Mating systems and limits to seed production in two *Dicerandra* mints endemic to Florida scrub

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Abstract. We used hand-pollination experiments to test the mating systems of and evaluate limits to seed production in two federally listed endangered plants endemic to the Lake Wales Ridge in Florida, USA: *Dicerandra frutescens* Shinners ssp. *frutescens* Huck and *D. christmanii* Huck and Judd (Lamiaceae). Both are nonclonal, short-lived perennials found in gaps created by disturbance (e.g., fire, roads) in Florida scrub. We found that both species require pollen and insect visitation to produce seeds. We detected pollinator limitation of seed production in *D. christmanii* but not *D. frutescens* ssp. *frutescens*, which we suggest is a function of time-since-disturbance or gap size rather than intrinsic differences between the two species. Both species are self-compatible. Inbreeding depression reduced seed set by 60% in *D. frutescens* ssp. *frutescens* but did not occur in *D. christmanii*. We conclude that pollinator limitation (in fire-suppressed populations of both species) and inbreeding depression (in *D. frutescens* ssp. *frutescens*) have the potential to limit seed production in these seed-dependent, rare species. Appropriate fire management should mitigate both of these risks, by maintaining large populations and conditions attractive to pollinators. Although these two species are very similar in reproductive biology, comparisons with other Florida scrub endemics and with rare plants in general suggest that potential threats to conservation via reproductive biology are difficult to predict, depending on combinations of ecology, life-history, and phylogenetic history.

Introduction

Understanding the reproductive biology of rare plants can be critical for their conservation (Kruckeberg and Rabinowitz 1985; Kaye 1999; Spira 2001). This is especially true when individuals are short-lived and regeneration occurs exclusively via seeds (Bond 1994; Schemske et al. 1994). In such species, population viability may be closely linked to seed dynamics, and conservation may depend on understanding the factors that limit seed production (Pavlik et al. 1993). When seed production is mediated by pollinators, seeds can be limited by pollinator abundance or behavior (Bierzychudek 1981; Larson and Barrett 2000). Pollen quality, in addition to pollen quantity, can limit seed production. Self pollen fails to produce seeds in self-incompatible species. Some small populations of self-incompatible plants are at risk of extirpation for this reason (Les et al. 1991; DeMauro 1993; Byers 1995; Ramsey and Vaughton 2000; Weekley and Race 2001; Wolf and

Harrison 2001). In addition, self pollen can limit seed production through inbreeding depression (Bosh and Waser 1999; Brown and Kephart 1999). In order to understand potential limitations on their seed productivity, we evaluated the mating systems of *Dicerandra frutescens* Shinners ssp. *frutescens* Huck and *D. christmanii* Huck and Judd (Lamiaceae), two federally listed endangered plants endemic to the Lake Wales Ridge in Florida, USA.

D. frutescens ssp. *frutescens* and *D. christmanii* are small woody perennials occurring in Florida scrub on yellow sands (Huck et al. 1989; Christman and Judd 1990; Menges 1992; Menges et al. 1999). Both species occupy the oak-hickory and sand pine scrub phases of Florida scrub (as designated by Abrahamson et al. 1984), which are dominated by several species of shrubby oaks and ericads, and have a variable overstory of scrub hickory or sand pine. Both plants are extremely narrowly distributed: about a dozen populations of *D. frutescens* ssp. *frutescens* are found in the vicinity of Lake Placid, Highlands County, Florida. (Recently, two additional populations in Polk County, Florida were designated *D. frutescens* ssp. *modesta*; Huck 2001.) *D. christmanii* is known from just five populations near Sebring, Highlands County, Florida. These two species are separated by just 10.5 km. They are distinct in a number of morphological and chemical characters (Huck et al. 1989; McCormick et al. 1993), but have very similar floral biology, pollination, microhabitats, life histories, and fire ecology (Huck et al. 1989; Menges 1992; Deyrup and Menges 1997; Menges et al. 1999).

Existing evidence indicates that seed production is critical for populations of *D. frutescens* ssp. *frutescens* and *D. christmanii*. Demographic studies of both species have shown that individuals are not long-lived (<10 years), and regeneration occurs exclusively through episodic recruitment of seedlings (Menges et al. 1999; E. Menges, unpublished data). Both species preferentially occupy open microsites (Menges 1992; Menges et al. 1999). Such open conditions are created by disturbance (e.g., fire or anthropogenic activity) and diminish with time-since-disturbance. However, individuals of *D. frutescens* ssp. *frutescens* do not survive disturbance (spring fire, removal of aboveground biomass, or defoliation; Menges 1992). *D. christmanii* is likely also intolerant to such disturbance. Seeds remain viable for more than 1 year (E. Menges and C. Weekley, unpublished data). Hence, persistence of *D. frutescens* ssp. *frutescens* and *D. christmanii* populations depends both on disturbance and on soil seed banks or seeds produced by undisturbed plants in the face of disturbance.

These two species of *Dicerandra* are among about 20 other federally endangered plants endemic to Florida scrub (Christman and Judd 1990; Dobson et al. 1997). As with these other species, the threats to *D. frutescens* ssp. *frutescens* and *D. christmanii* include habitat loss and fire suppression. Almost 20 years ago, Peroni and Abrahamson (1985) estimated that just 16% of the historical extent of scrub habitat on the Lake Wales Ridge remained. Loss of habitat can rapidly lead to the extinction of narrowly distributed species. Fire suppression is also a threat to *D. frutescens* ssp. *frutescens* and *D. christmanii*, since they thrive in the open conditions created by fire. The oak-hickory and sand pine scrub habitats where *D. frutescens* ssp. *frutescens* and *D. christmanii* are found are thought to have burned

at a frequency of once every 10–100 years (Myers 1990; Menges 1999), at least before fire suppression was enforced on a regional scale about 65 years ago. Prescribed burning has only recently been implemented in certain areas of Florida scrub.

Because seeds play an important role in the population dynamics and persistence of these species, we examined how pollen quantity (pollinator limitation) and pollen quality (self-incompatibility and inbreeding depression) affect seed production. Previously, it was concluded that pollinator limitation is unlikely in *D. frutescens* ssp. *frutescens* and *D. christmanii*, even though both are pollinated almost exclusively by a single species of bee-fly, *Exprosopa fasciata* (Huck et al. 1989; Deyrup and Menges 1997), because this insect is abundant, wide-ranging and a generalist in its feeding habits. However, these studies did not directly evaluate pollinator limitation. Huck (1987) reported that *D. frutescens* ssp. *frutescens* is self-incompatible; however, her data show that viable seeds were produced from self pollen. Here we report seed set resulting from hand-pollination experiments testing whether seed production requires pollen, whether insects are necessary and sufficient pollinators, and whether these species are self-incompatible.

Methods

We used five pollination treatments to determine the mating system of *D. frutescens* ssp. *frutescens*. We tested for spontaneous self-pollination by caging flowers, thus excluding insect visitors (label AUTO). To test for agamospermy (asexual reproduction in flowers, e.g. apomixis; label AGAM), flowers were similarly caged and all anthers were removed the morning the flower opened. We tested for self-compatibility (label SELF) by caging flowers and transferring pollen by hand from anther to stigma within flowers. A fourth treatment was similar: caged flowers were hand-pollinated, but the pollen came from another plant (label CROSS). The flowers used as a pollen source were caged to prevent insect visitation. Control flowers were not manipulated (label OPEN). Because of time constraints, and because *D. christmanii* and *D. frutescens* ssp. *frutescens* are so closely related (Huck et al. 1989), we only conducted the test for self-compatibility and the control treatment in *D. christmanii*. Pollination treatments were applied to naturally occurring plants of *D. frutescens* ssp. *frutescens* at Archbold Biological Station (ABS) south of Lake Placid, Florida, USA and to naturally occurring plants of *D. christmanii* in the Lake Wales Ridge National Wildlife Refuge (Flamingo Villas Tract) southeast of Sebring, Florida, USA in 1996.

Twenty-five plants of each species were arbitrarily selected to receive pollen. Another 20 plants were selected to provide pollen for the cross-pollination treatment (*D. frutescens* ssp. *frutescens* only). Treatments were assigned randomly to individual flowering stalks. Flowering stems were caged with a wire cylinder supported by a garden stake, which suspended a plastic mesh bag (Applied Extrusion Technologies, mesh size 0.9 mm) wrapped around the flowering stem. Hand-pollinations were performed daily from 28 August to 26 September, 1996 on

flowers of *D. frutescens* ssp. *frutescens*, and from 25 September to 10 October, 1996 on flowers of *D. christmanii*.

Flowering stalks were harvested when seeds in unmanipulated fruits on the plant appeared mature upon dissection or (in *D. frutescens* ssp. *frutescens*) when manipulated fruits started to abscise. In both species, each flower contains four ovules. We evaluated the development of a seed from each ovule in terms of the seed coat and endosperm: ovules either developed a seed coat or did not, and those with a seed coat did or did not contain endosperm. Seeds without endosperm were drier and more brittle than seeds with endosperm, and collapsed under gentle pressure. Some seeds fell from the capsules before we could recover them. We were able to determine whether 'missing' seeds had developed a seed coat based on the size of the scar left on the receptacle, but could not determine whether 'missing' seeds had endosperm or not.

We tested the effect of pollination treatment on the same two aspects of seed development: the development of a seed coat and, among those with a seed coat, the development of endosperm. We used a generalized linear model that is similar to a logistic regression, in that the response variable is a ratio of the number of 'successes' over the number of 'trials'. We used the logit link to linearize the data, and test statistics were corrected for overdispersion. The data from all flowers per flowering stalk (i.e., all flowers from a given plant and pollination treatment combination) were combined to avoid pseudoreplication. After combining the data from multiple flowers, the experiment has a randomized complete block design without replication, where each treatment level (i.e., pollination treatment) is represented once in each block (i.e., plant). We considered pollination treatment as a fixed effect and plant as a random effect. The effect of plant identity was tested with a likelihood ratio test comparing the scaled deviances of models with and without plant entered as a factor. This test has a Chi-square distribution.

The data on seed set and endosperm development in *D. frutescens* ssp. *frutescens* were tested with four and three *a posteriori* contrasts, respectively. The first contrast (of seed coat development) compared the treatments in which insects or pollen were eliminated to the treatments in which pollen was applied by humans or insects. The remaining contrasts (of data on seed coat and endosperm development) compared pairwise differences among the latter treatments (self, cross, and open). All tests were performed using PROC GLIMMIX in SAS (Littell et al. 1996). Plants of *D. frutescens* ssp. *frutescens* that were damaged during the course of the experiment were excluded from data analysis: styles in flowers of three plants were severed by ants, who foraged on the nectar that accumulated without insect visitation; and three additional plants suffered visibly from drought during the course of the experiment (1996 had the driest September on ABS records).

Results

Pollination treatment had a highly significant effect on seed set in *D. frutescens* ssp. *frutescens* ($F_{4, 66} = 53.75$, $P < 0.0001$), as did plant identity (Chi-square $= 5.97$,

Table 1. Counts of ovule fates, percent seed set, and percent endosperm development produced by each pollination treatment. Also shown are the sample sizes in each pollination treatment: the average number of flowers treated per plant (range in parentheses) and the number of plants treated.

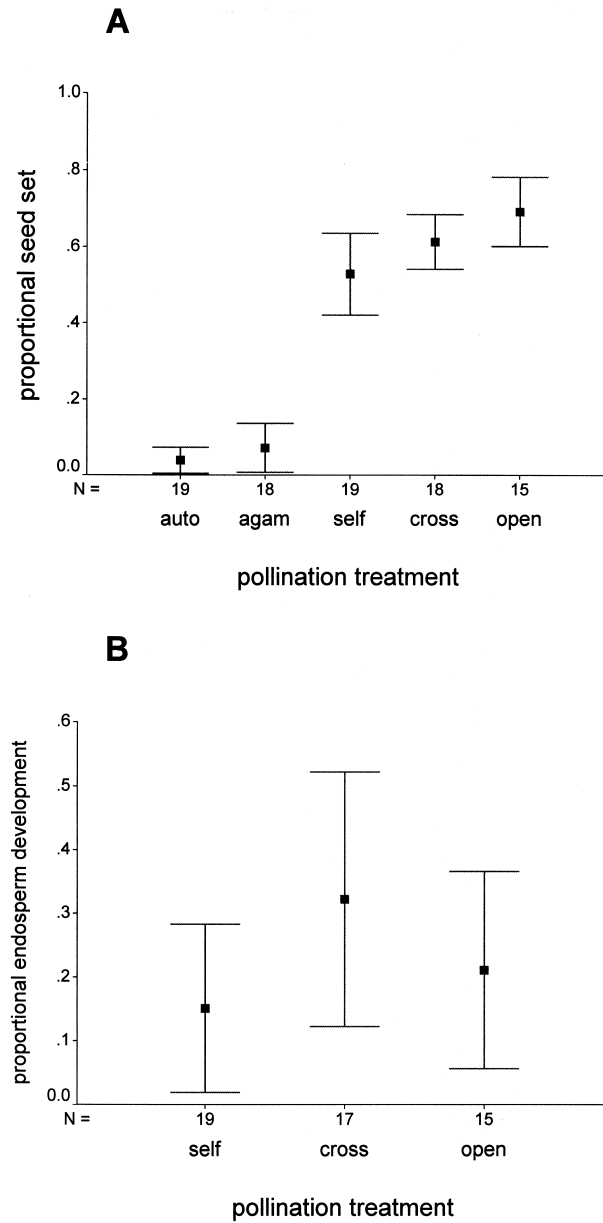| Ovule fate	Pollination treatment						
	D. frutescens ssp. *Frutescens*					*D. christmanii*	
	Auto	Agam	Self	Cross	Open	Self	Open
No seed coat, no endosperm	1608	1355	554	451	251	506	628
Seed coat, no endosperm	43	26	396	326	321	201	242
Missing	3	7	62	203	102	92	188
Seed coat, endosperm	6	0	92	196	140	834	592
Column totals	1660	1388	1104	1176	814	1633	1650
% Seed set	3	2	50	62	69	69	62
% Endosperm development	12	0	19	38	30	81	71
# Flowers treated/plant	22 (8–36)	18 (0–44)	15 (1–27)	15 (0–26)	11 (0–33)	16 (3–30)	17 (0–27)
# Plants	19	19	19	19	19	25	25

A

B

Figure 1. (A) Proportional seed set and (B) proportional endosperm development of *D. frutescens* spp. *frutescens* ovules subjected to five pollination treatments. The data used to create this figure are the same data that were tested: each data point summarizes seed set (A) or endosperm development (B) in multiple flowers per plant and pollination treatment combination. However, we used a generalized linear model (see Methods) rather than an analysis of variance to test the data, so the error bars (95% confidence intervals) in this figure do not exactly correspond to our test results. The treatment labels are explained in the text and in Table 1.
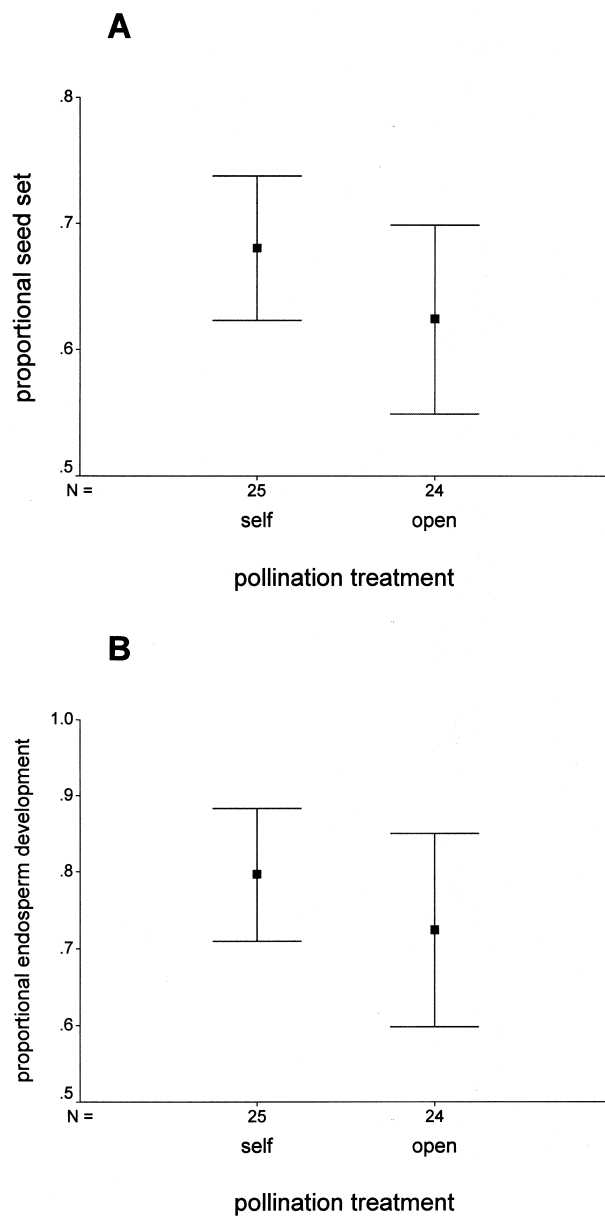
A

B

Figure 2. (A) Proportional seed set and (B) proportional endosperm development of *D. christmanii* ovules subjected to five pollination treatments. The data used to create this figure are the same data that were tested: each data point summarizes seed set (A) or endosperm development (B) in multiple flowers per plant and pollination treatment combination. However, we used a generalized linear model (see Methods) rather than an analysis of variance to test the data, so the error bars (95% confidence intervals) in this figure do not exactly correspond to our test results. The treatment labels are explained in the text and in Table 1.

Table 2. Characteristics of the reproductive biology of *D. frutescens* ssp. *frutescens* and *D. christmanii*.

	D. frutescens ssp. frutescens	*D. christmanii*
Requires pollen	Yes	No test
Requires pollinators	Yes	Yes (inferred)
Self-compatible	Yes	Yes
Inbreeding depression	Yes	No
Pollinator limitation	No	Some
Resource limitation	Yes	No

d.f. $= 1$, $P < 0.02$). Excluding insects, or this combined with emasculation, led to very low seed set (3% and 2% in the treatments testing for autonomous pollination and agamospermy, respectively; Table 1). The contrast between these two treatments and the remaining three was highly significant ($F_{1, 66} = 200.67$, $P < 0.0001$; Figure 1A). Pollen type also significantly affected seed set: ovules given self pollen were less likely to develop a seed coat than those given cross pollen ($F_{1, 66} = 5.81$, $P = 0.019$; Figure 1A). However, seed set in the self treatment (50%, Table 1) was 81% of seed set in the cross treatment (62%, Table 1), indicating that *D. frutescens* ssp. *frutescens* is self-compatible. Seed set in the control treatment was not significantly different from seed set in the cross treatment ($F_{1, 66} = 1.74$, $P = 0.192$; Figure 1A), but was significantly higher than seed set in the self treatment ($F_{1, 66} = 11.54$, $P = 0.001$; Figure 1A).

When we tested for an effect of pollination treatment on endosperm development in *D. frutescens* ssp. *frutescens*, we excluded the data from the treatments testing for autonomous pollination and agamospermy, which were mostly zeros (Table 1). Though the overall effect of pollination treatment was not significant ($F_{2, 30} = 2.86$, $P = 0.073$), ovules given self pollen were significantly less likely to develop endosperm than ovules given cross pollen ($F_{1, 30} = 5.51$, $P = 0.026$; Figure 1B). Ovules in the control treatment were no more or less likely to develop endosperm than ovules in the self ($F_{1, 30} = 2.75$, $P = 0.108$) or cross ($F_{1, 30} = 0.44$, $P = 0.515$) treatments, respectively (Figure 1B). Plant identity had a highly significant effect on endosperm development (Chi-square $= 14.76$, d.f. $= 1$, $P < 0.0005$).

Pollination treatment had a marginally significant effect on seed set in *D. christmanii* ($F_{1, 23} = 4.29$, $P = 0.050$; Figure 2A), but here seed set was higher in the self treatment than in the control treatment (69% versus 62%, respectively; Table 2). These data clearly indicate that *D. christmanii*, like *D. frutescens* ssp. *frutescens*, is self-compatible. Plant identity also significantly affected seed set (Chi-square $= 11.96$, d.f. $= 1$, $P < 0.001$). Seeds of *D. christmanii* were significantly more likely to contain endosperm if self pollen was applied by hand than if flowers were given open access to insects ($F_{1, 23} = 4.88$, $P = 0.037$; Figure 2B). Plant identity did not affect endosperm development (Chi-square $= 2.45$, d.f. $= 1$, $P > 0.05$).

Regardless of pollination treatment, ovules of *D. frutescens* ssp. *frutescens* developed into seeds at less than half the rate of ovules of *D. christmanii* (31% versus

65%, respectively; Table 1). This pattern is also reflected in endosperm development: among those that were recovered, 28% of *D. frutescens* ssp. *frutescens* seeds had endosperm, whereas 76% of *D. christmanii* seeds had endosperm. If we restrict the comparison to the treatments that are represented in both species (the self and open treatments), the discrepancy in seed set between *D. frutescens* ssp. *frutescens* and *D. christmanii* diminishes (58% versus 65%, respectively) but the discrepancy in endosperm development does not (24% versus 76%, respectively).

Discussion

Mating systems and limits on seed production

Both pollen and insects are necessary to produce seeds of *D. frutescens* ssp. *frutescens*. Very few seeds were produced when flowers of *D. frutescens* ssp. *frutescens* were emasculated and denied insect visitation (agamospermy treatment), or simply denied insect visitation (testing for autonomous pollination). Self pollen generated seeds when transferred from anthers to stigmas by hand (self treatment), so the low seed set in the treatment testing for autonomous pollination indicates that insects are necessary for pollination. Because *D. christmanii*'s floral structure is identical to that of *D. frutescens* ssp. *frutescens* (Deyrup and Menges 1997), we can infer that insects are necessary for its pollination as well.

We also found that *D. frutescens* ssp. *frutescens* and *D. christmanii* are self-compatible. Seed set and endosperm development in the self treatment of *D. frutescens* ssp. *frutescens* were 81% and 50% of seed set and endosperm development in the cross treatment, respectively. Although Huck (1987) concluded that *D. frutescens* ssp. *frutescens* is self-incompatible, her own data and the data from this experiment clearly show that viable seeds are produced from self pollen. We cannot make the comparison of seed set from pure self versus pure cross pollen in *D. christmanii*, but the data demonstrate that it is also self-compatible. Many ovules of *D. christmanii* (69%) developed into seeds when they were given self pollen, and many (81%) of these seeds contained endosperm.

Our data indicate that some inbreeding depression occurs in *D. frutescens* ssp. *frutescens* but not in *D. christmanii*. Self pollen was significantly less successful than cross pollen at causing ovules to develop either a seed coat or endosperm in *D. frutescens* ssp. *frutescens*. Overall, fecundity was reduced by 60% in response to pollination with self pollen, making inbreeding depression a significant concern in *D. frutescens* ssp. *frutescens*. In contrast, the self treatment generated somewhat higher seed set and endosperm development than the control treatment in *D. christmanii*, counter to the expectation under inbreeding depression. Seed set of *D. frutescens* ssp. *frutescens* was more similar between the cross and control treatments than the self and control treatments, suggesting that pollen loads applied by insects included mostly cross pollen. This corroborates the suggestion by Deyrup and Menges (1997) that outcrossing is promoted in flowers of *D. frutescens* ssp. *frutescens* by changes in the position of the style and stigma throughout the day.

Pollinator limitation did not occur in *D. frutescens* ssp. *frutescens*, but was a weak effect in *D. christmanii*. In *D. frutescens* ssp. *frutescens*, seed set in un-manipulated, freely pollinated flowers was no different from seed set in flowers hand pollinated with cross pollen. In contrast, seed set in unmanipulated flowers of *D. christmanii* was slightly less than seed set in flowers hand pollinated with self pollen, providing evidence for some pollinator limitation. Pollinator limitation is often shown to be conditional or situational, i.e., occurring in some places and times and not in others (Burd 1994; Dudash and Fenster 1997; Larson and Barrett 1999). In their study of *D. frutescens* ssp. *frutescens* pollination, Deyrup and Menges (1997) showed that pollinator visitation is more than three times higher to flowers occurring in sun than in shade. Plant density and number of flowers per plant, which are frequently correlated with insect visitation rates, were also higher in more open, sunny habitats (Deyrup and Menges 1997). All the plants used in our study occurred in gaps, but the plants of *D. frutescens* ssp. *frutescens* occurred in a much larger gap than the plants of *D. christmanii*. Our observation of some pollinator limitation in *D. christmanii* but none in *D. frutescens* ssp. *frutescens* is consistent with the positive relationship that Deyrup and Menges (1997) reported between time-since-fire or gap size and pollinator visitation. We suggest that pollinator limitation may be situational, depending upon gap size or time-since-fire rather than resulting from intrinsic differences between the two species.

The relationships between time-since-fire or gap size, plant numbers or size, and pollinator visitation or limitation observed in this study and in Deyrup and Menges (1997) suggest that reproduction of *D. frutescens* ssp. *frutescens* and *D. christmanii* may be positively density-dependent (Allee effect). Evidence of the Allee effect in plant reproduction has increased in recent years: fecundity has been shown to be a positive function of population size or density in experimental and natural plant populations (Kunin 1993, 1997a; Agren 1996; Oostermeijer et al. 1998). Below a certain number of plants (either an absolute number or density), reproduction may either completely fail, or be insufficient to replace individuals that die (Lamont et al. 1993; Steiner and Whitehead 1996; Groom 1998; Mawdsley et al. 1998; Robertson et al. 1999). Based on our data as well as those of Deyrup and Menges (1997), we predict that pollinator limitation of seed set should increase with time-since-disturbance; that is, the Allee effect may occur periodically in relation to disturbance and its effects on population size.

There was a striking difference between *D. frutescens* ssp. *frutescens* and *D. christmanii* in endosperm development. Including just the two pollination treatments that were conducted in both species ('self' and 'open'), 24% of *D. frutescens* ssp. *frutescens* seeds contained endosperm, compared to 76% of *D. christmanii* seeds. Pollen limitation is an unlikely explanation for this difference: more ovules of *D. frutescens* ssp. *frutescens* than *D. christmanii* developed to full-sized seeds in the open pollinated treatment (69% versus 62%). Nor is inbreeding depression sufficient to explain the difference: fecundity resulting from hand cross-pollination in *D. frutescens* ssp. *frutescens* was less than fecundity resulting from hand self-pollination in *D. christmanii* (62% and 69% seed set, respectively, and 38% and 81% endosperm development, respectively).

Other possible limitations to seed production, besides the amount or quality of pollen, are resources and seed predation (Zimmerman and Aide 1989; Pavlik et al. 1993; Kaye 1999). The individuals chosen for the study of *D. christmanii* occurred along a small trail created by off-road vehicle use, whereas the study plants of *D. frutescens* ssp. *frutescens* were located in a large opening adjacent to a sand road. In other words, the plants of *D. frutescens* ssp. *frutescens* occupied a more exposed site, and they suffered visibly from September's drought. One study plant of *D. frutescens* ssp. *frutescens* died within the month the study was conducted, probably because of drought stress. Seed predators (Thyreocoridae: *Cynoides ciliatus* ssp. *orientis*) witnessed in capsules of *D. frutescens* ssp. *frutescens* could be responsible for the lack of endosperm in some seeds, but their numbers are typically not great enough to generate the many empty seeds that we documented (M. Deyrup, personal communication). Fecundity data from these populations have been collected for several years (E. Menges, unpublished data). Analysis of these data will demonstrate whether differences in fecundity between these two species are temporally variable or chronic.

Two concerns about seed production revealed in this study, inbreeding depression and pollinator limitation, are related to fire suppression. Inbreeding depression is only likely to threaten population viability when the number of plants and hence overall seed production is low. Populations of *D. frutescens* ssp. *frutescens* and *D. christmanii* decline with fire suppression (E. Menges, unpublished data), as the open microhabitats that they favor close (Menges et al. 1999). Pollinator limitation should also be strongest as shrub cover closes with time-since-fire (Menges and Deyrup 1997).

Reintroducing fire where populations of *D. frutescens* ssp. *frutescens* and *D. christmanii* occur is an obvious antidote to these problems. However, reintroducing fire after long-term fire suppression can be difficult because of high or low ground fuel loads. In areas of high fuel loads, initial fires can be very hot and complete. With depleted seed banks in long-unburned areas (M. Finer, unpublished data), *Dicerandra* populations may rely on the seed production of unburned plants in patchy fires to recover from fire. Mechanical removal of at least some of the fuel that surrounds at least some *Dicerandra* individuals may help to recreate patchy burns when fuel loads are high. Because some fire-suppressed areas have woody fuels disconnected from ground fuels, mechanical pretreatments of large shrubs may make fuels more continuous and allow fire to move through *Dicerandra* patches.

Comparative reproductive biology

Overall, *D. frutescens* ssp. *frutescens* and *D. christmanii* are quite similar in their reproductive biology. Both require pollen and insect pollination to produce seeds; we predict that both species are subject to pollinator as well as resource limitation of seed set (Table 2). Both are self-compatible, but *D. frutescens* ssp. *frutescens* showed inbreeding depression whereas *D. christmanii* did not (Table 2). The rarer

of the two species may have purged its genetic load, either during the process of speciation or afterwards. (However, Menges et al. (2001) reported more isozyme variation in *D. christmanii* than in *D. frutescens* ssp. *frutescens*.)

We have reported elsewhere on the reproductive biology of four other plants endemic to Florida scrub on the Lake Wales Ridge (Evans et al. 2000, 2003). Together, the six Florida scrub endemics that we have studied illustrate a pattern of 'compensation' described by Bond (1994). Only the longest-lived and least dependent upon seeds, *L. ohlingerae*, is self-incompatible, and only the annual, *W. carteri*, is both self-compatible and capable of spontaneous self-pollination. The *Dicerandra*'s that we have discussed here, plus two other species, are short-lived herbaceous perennials that are self-compatible but depend on insects for pollination. The predominance of self-compatibility among the Florida scrub endemics that we studied confirms the prediction of this pattern by Kunin (1997b) and Gaston and Kunin (1997). However, these authors also predicted that many rare plants should be asexual, a trait absent among our Florida scrub endemics, and a recent survey (Murray et al. 2002) found no consistent pattern of self-compatibility in rare versus common plants. We also note the range of specialization with respect to pollination found among these Florida scrub endemics: two of six species are visited by many insects, whereas three of six are visited by one or a handful of species. We would argue that the reproductive biology of rare species (like common species) is only incompletely predictable, and this only in the light of ecology, life-history, and phylogenetic history.

Acknowledgements

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