Oecologia (1997) 110:493–500

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Sources of variation in floral nectar production rate in *Epilobium canum* (Onagraceae): implications for natural selection

Received: 9 January 1996 / Accepted: 18 December 1996

Abstract Sources of variation in floral nectar production were investigated in a natural population of *Epilobium canum* (Onagraceae), a hummingbird-pollinated herbaceous shrub. Field measurements showed significant phenotypic variation among plants in floral nectar production rates. Average variance among flowers within plants was approximately one-third to one-half as great as variance among plants, with coefficients of variation among flowers ranging from 6.5% to 116.7%. A greenhouse experiment using clonally propagated ramets from field plants showed significant genetic variation for nectar production rates; broad sense heritability was estimated to have a maximum value of 0.64. In the greenhouse, plants grown under low water or low light conditions produced approximately 25% less nectar on average than those grown under control conditions. However, significant genotype-environment interactions indicated that genets differed in their responses to the changes in conditions. Rank correlations for genet mean nectar production rates across environmental conditions were low, and in two out of three comparisons were not different from zero. It is concluded that although the opportunity for natural selection on nectar production rates exits in this population, the response to selection will likely be slow, and the opportunity for selection of a narrow-optimum nectar production phenotype may be limited.

Key words Nectar production · Genotype-environment interaction · *Epilobium canum* · Broad-sense heritability

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Introduction

Biologists since before Darwin have been aware that the production of floral nectar plays an important role in the pollination of flowers (Sprengel 1793). Darwin (1859) suggested, and recent studies have shown, that pollinator responses to differences in nectar availability can have important consequences for the reproductive success of plants (e.g., Pyke et al. 1988; Zimmerman and Pyke 1988; Mitchell and Waser 1992; Mitchell 1993). Because of this connection between nectar production and plant fitness, it has often been suggested that nectar production rates should be subject to natural selection. Furthermore, because the production of floral nectar is expected to involve some cost (Southwick 1984; Pyke 1991), it has been argued that selection should move nectar production characteristics toward some optimum value, where the difference between reproductive benefits and nectar resource costs is maximized (Pyke 1981; Zimmerman 1988; Rathcke 1992).

Studies have found that plants with higher rewards per flower may receive more visits from pollinators (Thomson et al. 1989; Real and Rathcke 1991), or have more of their flowers probed per visit (Hartling and Plowright 1978; Pyke 1978; Heinrich 1979; Waddington 1981; Zimmerman 1983; Galen and Plowright 1985; Cresswell 1990; Mitchell 1993). Pollinators may also spend more time at flowers with higher rewards (Zimmerman 1983; Galen and Plowright 1985; Neff and Simpson 1990). A smaller number of researchers have documented a connection between these behavioral responses of pollinators and increased plant fitness (Zimmerman 1983; Real and Rathcke 1991; Mitchell and Waser 1992; Mitchell 1993; Hodges 1995).

But the opportunity for natural selection also depends on the nature of variation in nectar production rates in the population in question. For selection to be possible, there must be sufficient phenotypic variation in nectar production rates that pollinators can detect differences among individuals. At least some of this vari-

ation must be heritable, so that the nectar production characteristics favored in the parental generation are expressed in the resulting offspring. Finally, if there is an interaction between genotype and environment in determining nectar production rates, the rate and direction of evolution will depend on the distribution of environmental conditions in the population and the relationship between phenotype and fitness in those environments (Via and Lande 1985).

Nectar production differs from other floral traits, such as size or color, in that it is a physiological trait, rather than a morphological one. As such, its expression may be affected by aspects of the plant's physical condition or environment that change over short spatial and temporal scales. Nectar availability has been found to vary with a wide variety of environmental conditions, including temperature, humidity, soil moisture, and nutrient availability (see references in Rathcke 1992). This sensitivity of nectar production rates to environmental factors may play a large role in determining the nature of phenotypic variation in natural populations, with implications for the operation of natural selection.

The environmental sensitivity of nectar production rates suggests that phenotypic variance among individuals would be high, unless physical conditions were substantially uniform across a population. But the scale at which environmental variation affects nectar production may be important as well. Because individual flowers on a plant may differ in their nectar production rates, the detection of differences among plants becomes essentially a statistical issue for the pollinators: estimating the mean nectar production rate of a plant from a small sample of its flowers. In large plants with low levels of physiological integration, environmentally-induced variation in nectar production within individuals could be large, making any sample of flowers only a rough estimate of the mean reward offered. Thus, the relative magnitudes of both within-plant and among-plant variation in nectar production rates are important in determining whether there is "sufficient" phenotypic variation for natural selection.

The sensitivity of nectar production rates to environmental conditions is also likely to affect the heritability of this trait. As variance due to environmental conditions increases relative to genetic variance, heritability decreases (Falconer 1989). Low heritability would limit the opportunity for a genetic response to selection (*sensu* Endler 1986), even if pollinator discrimination among nectar production genotypes led to differences in individual plant fitness. While there is some information on the heritability of nectar production rates in agricultural settings (Pedersen 1953a,b; Hawkins 1971; Teuber and Barnes 1979; Teuber et al. 1990), almost nothing is known about the heritability of this trait in natural populations (but see Mitchell and Shaw 1993).

Finally, because nectar production is part of a plant's total resource allocation strategy, we might expect there to be variation among genotypes in the degree to which nectar production rates are affected by environmental changes. In other words, there may be a significant genotype-environment interaction in nectar production rates. While such interactions are common in plant populations (Bradshaw 1965; Schlichting 1986), and have important implications for the rate and direction of evolution by natural selection (Via and Lande 1985, 1987), no published study has tested for the presence of such an interaction in nectar production rates.

This paper evaluates phenotypic and genetic variation in nectar production rates in a natural population of *Epilobium canum,* a hummingbird-pollinated plant, and addresses three specific questions:

1. What is the extent of phenotypic variation in nectar production rates within and among individuals in the population?
2. Is there evidence for the heritability of nectar production rates in this population?
3. Is there evidence for genetic variation in the response of nectar production rates to changes in environmental conditions such as light and water availability?

Methods

Study system

Epilobium canum (Onagraceae) is an herbaceous, perennial subshrub common in the foothills of the Sierra Nevada and the Coast Ranges of California. Individual plants produce tens to hundreds of red-orange, tubular flowers, 20–35 mm in length, which are pollinated by hummingbirds (Hickman 1993). The flowers generally last 3–4 days, and are protandrous; male and hermaphroditic phases are approximately equal in length. This study was conducted on a population of *E. canum* located in the Stebbins Cold Canyon Reserve, on the eastern edge of the central Coast Range, in Solano County, California (Weathers and Cole 1985). In this population, *E. canum* grows in large, spreading clumps (0.5–3 m diameter) along the bed and banks of a seasonal stream in the reserve. The population is roughly linear, with 100–150 plants scattered along the lower 1 km of the stream; nearest-neighbor distances range from less than 1m to more than 10 m. The plants bloom between August and November, and are visited almost exclusively by Anna's hummingbirds (*Calypte anna*).

Phenotypic variation in nectar production rate

I surveyed phenotypic variation in nectar production rates among *E. canum* plants in the Cold Canyon population in two different years. In 1992, I walked the dry creek bed and chose 28 plants from an area that represented approximately one-third of the linear distribution of the population. Because some large clumps could have represented more than one genetically distinct plant, I chose only those clumps that were uniform in their morphological characteristics, and separated from their nearest neighbors by at least one meter. On each plant, I sampled four haphazardly chosen male-phase flowers. I removed nectar from the flowers at approximately 0900 hours, using a graduated 50-µl syringe fitted with a blunt-tipped needle. The needle was inserted down the length of the corolla to the base of the flower, and all accumulated nectar was withdrawn. Flowers were bagged with nylon mesh to prevent pollinator visitation; at approximately 1200 hours and 1500 hours, all accumulated nectar was removed, and the volume recorded. The nectar was then expelled onto a small filter paper wick for analysis of sugar concentration using the anthrone method (Umbreit et al. 1972; McKenna and Thomson 1988). Nectar production rate was

calculated as the volume of nectar produced since the previous sampling, divided by the time elapsed.

In 1993, 25 plants were chosen using the same criteria as in 1992, but selected from those areas of the population that were not sampled in 1992. Initial nectar removal was at approximately 0800 hours, and flowers were sampled at approximately 1100, 1330, and 1600 hours. Four flowers were sampled per plant. Nectar production rate data for both years were analyzed using repeated-measures designs, under the GLM procedure of SAS (SAS Institute 1988).

Common garden experiments

To evaluate whether nectar production differences might have a genetic component, I collected stem cuttings from 20 different *E. canum* plants in the Cold Canyon population in the spring of 1992. Because the source plants were separated from one another by at least one meter, and in many cases differed in physical characteristics such as leaf shape or color, I assumed that they represented genetically distinct individuals (genets). The cuttings were allowed to grow for several months under greenhouse conditions, to establish a collection of "stock" plants for subsequent propagation. Cuttings were then taken from these stock plants for a common garden experiment.

Because a temperature gradient was suspected in the greenhouse, the common garden experiment was established in a randomized complete block design, with six contiguous blocks along a greenhouse bench, in the direction of the suspected gradient. Each block contained one clonal replicate (ramet) of each of the 20 original field genets, randomly located within the block. A preliminary analysis showed no significant differences among blocks, so the block term was dropped from the analysis, and ramets were considered replicates of the genets.

Only 14 of the 20 genets flowered sufficiently to allow replicated measurements of nectar production. When the ramets flowered, individual flowers were marked and nectar was sampled every 2 h over a 12-h day. Nectar sampling techniques were the same as those used for the field plants, except that flowers did not need to be bagged to prevent visitation. Ramet mean nectar production rates were calculated across flowers at each sampling time, and used in a repeated-measures analysis of variance.

To estimate the genetic variance in nectar production rate, I calculated the mean nectar production rate of each flower sampled, across all sampling times. These data were then used in a nested analysis of variance, with ramet nested within genet. I estimated genetic variance (V_g) as:

$$V_g = (\mathrm{MS}_{\mathrm{Genets}} - \mathrm{MS}_{\mathrm{Ramets(Genets)}})/r \ ,$$

where MS = mean square, and r = the average number of ramets sampled per genet (Falconer 1989; Mitchell and Shaw 1993). Clonal repeatability, or the ratio of V_g to total phenotypic variance (V_p) provides an estimate of the upper limit of broad-sense heritability of nectar production rates (Falconer 1989).

Effects of light and water availability on nectar production rates

Because floral nectar is primarily sugar and water, its production is likely to be affected by the availability of light and water to the plant. To evaluate the effect of decreasing these resources on plant nectar production rates, I took stem cuttings from a subset of the stock genets used for the 1992 greenhouse experiments. I chose eight genets that represented the full range of nectar production rates seen under greenhouse conditions, and propagated as many clonal replicates as possible given the available plant material. Once past the initial period of establishment, the surviving ramets (6–15 per genet) were divided evenly among three different treatments: control, low water, and low light. Control plants were grown under ambient greenhouse light, and received surplus water daily. Low-water plants also received ambient light, but were watered every other day with approximately half the amount of water that control plants received. This was enough water to keep the plants alive, but not enough to prevent them from wilting on the intervening days. Low-light plants received surplus water daily, but were grown under individual shade tents that allowed only 30% of ambient light to reach the plant. To eliminate position effects, the locations of all plants were randomized weekly throughout the 14-week experiment. As plants flowered, I measured the 6-h nectar production rates of four to five flowers on each ramet. Rates for individual flowers were averaged to produce a ramet mean nectar production rate, which was used in the analysis.

Not all genets flowered in the low-light treatment. To avoid a highly unbalanced analysis, the low-light and low-water treatments were compared to the control plants in separate ANOVAs. Genetic correlations across treatments were calculated using the mean nectar production rate for each genotype (across ramets) in each treatment.

Results

Phenotypic variation in nectar production rate

Data from the 1992 field survey showed a very strong correlation between the volume of nectar in a flower and the total amount of sugar represented by that volume ($r = 0.95$, $n = 299$, $P < 0.0001$, Spearman rank correlation). A similarly strong correlation was found from a subset of the plants sampled in 1993 ($r = 0.94$, $n = 48$, $P < 0.001$). Because of this close correlation between nectar volume and total sugar, nectar production rates subsequently were calculated on a volume basis only, and will be reported in microliters per hour ($\mu l \cdot hr^{-1}$) for the remainder of this paper.

The surveys of nectar production rates in the Cold Canyon population showed similar patterns of phenotypic variation between 1992 and 1993 (Fig. 1). Nectar production rates per flower were slightly higher in 1992 than in 1993 (population mean ± SE: 0.81 ± 0.04 $\mu l \cdot h^{-1}$ and 0.67 ± 0.03 $\mu l \cdot h^{-1}$, respectively). This

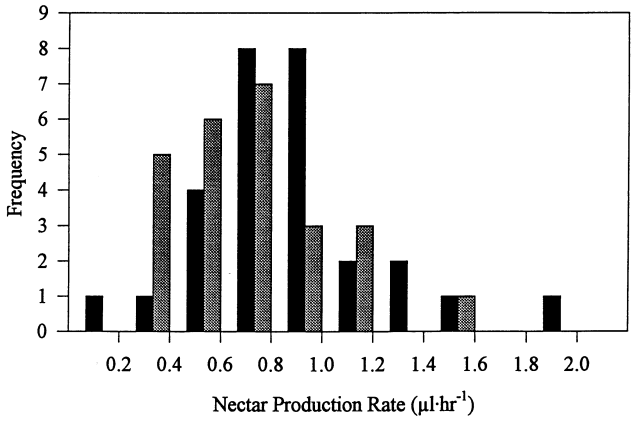

Fig. 1 Distribution of plant mean nectar production rates in surveys of *Epilobium canum* in Cold Canyon. Data are least-squares means from a repeated measures analysis of four flowers per plant, sampled two (1992) or three (1993) times during the day (*soid bars* 1992, *lighter bars* 1993)

difference could reflect year-to-year variation in nectar production rates, or may simply reflect the fact that different plants were sampled in the two years. Repeated-measures analysis of variance showed slightly different results between the two years (Table 1). Significant differences were found among plants in their mean nectar production rates in 1993 but not in 1992. These differences may result primarily from differences in sampling, however. The 1992 survey had relatively low power to detect variation among plants ($1\text{-}\beta < 0.30$), so the failure to find significant differences should not be taken to mean that true differences do not exist.

In both years, the average variance in nectar production rates among flowers within plants was approximately one-third to one-half the mean variance among plants (1992: $MS_{Plants} = 0.833$, $MS_{Flowers(Plants)} = 0.385$; 1993: $MS_{Plants} = 1.043$, $MS_{Flowers(Plants)} = 0.317$; Table 1). But plants exhibited a great deal of variance around these means. Coefficients of variation among flowers within plants ranged from 6.5% to 116.7% in 1992, and from 15.3% to 100.6% in 1993. Because the same flowers were sampled repeatedly through the day, values for the coefficient of variation at different times on the same plant were not independent, and the statistical significance of variability differences among plants could not be evaluated.

Common garden experiments

Nectar production rates per flower, across ramets and times of day, were substantially greater in greenhouse-grown plants than in the field (2.03 ± 0.05 $\mu l \cdot h^{-1}$), probably as a result of more favorable growing conditions. However, the coefficient of variation among genets in the greenhouse was comparable to that found among individual plants in the field (greenhouse: 48.32%; field: 1992, 39.49%; 1993, 45.80%).

A repeated measures analysis of flowers sampled every 2 h showed that differences among genets explained a significant portion of the observed variation in nectar production rates (Table 2). Average nectar production also varied with the time of day, but this variation was primarily due to low nectar production in the first sampling period (1.09 ± 0.15 $\mu l \cdot h^{-1}$) compared with the remaining times (joint mean: 2.16 ± 0.14 $\mu l \cdot h^{-1}$). There was significant variation among genets in the diurnal pattern of nectar production, however, as indicated by the significant genet-by-time interaction (Table 2).

Clonal repeatability (V_g/V_p) was estimated as 0.64 for the 14 genets used in this analysis. This result provides an upper limit for the broad-sense heritability of nectar production rates in the Cold Canyon population.

Table 1 Analysis of variance results for nectar production rate surveys of *Epilobium canum* plants in the Cold Canyon population in **A** 1992 and **B** 1993. Four flowers per plant were sampled two (in 1992) or three (in 1993) times during the day

A 1992

Effect	SS	*df*	*F*	*P*
Plant	22.502	27	1.211	0.283
Flower(Plant)	31.575	82	2.073	0.0007
Time of day	1.140	1	2.351	0.137
Time × Plant	13.285	27	2.648	0.0004
Total	84.157	215		

Model $R^2 = 0.8278$

B 1993

Effect	SS	*df*	*F*	*P*
Plant	25.032	24	2.965	0.0006
Flower(Plant)	23.112	73	1.795	0.0017
Time of day	0.7808	2	1.821	0.1725
Time × Plant	10.330	48	1.220	0.188
Total	83.443	281		

Model $R^2 = 0.7168$

Table 2 Analysis of variance results for nectar production rates of field-collected genets grown in common greenhouse conditions. One to three flowers were sampled on each of two to six clonal ramets per genet, at six times throughout the day. Mean values for each ramet at each time were used in the analysis

Effect	SS	*df*	*F*	*P*
Genet	220.77	13	4.390	0.0001
Ramet(Genet)	158.79	46	3.472	0.0001
Time of day	47.12	5	6.730	0.0001
Time × Genet	95.42	65	1.48	0.02
Total	751.46	347		

Model $R^2 = 0.7116$

Effects of light and water availability on nectar production rate

Nectar production rates in greenhouse-grown plants were significantly affected by changes in the availability of light and water (Fig. 2). On average, ramets grown under a 70% reduction in ambient light had 27% lower nectar production rates than ramets of the same genets grown under ambient light (1.92 ± 0.14 $\mu l \cdot h^{-1}$ and 2.62 ± 0.14 $\mu l \cdot h^{-1}$, respectively). However, the significant genet-by-treatment interaction indicates that the genets did not all responded in the same manner to reduced light availability (Table 3A). The rank correlation between a genet's nectar production rates in the two environments was not different from zero ($r = 0.1$; $df = 5$, $P = 0.87$), indicating that a high-nectar-producing genotype in one environment will not necessarily be a high producer in the other.

The effects of reduced water availability were similar to those of shading. On average, plants in the low-water treatment produced 26% less nectar than did those in

the control treatment (1.55 ± 0.10 $\mu l \cdot h^{-1}$ and 2.09 ± 0.10 $\mu l \cdot h^{-1}$, respectively). However, the significant genet-by-treatment interaction again shows that genets responded differently to the change in environmental conditions (Table 3B). As in the low-light treatment, the rank order of genotypes differs between the two treatments, but in this case there was a nearly significant positive correlation in genet ranks across the two environments ($r = 0.69$; $df = 8$; $P = 0.06$). The genet rank correlation between low light and low water conditions was also not significantly different from zero ($r = 0.40$; $df = 5$; $P = 0.50$).

Although the genotype-by-treatment interaction is significant for both the low light and low water treatments, the interaction term accounts for only about 11% of the total variance in nectar production rates in each analysis (Table 3). Treatment effects were also small relative to variance among genets; the reduction in light availability explained only 14% of the observed variance, while differences in water availability explained less than 8% of the total (Table 3). In contrast, variance among genets represented 30% of the total variance observed in the light manipulation and 52% of the variance in the water manipulation.

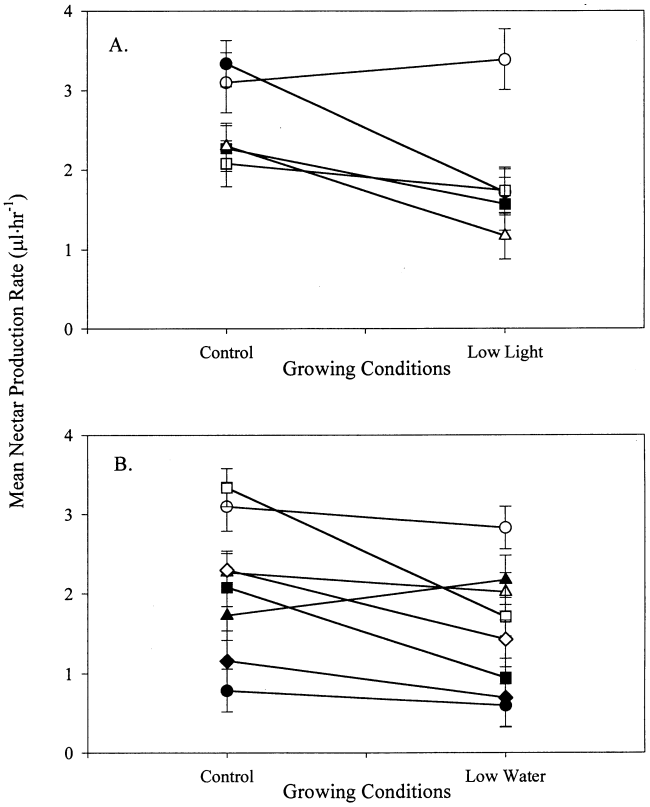

Fig. 2 Nectar production rates of field-collected *E. canum* genets grown under control and **A** low light or **B** low water conditions in the greenhouse. Means are across two to five clonal replicates per genet per treatment; *error bars* are standard errors

Table 3 Analysis of variance results for effects of light and water availability on nectar production rates. Two to five replicate ramets of eight genets were grown under each of three conditions: low light, low water, and control. Four to five flowers were sampled for nectar production rate on each ramet; the mean of these values for each ramet was used in the analysis. Only five of the eight genets flowered in the low-light treatment

A Low light versus control:

Effect	SS	*df*	*F*	*P*
Genet	11.380	4	6.62	0.0004
Treatment	5.277	1	12.29	0.0013
Genet × Treatment	4.312	4	2.51	0.059
Total	37.520	44		
Model $R^2 = 0.5994$				

B Low water versus control:

Effect	SS	*df*	*F*	*P*
Genet	29.236	7	14.76	0.0001
Treatment	4.315	1	15.25	0.0003
Genet × Treatment	6.009	7	3.03	0.010
Total	55.521	64		
Model $R^2 = 0.7503$				

Discussion

Phenotypic variation in nectar production rates

Evidence from field surveys of the Cold Canyon population of *E. canum* suggest that plants in the population differ significantly in their mean per-flower nectar production rates. Such phenotypic variation in nectar production rates appears to be widespread; significant differences among individuals in nectar production rates have been reported in a number of populations and a variety of species (Pleasants 1983; Marden 1984; Wyatt and Shannon 1986; Real and Rathcke 1988; Thomson et al. 1989; Hodges 1995).

Perhaps more interesting was the magnitude of variation in nectar production rates among flowers within a plant. Within-plant coefficients of variation ranged from less than 10% to over 100%. High within-plant variation in nectar production rates has been found in a number of other species as well (Steiner 1979; Herrera and Soriguer 1983; Marden 1984; Zimmerman and Pyke 1986; Real and Rathcke 1988), but it is not necessarily universal (Pleasants 1983; Mitchell 1993).

Natural selection requires that individuals be reliably discernible on the basis of the trait in question. High within-plant variation could make it more difficult for a pollinator to differentiate among plants based on mean nectar production rates, because any subset of flowers visited on a plant would only provide a rough estimate of the mean reward value of the plant as a whole. Clearly, within-plant variation in nectar production rates did not prevent the statistical detection of significant differences among plants. What is important for natural selection, however, is the degree to which the

pollinators can detect such differences. Observations at a subset of the plants in the Cold Canyon population showed no relationship between nectar production rates and either the number of pollinator approaches to a plant or the number of flowers probed per visit (Boose 1995), suggesting that pollinators might not be able to discriminate among plants in this population based on nectar production rates per flower.

On the other hand, it has been suggested that within-plant variation in nectar production rate may itself be adaptive (Pleasants 1983; Rathcke 1992). On plants with large floral displays, high within-plant variation in nectar rewards may induce pollinators to leave the plant after visiting only a small subset of the flowers available. This behavior could potentially increase outcrossing and reduce pollen transfer within the plant. Intraplant variation has also been shown to decrease nearest-neighbor visitation by bumblebees, increasing potential gene flow distances (Ott et al. 1985).

Individual *E. canum* plants are often quite large, with up to 250 flowers open at a time, so it is possible that the observed levels of within-plant variation have a beneficial effect in reducing within-plant pollen transfer. However, *E. canum* is self-compatible, and hand pollinations of field plants showed no evidence for inbreeding depression in fruit set, seed set, seed weight, or germination rate (D. Boose, unpublished work). While negative effects of inbreeding could be manifested later in the life cycle, initial evidence suggests that decreasing geitonogamous pollen transfer would confer little reproductive advantage in this population.

Feinsinger (1978) suggested that high intraplant variability in nectar production rates actually increases the amount of time a pollinator spends at a plant, by creating a pattern of "random reinforcement". For random reinforcement to be effective, however, pollinator visitation must be high relative to nectar availability (Feinsinger 1978). Otherwise, a pollinator's expected gains from searching for a small number of highly rewarding flowers on one plant would generally be less than those expected from moving to another plant. Rates of pollinator visitation are quite low in the Cold Canyon population of *E. canum*, with each plant receiving an average of only seven to ten flower probes per hour, and there was no evidence that the duration of visits to a plant was correlated with within-plant variability in nectar production rates (Boose 1995).

Thus it seems unlikely that within-plant variability plays an adaptive role in this population. Rather, such variation may limit the extent to which natural selection can "fine tune" nectar production rates, by setting a lower limit on the amount of phenotypic variation among individuals that can be detected by pollinators.

Heritability

The observed phenotypic differences among plants could be the result environmental variation, genetic variation, or some combination of the two. The clonal repeatability estimate calculated in the common garden experiment suggests that a large portion of the variation in nectar production rates could have a genetic basis. However, the calculated value (0.64) may overstate the true heritability of nectar production rates for two reasons. First, the common environment of the greenhouse was used specifically to reduce environmental variance in nectar production rates. Thus, a larger proportion of the total variance will be due to genetic factors, resulting in a higher heritability value. Heritability may be lower in the field, where variance due to environmental factors is likely to be higher (although total variability among individuals in the field was not greater than that among genets in the greenhouse). Second, because the plants were clonally propagated, some of the differences among genets may be due to non-additive genetic effects, which would not contribute to a genetic response to selection.

Evidence for genetic variation in nectar production rates has been found in cultivated alfalfa (Pedersen 1953a, b; Teuber and Barnes 1979; Teuber et al. 1990) and clover (Shuel 1952; Hawkins 1971), and in a wild population of *Mirabilis multiflora* (Hodges 1995), but only one previous study has estimated the heritability of nectar production in wild plants. Using paternal half-sibs and clonal replicates, Mitchell and Shaw (1993) calculated both broad-sense and narrow-sense heritabilities for nectar production in *Penstemon centranthifolius*, a perennial wildflower. As in my study, Mitchell and Shaw grew their plants under greenhouse conditions, which may inflate the heritability values somewhat, but their estimates of 0.53 for broad-sense, and 0.38 for narrow-sense heritability suggest the presence of significant additive genetic variation for this trait.

Effects of light and water availability

In my greenhouse experiments, I found that reducing light and water availability had measurable effects on nectar production rates, a result consistent with those of other manipulations of environmental conditions. Watering plants in the field has resulted in increased nectar production (Zimmerman 1983; Zimmerman and Pyke 1988); shading or defoliation has generally decreased nectar production (Pleasants and Chaplin 1983; Southwick 1984), but not always (Zimmerman and Pyke 1988).

In addition to the environmental main effects, however, the genotype-environment interaction indicated that genets responded differently to the same change in conditions. That is, there is genetic variation in the population for phenotypic plasticity (Via and Lande 1985). Genetic variation in phenotypic plasticity has been found in a number of morphological and life-history traits of plants (Bradshaw 1965; Schlichting 1986; Stratton 1992; Sultan and Bazzaz 1993; but see Young et al. 1994; Andersson and Shaw 1994), but to my knowledge this is the first demonstration of a genotype-environment interaction in nectar production rates.

A significant interaction between genotype and environment in determining phenotypic values can affect both the rate and direction of evolution in a trait (Via and Lande 1985). In general, the presence of such an interaction will slow the response to selection in a population, because it reduces the correlation between genotype and phenotype across environments. The magnitude of the effect will depend on the strength of that correlation, and the relative fitnesses of different phenotypes in different environments (Via and Lande 1985).

The low correlation among genet ranks across the experimental conditions suggests that selection on this trait may operate relatively independently in different environments. Even if selection acts in the same direction everywhere (e.g., favoring higher producing phenotypes in all conditions), the population-wide response to selection will be slowed because the favored phenotypes are produced by different genotypes in different environments. If selection acts in opposite directions (e.g., favoring higher producers when water is abundant but lower producers when water is scarce), then the response will be slowed even further; the positive rank correlation across these two conditions means that genotypes favored in one environment would be at a disadvantage in the other.

Conclusion

Despite the sensitivity of nectar production rates to changes in light and water availability, the presence of significant phenotypic and genetic variation suggests that natural selection could shape this important floral trait in the Cold Canyon population of *E. canum*. Because of the significant genotype-environment interaction, however, the response to selection may be slow. Furthermore, within-plant variation may limit the extent to which selection can fine-tune nectar production rates toward some optimal level, if it limits the amount of phenotypic variation that pollinators can detect. An accurate prediction of the likely evolutionary trajectory for this trait would require knowledge of the distributions of environmental conditions in the population, the effects of those environments on the expression of nectar production genotypes, and estimates of the relative fitnesses of the resulting phenotypes.

Acknowledgements This research was supported by grants from the UC Davis Public Service Research Program, the Center for Population Biology at UC Davis, the Hardman Foundation, and Sigma Xi. Valuable field assistance was provided by A. Braley, S. Eppley, L. Galloway, E. Nagy, D. Posner, and B. Roy. Previous versions of this manuscript were greatly improved by comments from K. Muller, R. Mitchell, W. Shriner, M. Stanton, R. Thorp, and one anonymous reviewer.

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