

Northwest Science Notes

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An Unusual Life History Strategy in *Lepidium papilliferum* (Brassicaceae), A Rare Mustard Endemic to Southwestern Idaho

Abstract

Lepidium papilliferum (Brassicaceae) is a rare mustard endemic to sagebrush-steppe habitat in southwestern Idaho. The species, commonly known as slickspot peppergrass, has been described as having two life history patterns with respect to flowering – annual and biennial. Annuals germinate, flower, and die all within their first year, whereas biennials exist as vegetative rosettes in their first year, overwinter, and then reproduce and die in their second year. In this article we identify a third, albeit uncommon, pattern of flowering for *L. papilliferum* whereby individuals engage in limited flowering and seed production late in their first year, and then, if they survive the winter, flower and set seed again in their second year. In a study conducted at two *L. papilliferum* populations from June 2007 to June 2008, we found that individuals that flowered late in their first season (N = 34) suffered 59% overwinter mortality, whereas biennials that put off all reproduction until their second year (N = 200) suffered significantly less overwinter mortality at 24% ($\chi^2 = 17.094$, $P < 0.001$). We discuss various possibilities for the adaptive significance of multiple flowering in *L. papilliferum* given the higher overwinter mortality for individuals that exhibit this life history strategy.

Introduction

Flowering plants have evolved a wide variety of life history strategies to maximize individual fitness in response to uncertainty of the conditions in which they live (Cole 1954, Hastings and Caswell 1979, Wilbur and Rudolf 2006). Three life history strategies that relate to patterns of longevity and flowering are widely recognized: annual, biennial, and perennial. Annuals germinate, reproduce, and die within a single season, whereas biennials typically germinate and grow in the first season, endure an overwintering or non-growing season, reproduce, and then die. By contrast, most perennials are capable of surviving through many

reproductive cycles during their lifetimes (Young and Augspurger 1991, Sutherland 2004, Tank and Olmstead 2008), although some long-lived species such as the century plant (*Agave* sp.) live for many years but reproduce only once.

Most plants are defined by single life history strategy, although there are some examples of species with multiple strategies (Reinartz 1984, Lacey 1988). Our investigation focuses on a rare mustard endemic to southwestern Idaho that is known to exhibit two life history strategies. *Lepidium papilliferum* (L.F. Hend.) A. Nels. and J.F. Macbr. (Brassicaceae), commonly known as slickspot peppergrass, exhibits both annual and biennial life forms throughout its range (Moseley 1994, Meyer et al. 2005). The species occurs in sagebrush-steppe habitat where it is restricted to microsites known as slick spots—shallow depressions of soil devoid

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of other plants and characterized by high levels of clay and salt as well as by subsurface water retention that is higher than that of surrounding areas (Quinney 1998). Following germination late in the spring, the germinants follow either an annual or biennial life history trajectory. Annuals flower, set seed, and die within a few months, whereas biennials forgo reproduction in their first summer of growth, overwinter as vegetative rosettes, and then reproduce in their second season before dying. Biennials that survive to reproduce are typically much larger than annuals, and produce many times the number of seeds (Meyer et al. 2005, personal observations of the authors). There are no accounts of individuals delaying flowering for more than a single season. Both life history forms co-occur in the same population, often within inches of one another. The life history trajectory an individual takes is thought to be influenced by environmental cues and the individual's state (Meyer et al. 2005, Quinney 2005); however, no specific mechanisms have been identified.

Our observations over several years of have revealed a third, and much less common, flowering pattern in *L. papilliferum* that is intermediate to the annual and biennial forms. Specifically, a small percentage of germinants begin life in what appears to be the vegetative phase of a biennial life cycle, but then late in the season (i.e., after annuals have already set seed and died) these individuals produce one or several shoots that develop flowers, fruits, and seed. The shoots wither and die after the fruits dehisce their seeds, but the main rosette persists. Our goal in the present study was to investigate whether individuals exhibiting this late-season flowering strategy survive to reproduce the following year, and if so, whether they suffer higher overwinter mortality than biennials.

Methods

We conducted our study from June 2007 to June 2008 at two populations of *L. papilliferum*—Kuna Butte (KB: UTM Zone 11, 542071 E 4804054 N; 25 km southwest of Boise, Idaho) and Big Gulch (BG: UTM Zone 11, 545035 E 4842856 N; 15 km northwest of Boise). At both sites we marked a total of 100 vegetative rosettes (selected randomly from up to 10 slick spots at each site) in early June with a uniquely numbered tag secured in the soil adjacent to each plant. We monitored

each rosette's status bimonthly for a year. For those vegetative rosettes that over-wintered successfully, we recorded whether or not they flowered and set seed in their second year.

In addition to tagging and monitoring vegetative rosettes, we searched both sites intensively for rosettes that showed signs of flowering late in the summer of their first year. Upon discovery, these individuals were tagged and monitored using the same protocol as for non-flowering rosettes. Although tagging of late-flowering individuals occurred later (i.e., early July) than it did for vegetative rosettes, no mortality occurred in vegetative rosettes until after late-flowering individuals had been tagged. Thus, our estimates of mortality within each group were unaffected by the timing of discovery and tagging. We located a total of 34 late-flowering rosettes, 17 at each site. At the end of the monitoring period we used a chi-squared contingency analysis (JMP, version 5.1, SAS institute, Cary, North Carolina, USA) to test for differences in overwinter survival between vegetative rosettes and flowering rosettes.

Results

Seventy-four of the 100 vegetative biennial rosettes monitored at KB, and 78 of the 100 monitored at BG, survived to reproduce and set seed during their second year. Because the difference in overwinter survival between sites was not statistically significant ($\chi^2 = 0.439$, $P = 0.51$), we pooled the data for subsequent analysis. Among the rosettes that flowered late in their first year, 8 of 17 at KB, and 6 of 17 at BG, survived to reproduce a second time the following summer. Again, because the difference in overwinter survival between sites was non-significant ($\chi^2 = 0.486$, $P = 0.49$), we pooled the samples. Combining data from both sites, non-flowering rosettes were significantly more likely than flowering rosettes to survive winter and reproduce the following summer (152 of 200 [76%] versus 14 of 34 [41%], respectively; $\chi^2 = 17.094$, $P < 0.001$).

Discussion

Slickspot peppergrass is typically described as a monocarpic species with two life history strategies – annual and biennial, both of which involve a single episode of reproduction during the plant's lifetime (Moseley 1994, Quinney 1998, Meyer et

al. 2005). We identified a third, albeit uncommon, flowering pattern which involves two episodes of reproduction, one late in the first year and one in the second. Individuals exhibiting this dual flowering strategy begin life in what appears to be the vegetative phase of the biennial life cycle. However, in mid to late summer they sprout one to several shoots, which proceed to flower, fruit, and set seed. No more than 25 fruits are typically produced during late-season flowering. Once seeds are released the shoots wither and die, leaving a rosette that once again resembles the vegetative state of a biennial. Although we did not quantify seed production by individuals that survived winter, there were no obvious differences in fruit set between biennials and individuals that flowered the previous year. In future studies it would be informative to record metrics such as plant diameter before and after winter to see if growth and reproductive output are influenced by an individual's life history strategy.

The mechanisms that lead to the various life history trajectories in *L. papilliferum* are not well understood. Meyer et al. (2005) suggested that phenotypic plasticity is the most likely explanation for the annual versus biennial life histories in *L. papilliferum*, based on the premise that genotypic differences in life histories would lead to the elimination of the less fit strategy, and their finding that biennials have lower mean lifetime fitness than annuals because of higher mortality. The phenotypic plasticity hypothesis maintains that all *L. papilliferum* germinants have the potential to become either annuals or biennials, and that the life history trajectory an individual takes depends on the reaction norm between its physiological state (e.g., size, nutrient reserves) and local microclimate (e.g., soil moisture, nutrient availability).

Phenotypic plasticity may explain late season flowering in the first year by rosettes that initially appeared as typical biennials. For example, rosettes in poor physiological condition may opt for limited reproduction late in their first year to offset their elevated probability of death over the winter. From an evolutionary sense, an individual's investment in current reproduction is expected to increase when prospects for future reproduction are diminished (Wilbur and Collins 1973, Lacey 1986). This explanation is consistent with our find-

ing that overwinter mortality was higher among individuals that flowered late in their first year than among individuals that deferred all reproduction until their second year (59% versus 24%, respectively). However, we cannot rule out the possibility that high overwinter mortality among individuals that flowered late in their first year reveals a cost of reproduction. Increased overwinter mortality among rosettes that flowered in their first year may indicate that investment in reproductive structures diverted resources that would otherwise have been used for maintenance (Reznick 1985, Avila-Sakar et al. 2001).

It is noteworthy that overwinter mortality in our study was lower than previously reported for biennials. Specifically, Meyer et al. (2005) reported that 77% of biennials failed to survive the summer and winter of 1995-96, whereas only 24% failed to survive in our study. These differences may be explained by the relatively mild conditions experienced in the winter of 2007-2008. Under less favorable climatic conditions higher mortality rates would be expected for all *L. papilliferum* rosettes, and the differences in mortality between late-flowering rosettes and vegetative rosettes may become even more pronounced than in the present study.

It remains an open question whether a diversion of resources from maintenance to flowering would be sufficient to explain the significant increase in overwinter mortality among individuals that flowered late in their first year, or whether it was simply a factor that contributed to higher mortality among individuals that already had reduced prospects for survival. Moreover, additional information is needed to establish whether or not it is the rosettes in poor condition that proceed to reproduce late in their first year. Experimental manipulations of growing conditions may be the key to understanding the mechanisms that control life history trajectories in this rare and enigmatic plant.

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