

Seedling emergence and survival of *Warea carteri* (Brassicaceae), an endangered annual herb of the Florida Scrub

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Abstract: Seedling emergence and survival to flowering are critical processes in the life history of annual plants. We evaluated the importance of year and habitat on seedling emergence and the effects of year, habitat, timing of seedling emergence, and seedling density on survival of *Warea carteri* Small, an annual mustard endemic to Florida scrub. We tagged 1329 seedlings in 78 permanent 0.25 m² quadrats in two habitats (scrub and disturbed) between 1999 and 2002 and followed seedlings monthly. Most (>80%) seedling emergence occurred between September and December. Emergence peaked 2 months earlier and was more variable in disturbed sites than in scrub. Seedling survival among years ranged from 3.5% to 12.0%. Seedling density varied from 1 to 75 per 0.25 m² quadrat, with an overall median of 6.0. Survival was not density dependent. Median age at flowering ranged from 11.7 to 15.2 months, with late season recruits most likely to survive to flowering. *Warea carteri* recruits like a winter annual but flowers like a summer annual. Its delayed germination and a 12–15 month life span contribute to population cycling. Complete reproductive failure in unfavorable years, high seed production in favorable years, low rates of seed germination, and a persistent seed bank are consistent with predictions for an annual species in a variable habitat.

Key words: annuals, delayed germination, density dependence, disturbed habitats, summer annual, winter annual.

Résumé : L'émergence des plantules et leur survie jusqu'à la floraison constituent des étapes critiques dans le cycle vital des plantes annuelles. Les auteurs ont évalué l'importance de l'année et de l'habitat sur l'émergence des plantules, ainsi que de l'année, de l'habitat, du moment de l'émergence des plantules, et de la densité des plantules sur la survie du *Warea carteri* Small, une moutarde endémique du maquis en Floride. Ils ont marqué 1329 plantules dans des quadrats de 78,25 m² dans deux habitats (maquis et perturbé), entre 1999 et 2002, et ils ont suivi les plantules mensuellement. La plupart des plantules émergent de septembre à décembre. L'émergence, plus variable dans les sites perturbés, atteint un maximum deux mois plus tôt. Au cours des années, la survie va de 3.5 à 12.0 %. La densité des plantules varie de 1–75 par parcelle de 0,25m², avec une médiane générale de 6,0. La survie ne dépend pas de la densité. L'âge médian de la floraison va de 11.7 à 15.2 mois, les recrues de la fin de saison ayant plus de chance de survivre. Le *Warea carteri* recrute comme une plante annuelle d'hiver, mais fleurit comme une annuelle estivale. Sa germination tardive et son cycle de vie de 12–15 mois contribuent au cyclage de la population. Un échec complet de la reproduction au cours d'années défavorables, une forte production de graines au cours des années favorables, un faible taux de germination, et une banque de semence persistante correspondent aux prédictions pour une espèce annuelle dans un habitat variable.

Mots-clés : annuelles, germination retardée, dépendance de la densité, habitats perturbés, annuelle estivale, annuelle d'hiver.

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Introduction

Seedling establishment is a critical stage in the life history of any plant species that relies on sexual reproduction for the persistence of its populations (Grubb 1977; Harper 1977). Seeds must reach "safe sites" that promote germination and provide an environment favorable to seedling survival and growth. Perennial plants maintain their populations through the longevity of individuals and (or) clonal reproduction (e.g., Forbis and Doak 2004) and thus may require only infrequent recruitment to maintain viable populations

(Pierson and Turner 1998; Wiegand et al. 2004). In contrast, annual plants without persistent seed banks rely on the yearly recruitment of seedlings and on their development into sexually reproductive adults. Failure of seedling recruitment can result in local extinction (Morgan 1985). However, many annual plants have persistent seed banks, which may buffer populations from environmental extremes (Cohen 1966; Kalisz and McPeck 1992, 1993), allow populations to recover after several years without aboveground reproductive plants (Menges and Quintana-Ascencio 2004), and reduce extinction risk (Stocklin and Fischer 1999).

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Seedling recruitment rates vary in time and space (Crawley 1990; Oostermeijer et al. 1996; League and Veblen 2006) in response to seasonal weather patterns and local habitat conditions. Seedling survival is a product of many factors, including seedling density (Gilbert et al. 2001), timing of seedling emergence (Harper 1977; Fernandez-Quintanilla et al. 1986; Weiner 1988; Dyer et al. 2000; Turkington et al. 2005; Verdu and Traveset 2005), herbivory (Fenner 1987), and pathogens (Augspurger and Kelly 1984). While density-dependent seedling survival is prevalent in many tropical forests (Clark and Clark 1984), it also occurs over a wide latitudinal range (Lambers et al. 2002). However, many studies have failed to find evidence that seedling survival declines with density (Ehrlén and Eriksson 1996; Connell and Green 2000).

Seedling survival rates may also vary among cohorts that emerge at different times in the annual cycle (Miller 1987; Verdu and Traveset 2005). For example, early emergents may have an advantage over later ones because of competition for light (Miller et al. 1994) or avoidance of mortality due to flooding (Jones et al. 1997) or drought (Lonsdale and Abrecht 1989). Presumably, early emergents are better able to deal with environmental stress because of their greater size (Turkington et al. 2005; Verdu and Traveset 2005). On the other hand, early emergents may suffer higher rates of mortality because of their longer exposure to predation or pathogens (Marks and Prince 1981; Jones and Sharitz 1989; Rice 1990).

Carter's mustard (*Warea carteri* Small; Brassicaceae) is a federally listed endangered annual plant endemic to fire-prone xeric upland habitats on central Florida's Lake Wales Ridge (US Fish and Wildlife Service 1999). It is characterized by dramatic fluctuations in aboveground population size, particularly in response to fire² (Menges and Gordon 1996). Seedling recruitment is protracted and may occur prior to the onset of flowering by the previous annual cohort. Thus, there is some overlap between annual cohorts.

In addition to its preferred natural habitats, Carter's mustard also occurs along roadsides, firelanes, and trails. Although roadsides and similar anthropogenic habitats offer open conditions and thus opportunities for less competitive species, these disturbed habitats may favor weedier life history adaptations than intact upland habitats (Quintana-Ascencio et al. 2007). Periodic disturbances caused by animal or human traffic differ from the less frequent but more widespread effects of fire, and this may in turn create differences in population dynamics of a species, such as Carter's mustard, that can survive in both roadside and scrub habitats. Demographic mechanisms that may differ include seedling emergence, survival to flowering, and timing of flowering. Because population persistence in annual plants is so often dependent on yearly renewal of the seed bank, survival to flowering is a key metric of demographic success. In addition, plant age and size at flowering are important measures of the effects of habitat, density, and time of emergence on population dynamics.

Our goals in this study were (i) to compare patterns of seedling emergence and survival of Carter's mustard in two contrasting habitats (scrub vs. disturbed sites), (ii) to test the

hypothesis that seedling survival is density dependent, (iii) to assess the effect of timing of emergence on seedling survival, and (iv) to determine ages and sizes at flowering.

Methods

Study species and study sites

Carter's mustard is a south-central Florida endemic formerly known from the Atlantic Coastal Ridge in Miami-Dade and Brevard Counties, but currently restricted to the Lake Wales Ridge in Highlands and Polk Counties. On the Lake Wales Ridge, Carter's mustard occupies a variety of pyrogenic xeric upland habitats from scrubby flatwoods to sandhills, as well as roads and trails traversing its preferred habitats (US Fish and Wildlife Service 1999). It is an edaphic generalist on nutrient-poor, moderately to extremely well-drained upland soils (Menges et al. 2007). Fire promotes population booms in the first year postfire (Menges and Gordon 1996), generally followed by population crashes and subsequent damped fluctuations in years between fires.² Populations occupying mechanically disturbed sites may exhibit less extreme fluctuations in aboveground size (Menges and Gordon 1996).

Carter's mustard is a single-stemmed, multi-branched herb to 1 m in height. Leaf morphology is highly variable, especially in seedlings. Seedlings often persist as rosettes throughout the October–May dry season before bolting with the onset of the June–September rainy season. Flowering occurs from late September through October, and fruiting occurs from mid-October to December. Plants bear several to many ping-pong ball-sized inflorescences, each comprising 10–25 white four-petaled flowers. Flowers are bisexual, self-compatible, and autogamous, although most fruit set is due to insect visitation (Evans et al. 2000). Fruits are siliques that shed their seeds from the plant by dehiscent. Most seeds fall beneath or near the parent plant, and there is no obvious means of secondary dispersal. Field germination experiments have shown that most germination is delayed by about 1 year, which creates an overlap of generations. Disturbances create favorable conditions for germination and seedling survival, and synchronize seedling establishment, thereby generating a cycle of population sizes with a 2-year period.²

We conducted the study in two Florida scrub populations, at Lake Wales Ridge State Forest (27°11'N, 81°21'W) in Polk County and at Archbold Biological Station (27°10'N, 81°21'W) in Highlands County. At the State Forest, we established seedling quadrats at four sites in oak–hickory scrub and along trails through the scrub. At Archbold, seedling quadrats occupied two scrubby flatwoods sites. The climate in south-central Florida is characterized by a 4-month summer rainy season (June–September) and an 8-month dry season (October–May; Chen and Gerber 1990).

Study sites comprised two habitat types: disturbed sites differed from Florida scrub sites in having been radically altered by mechanical disturbance in the past or in being subject to recurrent disturbance by animals or humans. Approximately 40 years prior to this study, one site was root-raked, a procedure used by citrus growers to remove

²P.F. Quintana-Ascencio, E.S. Menges, C.W. Weekley, M.I. Kelrick, and B. Pace-Aldana. Submitted for publication.

the belowground parts of clonal oaks (*Quercus* spp.) and re-pent palmettos (*Serenoa repens*, *Sabal etonia*); the site remains largely devoid of woody plants and palmettos. Trails through intact scrub are kept open and frequently impacted by passing deer, feral hogs, and humans. In contrast with these mechanically disturbed sites, fire is the natural disturbance in Florida scrub.

Sampling protocol

Relying on previously marked patches of flowering Carter’s mustard, between 1999 and 2002 we established 78 permanent 0.25 m² quadrats. Most quadrats were centered on extant seedlings; we also occasionally set up quadrats near large flowering adults in the expectation of subsequent seedling emergence. Although not all quadrats were occupied every year, quadrat occupancy was always >70% (range 71.0%–77.4%). The small area encompassed by the quadrats facilitated close scrutiny and early identification of seedling emergents. We followed individually marked seedlings monthly from emergence to flowering or death, recording survival, size, and reproductive status.

Analysis

To analyze patterns of seedling emergence and survival, we created a series of four nonexclusive binary logistic regression models with year and habitat as the main effects. We used the corrected Akaike information criterion AIC_c (Burnham and Anderson 2002) to assess the relative support for the various models. In analyses with competing models, we used model averaging to judge the strength of each variable. Using density per quadrat for the 3 years of the study, we also performed a logistic regression to evaluate the effects of seedling density on seedling survival. For graphical presentation, we grouped densities into classes.

To evaluate the effects of timing of emergence on survival, we grouped monthly cohorts into early (June–August), peak (September–December), and late (January–May) season cohorts; peak season months had seedling emergence rates >10%. Survival to flowering in the resulting seasonal cohorts was analyzed with χ^2 tests. We used survival analysis to quantify differences in the median age of flowering plants in the two habitats. All statistical procedures were performed in SPSS version 11.5 (SPSS 2003); for survival analysis, we used the Life Table procedure.

Results

Seedling emergence

Most Carter’s mustard seedling emergence occurred between September and December, but patterns of emergence varied between habitats and among years. Of the 1329 emergents tagged in monthly censuses between 1999 and 2002, we recorded 83.6% between September and December, at the end of the June–September wet season, and in the early dry season (Weekley et al. 2007). The overall pattern of emergence was similar for scrub and disturbed sites (Fig. 1), with both habitats recruiting >80% of their seedlings during this 4-month period. However, emergence peaked 2 months earlier in the disturbed sites than in the scrub. Early (June–August) recruitment was similar for the two habitats (10.8% for disturbed, 9.8% for scrub), but late

Fig. 1. Percentage of seedlings emerging by month and by habitat, summed for three annual cohorts of Carter’s mustard, 1999–2002.

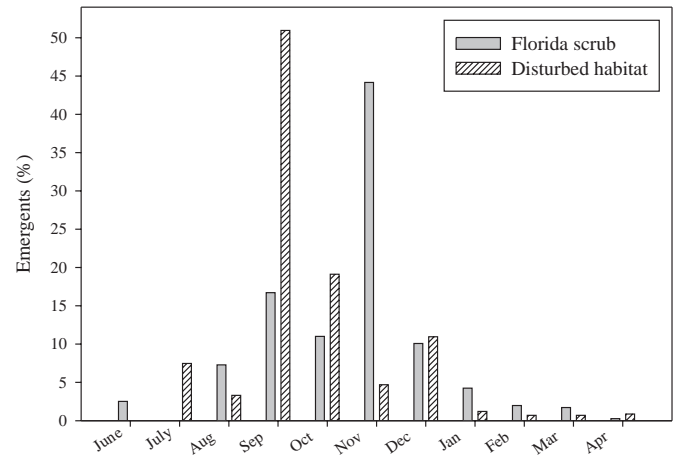
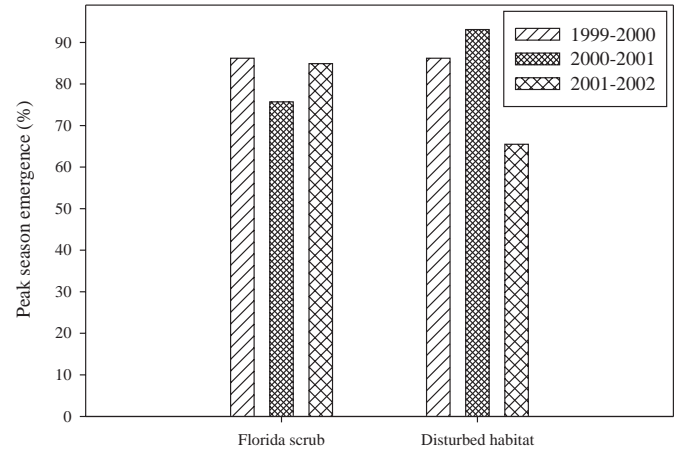


Fig. 2. Percent annual peak season emergence rate for Carter’s mustard seedlings in Florida scrub and disturbed habitats, 1999–2002.



(January–April) recruitment was over twice as high in scrub (8.2%) as in disturbed sites (3.4%).

Patterns of seedling emergence between the two habitats also varied among years (Fig. 2). In 1999–2000, there was no difference in the proportion of seedlings emerging in peak (September–December) versus nonpeak (June–August and January–April) seasons in scrub and disturbed habitats (86.2% emergence for both habitats). In 2000–2001, however, disturbed sites had higher emergence during the peak season than scrub (95.1% vs. 75.7%), while the situation was reversed in 2001–2002, with peak season emergence higher in scrub than in disturbed sites (84.9% vs. 65.5%). Annual peak season emergence rates were less variable in scrub than in disturbed sites, with a coefficient of variation for scrub of 6.9% versus 17.6% for disturbed sites

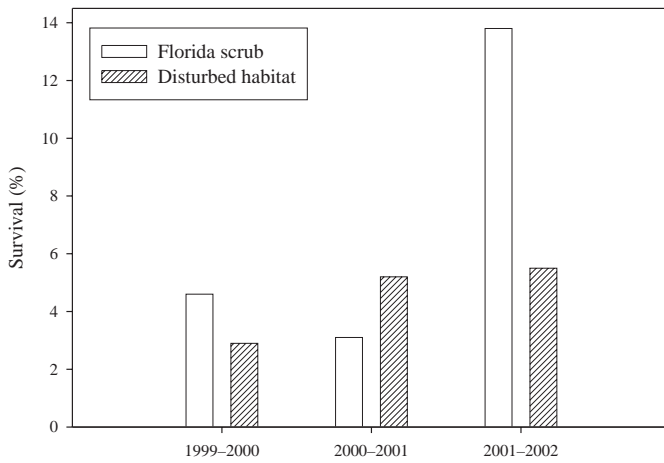
In the binary logistic regression models, neither year nor habitat alone was sufficient to explain variation in patterns of peak versus nonpeak seedling emergence (Table 1), but the model with both factors and their interaction was strongly supported by AIC_c.

Table 1. Akaike information criterion (AIC_c) results of binary logistic regression models with the proportion of peak versus nonpeak season emergents as the dependent variable.

Model	<i>K</i>	-2log likelihood	AIC _c	Δ _{<i>i</i>}	<i>w_i</i>
Year + habitat + year × habitat	6	1128.777	1140.84	0	1.000
Habitat	2	1182.831	1186.84	46.00	0.000
Year	3	1180.863	1186.88	46.04	0.000
Year + habitat	4	1179.584	1187.61	46.77	0.000

Note: *K*, number of parameters in the model; -2log likelihood, test parameter from the logistic regression model; AIC_c, corrected Akaike information criterion; Δ_{*i*}, AIC_{*i*} - AIC_{min}; and *w_i*, Akaike weight indicating the degree of support for each model (values range from 0 to 1). *N* = 1329 for all models.

Fig. 3. Percent seedling survival by year and habitat for three annual cohorts of Carter's mustard.



Seedling survival

Seedling survival also was affected by habitat and year. Over the 3 years, 7.7% of recruits (102/1329) survived to the flowering season (late September–October), and all but 9 of these survivors flowered. Overall survival varied from 3.5% in 1999–2000 to 12.0% in 2001–2002. In 2 of 3 years, percent seedling survival to flowering was greater in scrub than in disturbed sites (Fig. 3). AIC_c evaluation of the binary logistic regression models offered support to both single and multifactor models, but the strongest model incorporated habitat, year, and their interaction (Table 2). Model averaging revealed that habitat is the strongest variable in all models (sum of Akaike weights = 0.8815 for habitat vs. 0.6627 for year).

Effect of density on seedling survival

Over the 3 years, seedling density per quadrat ranged from 1 to 75 with a median of 6.0 for both scrub and disturbed sites (mean ± SD: 9.1 ± 11.2). However, median density differed significantly among years (Kruskal–Wallis $\chi^2 = 9.345$, *df* = 2, *p* = 0.009), with the highest density in 2000–2001 (10.5 seedlings per quadrat) and the lowest in 1999–2000 (4.0 seedlings per quadrat). Density did not differ annually between the two habitats (Fig. 4; Mann–Whitney *U* tests: *p* > 0.05 for all years). In the logistic regression model, density was not a significant predictor of survival (*p* = 0.951). Survival showed no clear pattern with density class (Fig. 5).

Differential survival among early, peak, and late season cohorts

Overall, 74.2% of the plants that survived to flower be-

longed to the peak season cohort. Summed over all years and sites, there was a significant difference in the percentage of plants surviving to flowering among the three seasonal cohorts ($\chi^2 = 17.162$, *df* = 2, *p* < 0.001; Fig. 6), with late cohorts having higher survival to flowering (18.3%) than either peak season (6.2%) or early cohorts (6.6%). For scrub sites, there was a significant difference among cohorts summed over the 3 years ($\chi^2 = 9.290$, *df* = 2, *p* = 0.010): percent survival ranged from 6.8% for early cohorts, to 8.1% for peak season cohorts, to 19.4% for late cohorts. For disturbed sites, the pattern was similar (6.5%, 3.9%, and 15.0% for early, peak, and late cohorts, respectively), but significance could not be tested because of low expected frequencies. In 2001–2002, survival was higher in the late cohort than in the peak season or early cohorts (28.6% vs. 10.2% and 10.4%, respectively; $\chi^2 = 19.129$, *df* = 2, *p* = 0.001). For the other 2 years of the study, high overall mortality precluded any statistical tests.

Age and size at flowering

Median age at flowering varied from 11.7 to 15.1 months for the three annual cohorts. It did not differ between scrub and disturbed sites in 1999–2000 (Wilcoxon (Gehan) statistic = 1.556, *df* = 1, *p* = 0.212) or in 2001–2002 (Wilcoxon (Gehan) statistic = 0.459, *df* = 1, *p* = 0.498), but there was a significant difference in 2000–2001 (Wilcoxon (Gehan) statistic = 6.289, *df* = 1, *p* = 0.012), with median age about 3 months greater in the scrub sites (14.4 vs. 11.7 for disturbed). All flowering plants were ≥26 cm in height, while 60% of plants <26 cm in height failed to flower.

Discussion

Carter's mustard recruits like a winter annual but reproduces like a summer annual. Like a winter annual, it recruits largely in the fall before its main growing season. Approximately 3/4 of seedling emergence occurred during a 4-month period running from September (late rainy season) to December (mid dry season). Although most seedling emergence took place at the end of the June–September rainy season, additional emergence peaks sometimes followed heavy winter rainfall (e.g., November 2001). Like a summer annual, Carter's mustard flowers in the fall following emergence, whereas winter annuals typically flower in the spring. As a result of this pattern, most plants flowered when they were slightly older than 12 months of age. If an annual is strictly described as a plant living no longer than 12 months, then Carter's mustard is not an annual at all. However, labeling Carter's mustard a biennial would be problematic, as most biennials have substantial growth

Table 2. Akaike information criterion (AIC_c) results of binary logistic regression models with proportion of peak versus nonpeak season survivors as the dependent variable.

Model	<i>K</i>	-2log likelihood	AIC _c	Δ _{<i>i</i>}	<i>w_i</i>
Year + habitat + year × habitat	6	635.501	647.56	0	0.431
Habitat	2	644.048	648.06	0.49	0.337
Year	3	644.130	650.15	2.58	0.118
Year + habitat	4	642.218	650.25	2.68	0.113

Note: *N* = 1329 for all models. Column headings are as in Table 1.

Fig. 4. Boxplots showing seedling densities (number of seedlings per 0.25 m² quadrat) of Carter’s mustard by year and habitat. Solid lines within boxes are medians, broken lines are means, upper and lower horizontal bars are 75th and 25th percentiles, respectively. Upper and lower “whiskers” show 90th and 10th percentiles, respectively, and circles indicate extreme outliers.

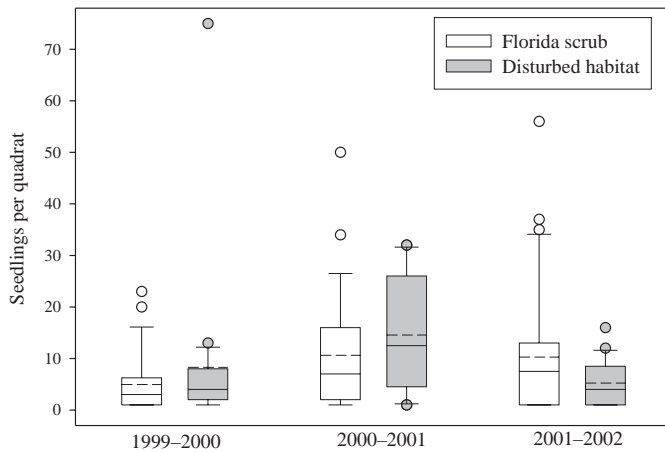
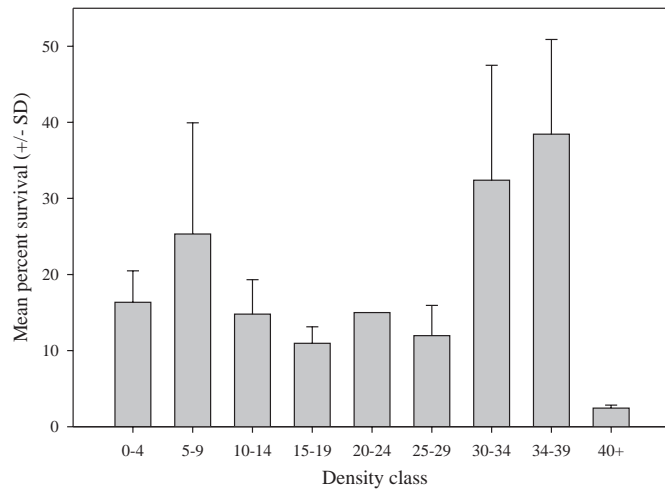


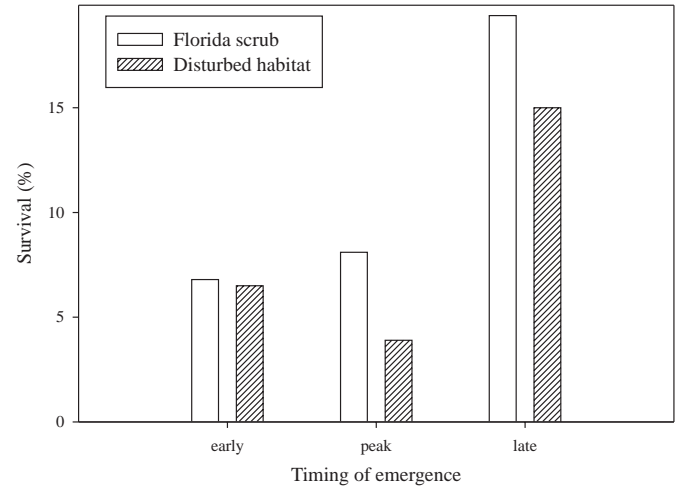
Fig. 5. Mean percent survival to flowering by density class (±SD) for Carter’s mustard summed for three annual cohorts.



during two growing seasons (Harper 1977, p. 542). The mild winter of subtropical south-central Florida may blur life history classifications usually applied to plants in climates with greater seasonal temperature extremes.

Demographic variation in Carter’s mustard is strongly affected by fire. Within the xeric uplands of the Lake Wales Ridge, Carter’s mustard is a habitat generalist (US Fish and Wildlife Service), occurring in sites that historically burned

Fig. 6. Percent seedling survival by timing of emergence for Carter’s mustard seedlings in two habitats, summed over 3 years.



both frequently (e.g., sandhills, 2–4 years) and infrequently (e.g., scrubby flatwoods, 5–20 years; Menges 1999). Because of delayed germination², Carter’s mustard is characterized by overlapping cohorts. In its natural habitats, fire, by killing one cohort, initiates an alternating 2-year cycle of boom and bust. This strong aboveground variation is buffered by high seed production in surviving individuals (interquartile ranges 7–48 fruits per plant, 1–13 seeds per fruit, median seeds per plant = 117; E.S. Menges, unpublished data, 1996) and the presence of a persistent seed bank.² Because the seed bank is long-lived, Carter’s mustard may reappear after many years of absence, especially following fire (Menges and Gordon 1996).

Differences in seasonal rainfall patterns provide the most obvious explanation for annual differences in survival observed over the 3 years of this study. Carter’s mustard occurs in a variable but largely predictable climate with a 4-month summer rainy season and an 8-month dry season (Chen and Gerber 1990). Although seasonality of rainfall is predictable, the climate is variable, in that winter storms and El Niño events may result in relatively wet winters in some years. Thus, overall seedling survival was highest (12.0%) in the wettest year (October–September 2001–2002: 1321 mm at the State Forest, 1681 mm at Archbold) and lowest (3.5%) in the driest year (October–September 1999–2000: 1213 mm at the State Forest, 829 mm at Archbold).

Despite considerable variation in seedling densities among populations and years, we found no evidence of density-dependent seedling mortality in Carter’s mustard. Although density-dependent mortality is often detected in seedling

survival studies (e.g., Symonides 1979; Keddy 1981; Law 1981; Smith 1983; Clark and Clark 1984; Gilbert et al. 2001; Lambers et al. 2002), there are also many examples where such effects are weak or absent (e.g., Torstenson 1987; Nilsson 1995; Ehrlén and Eriksson 1996; Connell and Green 2000). Lack of density dependence in Carter's mustard may reflect sensitivity to nearby shrubs, rather than conspecifics, a pattern likely for other subordinate Florida scrub plants (Hawkes and Menges 1995; Menges and Kimmich 1996; Quintana-Ascencio and Morales-Hernández 1997).

Although many studies have shown that cyclical population fluctuations are the result of density dependence (Symonides et al. 1986), other factors may also cause population cycling in annual or biennial plants (Thrall et al. 1989). The absence of density-dependent seedling mortality in Carter's mustard is consistent with demographic models, indicating that population fluctuations with a period of 2 years are caused primarily by delayed germination rather than by density dependence².

The higher overall survival of late season cohorts compared with early or peak season cohorts was driven largely by higher survival in scrub than in disturbed sites and in the 2001–2002 annual cohort. Thus, late season cohorts are favored only under specific circumstances. While many studies have shown that early emergents are favored over later ones in survival, growth, and fecundity (reviewed in Verdu and Traveset 2005), far fewer studies have demonstrated an advantage for late emergents (however, see Baskin and Baskin 1972; Lacey 1982). In a meta-analysis based on 55 studies of seedling emergence times, Verdu and Traveset (2005) concluded that early emergence had no effect on survival, but did provide benefits in seedling growth and fecundity. They also found that the survival benefit of early emergence was greater in perennials than in annuals. The apparent absence of higher survival in early season cohorts of Carter's mustard is consistent with these conclusions.

One potential advantage of late emergents is their reduced exposure to seasonal hazards such as drought. In Carter's mustard, plants emerging in the first summer or fall (i.e., early or peak season emergents) must be able to survive up to 8 months of relatively dry conditions, while seedlings emerging halfway through the dry season would avoid some of the driest conditions.

Seedlings emerging as early as the first June of the annual cohort or as late as the following April survived to flowering. Plants as young as 7 months and as old as 16 months flowered, with 16.1% of flowering plants <11 months old and 22.6% >13 months old. Since all plants ≥ 26 cm in height flowered, irrespective of age, plant size appears to be a more important determinant of flowering than age. Short-statured survivors that failed to flower ($n = 9$) came from all three seasonal cohorts and may have been victims of vertebrate herbivory. However, late emergents may be smaller at the time of flowering, which may reduce their fecundity.

Nonetheless, Carter's mustard exhibits some variability in the timing of emergence through individual years. Because early emergence may favor size and fecundity (Verdu and

Traveset 2005), and late emergence may favor survival to flowering, there may be stabilizing selection for peak emergence between September and December. Alternatively, staggering germination over a period of several months may constitute a bet-hedging strategy in a variable environment.

Within the Florida scrub flora, Carter's mustard and the congeneric clasping warea (*Warea amplexifolia* (Nutt.) Nutt.) are all but unique in being annual plants. *Paronychia chartacea* subsp. *chartacea* Fernald is sometimes considered an annual, but recent evidence suggests that it is more accurately characterized as a short-lived perennial.³ The annual habit in plants is favored in environments subject to frequent disturbance, when the probability that a seed will establish a flowering plant within one season is greater than the probability that an adult will survive to another flowering season (Watkinson and Davy 1985). Cohen's (1966) model predicts that in habitats where complete reproductive failure may occur in unfavorable years, an annual species will have high seed production in favorable years, low rates of seed germination, and a seed bank capable of persisting for at least 1 year.

Although growing in an ecosystem dominated by perennials, the annual Carter's mustard conforms to Cohen's predictions of life history traits evolved in variable environments.

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