ALLOCATION OF REPRODUCTIVE RESOURCES WITHIN AND AMONG INFLORESCENCES OF LAVANDULA STOECHAS (LAMIACEAE)

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Patterns of fruit set were studied in Lavandula stoechas, a Mediterranean shrub commonly occurring in southern Spain. The small, hermaphroditic flowers of this shrub are aggregated into dense, headlike inflorescences and exhibit extensive variations in fecundity. It was shown that as the number of developing fruits in the inflorescence increased, the probability of a flower setting fruit, the size of seeds, and their germinability decreased, most likely because of strong within-inflorescence resource limitation. An experiment was designed to ascertain whether increased fertility in late-opening flowers could be induced through reallocation of reproductive resources between different inflorescences. The experiment consisted of removing half of the inflorescence buds from a set of plants and comparing their fecundity with that of intact individuals. Thinning did not increase the proportion of flowers setting fruit which, in fact, was slightly lower than that of intact individuals (probably due to some reduction of floral display brought about by thinning). Although treated plants produced heavier seeds than controls, results suggest that inflorescences of L. stoechas behave as autonomous modules among which resources cannot be reallocated. Predispersal seed predation by insects accounted on average for a 31% reduction in fruit set. Predation was found to be nonrandomly distributed within inflorescences, with most damage concentrated on late fruits (i.e., those with smaller and less germinable seeds).

Plants often have their flowers aggregated into higher-level units termed inflorescences. Species differ widely in the organization, compactness, and size of their inflorescences (Weberling, 1965), but in some cases flowers are so perfectly integrated and packed that the whole inflorescence may become a pollinator attraction unit by resembling a single flower (pseudanthium), as in the capitula of the Compositae (Faegri and Van der Pijl, 1979). It is accepted that inflorescences represent gamet-packages molded mainly by selection pressures related to pollination, resource distribution, and fixed costs of associated structures (Schoen and Dubuc, 1990).

The aggregation of flowers into semiautonomous, physiologically integrated units (Watson and Casper, 1984) sometimes results in a conflict between different floral functions (Wyatt, 1982). For example, many-flowered inflorescences increase pollinator attraction (Wilsson and Price, 1977; Cruzan, Neal, and Willson, 1988; Palmer, Travis, and Antonovics, 1988), but as pollination takes place, interovary competition for resources can dramatically affect fruit and seed set (Stephenson, 1979, 1980; Bawa and Webb, 1984; Holtsford, 1985). Thus, the flowers in an inflorescence may have different reproductive values for the plant but be morphologically identical. Among-flower variation in fecundity that occurs in hermaphroditic plants has resulted in a considerable body of literature on ‘surplus’ flowers (Willson and Price, 1977; Stephenson, 1981; Queller, 1983), serial adjustment of reproductive resources (Lloyd, 1980; Lloyd, Webb, and Primack, 1980), flower/fruit ratios (Sutherland, 1986, 1987), and selective fruit abortion (Bookman, 1983; Stephenson and Winsor, 1986).

There is evidence that plants can easily reallocate reproductive resources within inflorescences. Following flower or pod thinning, for example, larger seeds can be produced (Maun and Cavers, 1971) or the probability of setting fruit can change (Stephenson, 1979, 1980). Much less is known, however, on the relationship among flowers on different inflorescences. For example, to what extent does the probability of setting a fruit depend on the number of flowers elsewhere on the plant?

The goals of the present study were to investigate the within-inflorescence pattern of fe-
cundity in *Lavandula stoechas* (Lamiaceae) and to gain some knowledge on the extent to which dense inflorescences act like independent reproductive modules. In *L. stoechas*, the architecture of the inflorescence determines a distinct pattern of flower opening that can be tracked when flowering has ceased, thus making the plant suitable for studying among-flower variations in fecundity and the factors associated with it. In addition, the whole set of inflorescence buds corresponding to a reproductive episode appear simultaneously on the plant just before the onset of flowering, which allows manipulation of overall flower number. Previous studies have demonstrated that neither the rate of nectar secretion (Muñoz and Devesa, 1987) nor the number of seeds per fruit (Devesa, Arroyo, and Herrera, 1985) are evenly distributed within inflorescences.

**MATERIAL AND METHODS**

The plant— *Lavandula stoechas* L. (Lamiaceae) is a xerophytic, aromatic shrub up to 1 m high that commonly occurs in shrubland communities of southern Spain. It grows on a wide range of soil types under dry, sunny conditions at elevations below 1,500 m. Populations differing in floral and inflorescence traits have been given varietal or subspecific status (Devesa, Arroyo, and Herrera, 1985). The results reported here refer to subspecies *sam-paiana* Rozeira, characterized mainly by comparatively short and few-flowered inflorescences. Plants grow and flower in most populations during late winter and early spring (February through May; Herrera, 1986) and are dormant during summer and autumn. A variety of Lepidoptera, Diptera, and Hymenoptera (mostly honeybees) pollinate *L. stoechas* in southern Spain (Herrera, 1988).

The flowers of *L. stoechas* are hermaphroditic and tubular (Fig. 1), have a dark purple, tubular corolla, and secrete minute amounts of sugar-rich nectar (Herrera, 1985). The pollen : ovule ratio is near 1,000. *L. stoechas* is self-compatible, but self-pollination seldom if ever takes place because of very strong protandry (Devesa, Arroyo, and Herrera, 1985; Muñoz and Devesa, 1987). Inflorescences are headlike, nearly cylindrical aggregations of dichasium at the top of a peduncle, terminated by several showy, sterile, purple bracts (Fig. 2). The dichasium are arranged into four vertical columns at right angles, each column bearing four to five dichasium, and each dichasium bearing five flowers (Fig. 3). The first flower to open in any dichasium is referred to here as a central flower, and those opening later in the sequence are referred to as lateral flowers. An inflorescence bears 60—100 flowers, of which four of the lateral type will be found for each of the central type. Anthesis of central flowers is remarkably synchronous and restricted to the first 10 days of the 40—50 day blooming period of an inflorescence. Within any inflorescence, the anthesis of central flowers never overlaps that of lateral flowers. The ovary develops into zero to four nutlets (seeds, hereafter), each of which is 1 mm long. Upon detachment from the receptacle, seeds remain enclosed within the calyx until dispersal. Ovaries from central flowers set an average of three seeds, while those from lateral flowers set just one seed on average (Devesa, Arroyo, and Herrera, 1985). Regardless of whether they contain any seed or not, calyces are not shed until the inflorescence disintegrates, which occurs several months after seed dispersal. At fruiting, calyces from lateral and central flowers can easily be identified.

**Study site and field procedures—** Field work was conducted at the Reserva Biológica de Donana (Donana National Park, southern Spain), a sandy, coastal area with a Mediterranean climate where shrubland is the dominant vegetation (Rivas-Martínez et al., 1980). Rainfall, which is highly seasonal, averages 600 mm/yr. At the study site, a population of *L. stoechas* grows on old, stabilized sand dunes, intermingled with other sclerophyllous shrub species. In February 1989, ten similarly sized *L. stoechas* individuals, each bearing 22—74 inflorescence buds, were selected and tagged. Plants were then randomly assigned to one of the following manipulations: 1) every second inflorescence bud was carefully clipped (thinning treatment); or 2) no manipulation (control). At that time, plants in the population bore a complete set of half-sized buds (Fig. 4). After flowering, and slightly before the onset of seed dispersal (June), four heads were collected at random from each plant, and a number of calyces therein sampled for the presence of ripe, brown nutlets.

**Sampling—** To test for within-inflorescence variation in fecundity, sampling of calyces was stratified so as to include all of the central flowers (10—15) and 15 lateral flowers per head. In total, fruit production was monitored in 975 calyces (from 377 central and 598 lateral flowers) from 40 inflorescences and ten plants. In *L. stoechas*, calyces may contain either only black and unenlarged (presumably unpollinated) ovules and/or aborted, pale-yellow seeds (i.e., the flower has failed to set fruit), or one
to four brown, viable seeds. Additionally, close examination of apparently viable seeds under a dissecting microscope revealed that some had been bored and their content removed by predators (parasitic hymenopteran larvae; J. Herrera, personal observation). Invariably, the larvae destroyed all seeds within attacked calyces. When examining fruit set per inflorescence, a separate record was kept of the proportion of ovaries setting either viable or bored, unviable seed.

Estimates of fecundity — Fruit set was defined as the number of calyces containing at least one brown (preyed or not) seed, divided by the number of flowers. The predation rate was defined as the ratio of preyed fruits to total fruit number. Effects of inflorescence removal,
TABLE 1. Within-inflorescence variability in the fecundity of thinned and control L. stoechas plants (in each case, N = 5)*

<table>
<thead>
<tr>
<th>Flower type</th>
<th>Variables</th>
<th>Untreated plants</th>
<th>Thinned plants</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fruit set</td>
<td>81.4(3.3)</td>
<td>65.7(4.8)</td>
</tr>
<tr>
<td></td>
<td>Seed mass</td>
<td>3.9(0.1)</td>
<td>4.2(0.1)</td>
</tr>
<tr>
<td></td>
<td>Predation</td>
<td>12.7(4.4)</td>
<td>18.3(7.1)</td>
</tr>
<tr>
<td>C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Overall</td>
<td></td>
<td>76.7(2.4)</td>
<td>69.0(2.8)</td>
</tr>
</tbody>
</table>

* Values are means for 20 inflorescences, and numbers in brackets are standard errors. Fruit set and predation rate are percentages. Seed masses are in mg. See Table 2 for the significance of differences.

b C, central; L, lateral flowers.

table 2. Results from analyses of variance for effects of inflorescence removal (Treatment), type of flower ((Flower), and plant identity (Plant) on fecundity in L. stoechas

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Source</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fruit set</td>
<td>Treatment</td>
<td>1</td>
<td>3.755</td>
<td>0.057</td>
</tr>
<tr>
<td></td>
<td>Flower</td>
<td>1</td>
<td>0.897</td>
<td>0.347</td>
</tr>
<tr>
<td></td>
<td>Plant</td>
<td>8</td>
<td>1.907</td>
<td>0.073</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>69</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seed mass</td>
<td>Treatment</td>
<td>1</td>
<td>12.073</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Flower</td>
<td>1</td>
<td>29.846</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Seediness</td>
<td>3</td>
<td>0.341</td>
<td>0.796</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>74</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predation rate</td>
<td>Treatment</td>
<td>1</td>
<td>0.775</td>
<td>0.382</td>
</tr>
<tr>
<td></td>
<td>Flower</td>
<td>1</td>
<td>26.299</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Plant</td>
<td>8</td>
<td>2.632</td>
<td>0.014</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>69</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a Refers to whether the seed was in a fruit with one, two, three, or four seeds.

to the inflorescence axis (Fig. 3) set fruit at a higher rate than late-opening flowers (Devesa, Arroyo, and Herrera, 1985; this study, Table 1). This is most unlikely to result from changes in pollen deposition rates through the flowering

RESULTS

Mean number of heads exposed to pollinators after manipulation was 33.8 per plant (SE = 5.8, range 22—55) for controls, and 19.4 per plant (SE = 4.0, range 11—32) for thinned individuals. Among controls, central flowers set fruit at a significantly higher rate than lateral flowers (t = 2.368, P = 0.023), while this pattern vanishes if thinned individuals are considered (t = 0.831, P = 0.411). Maximum dis-
flowers on thinned plants developed in fruits with seeds that were heavier than those from flowers on controls (Tables 1, 2). My suggestion is that such an increase in seed mass reflects a within-inflorescence compensation for the lower fruit set of central flowers. However, plants do not appear to reallocate resources among inflorescences, as indicated by the fact that bud removal did not increase percent fruit set of treated plants. In this regard, it is remarkable that the fecundity of late-opening flowers on thinned plants remained virtually identical to that of equivalent flowers on controls (Table 1). The compact inflorescences of *L. stoechas* probably behave to a great extent as isolated modules of resource allocation.

Explanations for the lack of response of lateral flowers to inflorescence removal should relate to an interaction between growth and reproduction. The formation of new foliage in *L. stoechas* is simultaneous to flowering, and it was observed that thinned plants exhibited an unusually vigorous growth (unpublished data). Leaf buds nearest to the removed inflorescences might outcompete the remaining inflorescences for the resources not expended on flower, fruit, and seed production. Thus, a compensation for the loss of reproductive potential among flowers on the same inflorescence could often occur (for example, through increased seed mass), while between-inflorescence compensation is likely to be impeded through interactions with vegetative growth.

**Predation**—*L. stoechas* predators apparently discriminate between fruits according to their position on the inflorescence. Many plant species experience high levels of predispersal seed predation (i.e., Janzen, 1971; Andersen 1988), and it is not uncommon to find that predation is nonrandomly distributed among the available fruits. Differential predation can operate in other species on the basis of phenology (Augspurger, 1981) or fruit seediness (Zimmerman, 1980; Herrera, 1984). The mechanism by which early fruits of *L. stoechas* mostly escape predation while late fruits are heavily preyed is unknown, but whatever the proximate cause, it results in the destruction of fruits with fewer, smaller, and less germinable seeds (Table 1; Fig. 5). This is similar to what happens in *Bartsia alpina* (Scrophulariaceae; Molau, Eriksen, and Knudsen, 1989). Investigations are currently in progress to determine if differential predation could exert a selection pressure on inflorescence architecture and/or promote phenological escape in this shrub.


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