts *et al.*, 2012). Vegetative reproduction is extremely rare in natural populations. Clonal reproduction by layering in *R. nudiflora* is possible, but is unlikely without human intervention. Pollinators are generalist bees (*Apis mellifera*, *Trigona fulviventris*) and butterflies (*Microtia elva*), both abundant in the study area.

Experimental design

In early April 2010, we randomly placed 11 plots (2 × 2 m) throughout an area of c. 2 ha. Inside the plots, we tagged all the plants that did not have reproductive structures but only a few leaves at the time. We divided each plot into two 2 × 1 m subplots, one of which was shaded with nylon mesh suspended 90 cm above the forest floor and supported by four thin wood poles (2 cm diameter); this mesh intercepted about 50% of ambient photosynthetic photon flux density. To avoid shading contiguous subplots, shaded subplots were oriented from east to west. The use of this mesh does not disturb flower visitor or seed predator behaviour, and the light environment prevailing under the mesh is similar to what *R. nudiflora* experiences in the understory of a heavily disturbed forest (Munguía-Rosas *et al.*, 2012). At the beginning of the study, there were 5–14 plants tagged per subplot. New *R. nudiflora* recruits and other plants that germinated during the study were removed. In total, 214 plants were initially tagged: 117 in shaded subplots and 97 in open subplots.

Data collection

We counted all open CH flowers, CH fruit and CL fruit on the tagged plants two to four times per month during the growing season (from early April to late December) for 2 years (2010, 2011). We did not count CL flowers because, with our observation schedule, it was not possible to distinguish early CH floral buds from fully developed CL flowers. CH and CL fruit were easily differentiated because CL fruits are smaller and, in contrast to CL fruit, CH fruit usually bears the remnants of the style. For the three reproductive structures (CH flowers, CH fruit and CL fruit), we recorded the date of the onset of production (Julian calendar;

January 1st = day 1) when we detected reproductive structures for first time and the end of production (last time we saw the reproductive structure) on a per-plant basis. Daily rainfall data were obtained from the closest weather station (Merida City).

Data analysis

We assessed the effect of light availability and between-year variation on the phenology (onset and end of production) of CH flowers, CH fruit and CL fruit. Also, we assessed the consistency of the effect of light availability on phenology for the 2 years (light availability \times year interaction). We analysed this data using generalised mixed-effects models with a gamma error distribution and reciprocal link function (Crawley, 2002, 2007). In all cases, the response variable was either the onset or end of production, each analysed as Julian days; therefore, we fitted two models per reproductive structure (CH flowers, CH fruit, CL fruit), one per response variable. In all models, light availability and year, as well as their interaction, were considered fixed effects. The hierarchical organisation of plots, subplots and plants was included as a random effect to account for any spatial and temporal correlation of data. Analyses were performed with the `glmmPQL` function from the `MASS` library for R 2.14.1 software (R Development Core Team, 2011), which fits generalised mixed-effects models using the penalised quasi-likelihood method (Venables & Ripley, 2002). We used a simple main effects analysis to assess any differences between light levels in a given year (Woodward & Bonette, 1991).

To assess between-year variation in phenology at the individual level, we calculated the repeatability of the onset and end of production for CH flowers, CH fruit and CL fruit for each light level. Repeatability expresses the total variation that is reproducible among repeated measures of the same subject (reviewed by Nakagawa & Schielzeth, 2010). We calculated the adjusted repeatability with the linear mixed-effects model (LMM)-based method and the restricted maximum likelihood estimation (REML) method recently outlined by Nakagawa and Schielzeth (2010). Linear mixed-effects model-based methods estimate the variance of the individual random effect (σ_x^2) and the variance of the random error (σ_e^2) from a mixed-effects model. Linear mixed-effects model-based repeatability (RM) is then calculated as:

$$RM = \frac{\sigma_x^2}{\sigma_x^2 + \sigma_e^2} \quad (1)$$

RM was adjusted by excluding the effect of the split-plot design from the variance components [see Nakagawa

and Schielzeth (2010) for details]. Repeatability significance was assessed with a 95% confidence interval, calculated with a parametric bootstrap using 1000 permutations run in the `rpt.remlLMM.adj` function from the package `rptR` (Nakagawa & Schielzeth, 2010) for R 2.14.1 software (R Development Core Team, 2011). The normal distribution of the residuals suggests an acceptable fit to the data; in fact, this fit was much better than any other distribution family currently implemented in the `rptR` package (Poisson and binomial). Phenotypic flexibility can be intuitively inferred from repeatability (i.e. plasticity = 1-RM; Nakagawa & Schielzeth, 2010).

We calculated the proportion of plants in the population bearing CH flowers, CH fruit or CL fruit per sampling date under the two light conditions (open vs. shaded subplots) for each year (2010, 2011). We used the proportion rather than the number of plants because some died over the course of the study. We assessed the relationship between the proportion of plants producing the three reproductive structures mentioned above and the daily mean rainfall during 10 days before each phenology sampling day using linear regression models. The light level and its interaction with rainfall were included in the model. Five models were fitted in total, one for each year (2010 and 2011) and response variable (proportion of plants bearing CH flowers, CH fruit or CH fruit). Proportions were transformed (arsine of the square root) prior analysis to improve normality. In our experience, 10 days is sufficient time for the plants to respond to rainfall and produce flowers and fruit.

Results

During 2010, at the population level, the proportion of plants with CH flowers was bimodal in the open and shaded subplots (Fig. 1A and B). The first flowering pulse was observed in mid-May (around Julian day 163 of the year) and the second in mid-August (around Julian day 226). The two pulses were largely matched, in terms of date, between open and shaded subplots (Fig. 1A and B). Interestingly, in 2010, the second pulse of CH flowers lasted longer than the first pulse under both light intensity levels (Fig. 1A and B). The proportion of plants bearing CH fruit had the same phenology pattern we observed for CH flowers (Fig. 1A and B). The proportion of plants bearing CL fruit varied slightly throughout the year, but with an abrupt, short pause in mid-August (around Julian day 230), a pause that coincided with the second, larger pulse of CH flower and fruit production that year (Fig. 1A and B). The phenology of CL fruit was very similar in the open and shaded subplots (Fig. 1A and B).

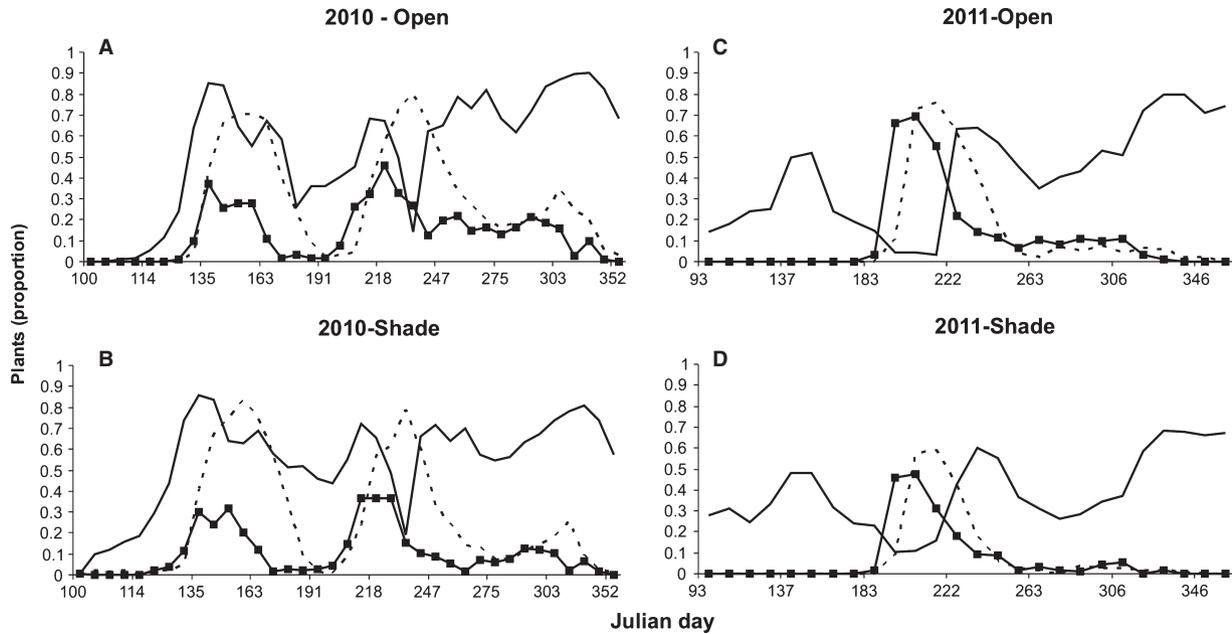


Fig. 1 Reproductive phenology of the weed *Ruellia nudiflora*. Phenology (proportion of plants bearing a given structure) of chasmogamous flowers (flowers—■—), chasmogamous fruit (CH fruit—---) and cleistogamous fruit (CL fruit—) is shown against the Julian day (January 1st = 1). Plant phenology was followed for 2 years: 2010 (A, B) and 2011 (C, D) under two experimental levels of light availability: ambient light (Open conditions; A, C) and about 50% ambient light (Shaded conditions; B, D).

Table 1 Mean Julian day (\pm SE; January 1st = 1) that the weed *Ruellia nudiflora* starts (Onset) and ends (End) the production of chasmogamous flowers (flowers), chasmogamous fruit (CH fruit) and cleistogamous fruit (CL fruit) under two experimental levels of light availability: ambient (Open) vs. 50% ambient light (Shaded)

Structure	Trait	Year/light level			
		2010		2011	
		Open	Shaded	Open	Shaded
Flower	Onset	157 \pm 4.15 ^a	154 \pm 4.27 ^a	199 \pm 1.98 ^b	196 \pm 0.86 ^b
	End	266 \pm 4.88 ^a	251 \pm 6.38 ^b	243 \pm 4.81 ^c	221 \pm 3.59 ^d
CH fruit	Onset	158 \pm 4.31 ^a	156 \pm 4.32 ^a	205 \pm 1.19 ^b	203 \pm 1.24 ^b
	End	288 \pm 4.83 ^a	278 \pm 4.83 ^b	245 \pm 4.41 ^c	230 \pm 3.11 ^d
CL fruit	Onset	129 \pm 1.88 ^a	121 \pm 1.57 ^a	159 \pm 7.04 ^b	146 \pm 6.59 ^b
	End	345 \pm 0.07 ^a	339 \pm 0.14 ^a	343 \pm 0.32 ^a	341 \pm 0.26 ^a

Different superscript letters indicate statistically significant differences, assessed using a simple main effects analysis after fitting mixed-effect linear models where light intensity, the year and their interaction were included as fixed effects; the hierarchical structure of the design was considered to be a random effect (not shown).

During 2011, the proportion of plants bearing CH flowers and CH fruit was unimodal, unlike the bimodal pattern seen the previous year (Fig. 1). The highest proportion of plants with CH flowers and CH fruit in 2011 was seen from early July to mid-September (Julian days 183–263) in open and shaded subplots (Fig. 1C and D). Also, this period (Julian days 183–263) coincided with the lowest proportion of plants bearing CL fruit under both light levels (Fig. 1C and D).

Individual plants in the shaded subplots exhibited a significantly earlier end of production of CH flowers ($F_{1,9} = 13.14$, $P < 0.01$) and CH fruit ($F_{1,9} = 10.22$,

$P = 0.01$) than did the plants in the open subplots (Table 1). However, the onset in the production of CH flowers ($F_{1,9} = 1.55$, $P = 0.24$), CH fruit ($F_{1,9} = 0.26$, $P = 0.62$) and CL fruit ($F_{1,9} = 4.86$, $P = 0.06$), as well as the end of CL fruit production ($F_{1,9} = 1.02$, $P = 0.34$) did not differ between the two light levels (Table 1). Year had a significant effect on at least one of the two phenological traits (onset and end of production) for the three reproductive structures. CH flowers were produced significantly earlier ($F_{1,161} = 155.73$, $P < 0.01$) and production ended significantly later ($F_{1,161} = 28.29$, $P < 0.01$) in 2010

than in 2011 (Table 1). The same pattern [significantly earlier production onset ($F_{1,161} = 168.14$, $P < 0.01$) and significantly later end of production ($F_{1,161} = 121.08$, $P < 0.01$) in 2010 than 2011] was observed for CH fruit (Table 1). In contrast to CH reproductive structures, only the onset of CL fruit production was significantly earlier ($F_{1,161} = 33.78$, $P < 0.01$); the end of production was not delayed ($F_{1,161} = 0.02$, $P > 0.05$) in 2010 relative to 2011 (Table 1). In no case was the light availability \times year interaction statistically significant ($F_{1,161} = 0.02$ – 1.22 , $P > 0.05$ in all cases).

At the individual level, repeatability was not statistically different from zero in any of the cases (Table 2). Temporal variation in the proportion of plants bearing CH flowers, CH fruit or CL fruit was not related to rainfall, light availability or their interaction during 2010 or 2011 (Table 3).

Discussion

The results of our research show that the phenology of *R. nudiflora* was highly variable at both the population and the individual levels. We found that the same population exhibited either unimodal or bimodal phenology in different years. Extremely low repeatability also confirms our expectation that individual phenology is a highly plastic trait. Contrary to our expectations, plasticity was not limited by shade, suggesting that the extraordinary phenotypic plasticity exhibited by *R. nudiflora* does not represent a high energetic cost for

Table 2 Repeatability of two phenological traits (onset and end of production) for three reproductive structures in the weed *Ruellia nudiflora*: chasmogamous flowers (flower), chasmogamous fruit (CH fruit) and cleistogamous fruit (CL fruit). The plants were exposed to two levels of light: ambient (Open) and about 50% ambient light (Shaded)

Variable	Light level	Repeatability	95% CI
Flowering start	Open	0	0, 0.22
	Shaded	0	–
Flowering end	Open	0	–
	Shaded	0.09	0, 0.32
CH Fruit start	Open	0	–
	Shaded	0	–
CH Fruit end	Open	0	–
	Shaded	0	–
CL Fruit start	Open	0	0, 0.19
	Shaded	0	0, 0.19
CL Fruit end	Open	0	–
	Shaded	0.03	0, 0.29

Repeatability was calculated using the LMM-based method and the REML estimation method. The 95% confidence interval for repeatability is also shown. Missing confidence intervals (–) indicate that the exact repeatability calculated was 0. None of the repeatability values were statistically different from zero.

Table 3 Results of the regression models run to assess the relationship between the proportion of plants bearing reproductive structures [chasmogamous flowers (flowers), chasmogamous fruit (CH fruit) and cleistogamous fruit (CL fruit)] and rainfall

Structure	Source of variation	Year ($F_{1,46}$)	
		2010	2011
Flower	Rainfall	0.06	2.51
	Light	0.42	0.97
	Rainfall \times Light	0.18	0.04
CH fruit	Rainfall	0.21	1.16
	Light	0.16	0.86
	Rainfall \times Light	0.01	0.02
CL fruit	Rainfall	2.38	0.47
	Light	0.03	0.02
	Rainfall \times Light	0.13	0.01

The light availability factor (two levels: open spaces and under a shade cloth) and its interaction with rainfall were also included in the model. A separate model for reproductive structure (Structure) and year (2010, 2011) was fitted (five models in total). No statistically significant associations were found.

this plant species. Instead, moderate levels of shade induced a plastic response in the phenology of its reproductive structures; specifically, this plant may shorten the production time of CH in response to low light availability. Variation in phenology was not explained by rainfall; therefore, rainfall was not producing the between-year variation observed in phenology of *R. nudiflora*. The plasticity observed in *R. nudiflora* may account for the successful invasiveness exhibited by this species, as well as the persistence of populations that have already invaded habitats. Our results may have useful management implications; for instance, different management strategies might be required in open and shaded areas as light availability determines, to some extent, which reproductive strategy [i.e. mainly selfed (CL) or mainly out-crossed (CH)] would be favoured, and this is frequently correlated with progeny vigour (e.g. Snow & Spira, 1993).

Although some authors have emphasised that the ecological context may have an effect on the plastic response of plants (Valladares *et al.*, 2007), our results suggest that the light environment has no effect on the reproductive phenology of *R. nudiflora* at the population (see Fig. 1) and individual levels (see Table 2). On the contrary, the analysis at the plant level revealed that shade induced some plastic response in the pattern of allocation to different reproductive structures: shade had a significant and negative effect on the production onset of CH flowers and fruit, but had no effect on CL fruit phenology. Therefore, not only did shade not limit the plastic response of *R. nudiflora*, it also induced a plastic response in individual phenology. This finding agrees with those of other studies whose

authors found that shade amplifies the plasticity of responses in traits that enhance resource capture (e.g. stem elongation and early flowering) in other plant species (Schmitt *et al.*, 1995; Dudley & Schmitt, 1996; Callahan & Pigliucci, 2002). At the individual level, this plasticity may allow cleistogamous plants to maximise fitness by opportunistically allocating resources to costly CH structures only under optimal conditions (high levels of light) and also continuing to produce energetically cheap CL structures under a wide variety of environmental conditions, including in suboptimal environments. As recently suggested by some authors (Auld *et al.*, 2007), we suspect that phenotypic plasticity is less costly than previously thought (Dewitt *et al.*, 1998) and this is why we found that the light environment does not have a perceptible effect on the phenological plasticity of *R. nudiflora*.

Although there was a clear between-year difference in the amount of rainfall, we have shown that temporal variation in the phenology of *R. nudiflora* was not explained by variation in rainfall (see Table 3). Although the environmental variable responsible for *R. nudiflora*'s phenological variation remains unidentified, we have successfully shown that the light environment did not limit the plastic response of this species to temporal variation in other(s) unidentified environmental factor(s), whatever they may be.

Phenotypic plasticity is commonly considered to be a trait that is associated with invasiveness in alien plants. It is expected that some invasive plants express advantageous genotypes in a broader range of environments than non-invasive species do and that this enhances the ability of the former to occupy a wider range of environments. Additionally, phenotypic plasticity is an important mechanism for population persistence in the face of high temporal environmental stochasticity (Richards *et al.*, 2006; Richardson & Pyšek, 2006; Barrett *et al.*, 2008; Wolkovich & Cleland, 2011). For *R. nudiflora*, the phenotypic plasticity we observed in reproductive phenology may optimise resource allocation and this may enable this species to colonise a wider array of habitats, in addition to promoting chronic persistence where it has already invaded habitats, including those thought to be suboptimal for the species. For instance, shady sites are considered suboptimal for the establishment of the study species (Cervera & Parra-Tabla, 2009) and that is why *R. nudiflora* produced CH structures for shorter periods of time when shaded than when in open sunny sites. This ability of cleistogamous plants to shift from one reproductive strategy to another (CH vs. CL) in response to environmental conditions could be an example of phenotypic adaptive plasticity (Oakley *et al.*, 2007). This plasticity may allow for the

persistence of *R. nudiflora* under a wider variety of habitats than those used by other non-cleistogamous species.

The plasticity of *R. nudiflora* is certainly a sizable challenge for weed managers. However, some of our findings are helpful for fine-tuning management strategies. For instance, we know that shady habitats negatively affect the duration (i.e. onset and production end) of CH structures, leading to a CL-biased seed crop; CL seeds are smaller and have lower genetic variability than CH seeds. Therefore, sunny habitats may be dominated by more vigorous plants (because of the genetic background and the size of the seeds) than shady ones are, indicating that these two types of habitat may need different management strategies to eradicate populations of this weed species.

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