Population Differentiation and the Effects of Herbivory and Sand Compaction on the Subterranean Growth of a Desert Lily

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Abstract

Differences in level of herbivory can select for local adaptation and genetic differentiation of plant populations in different environments. Mean bulb depth of the desert lily *Pancratium sickenbergeri*, differs considerably among populations differing in the level of herbivory by the dorcas gazelle. The gazelle digs in the sand to remove most of the bulb of the lily. Deeper bulbs have less material removed by herbivory than shallow bulbs and have higher fitness. A possible confounding factor is the degree of sand compaction, which may retard the downward growth of the bulb. We conducted a common garden experiment with 2 sand types with seeds from source populations with different levels of herbivory. There was a large genetic difference among populations. Two of 3 analyses indicated that there was an interaction between population and sand type, indicating that there is a heritable component of plasticity.

Studies of the evolution of plant resistance to herbivores require an understanding of the origin and dynamics of genetic variation for resistance traits in natural populations (Simms and Rausher 1992). Life-history traits, that is, growth and resistant patterns, are quantitative traits under continual selection, and the genetic variation of such traits should be low compared with traits less directly connected to fitness. Nevertheless, the heritabilities of life-history traits are often large (Stearns 1992; but see Price and Schluter 1991 and Hoffmann and Merila 1999). An explanation for the maintenance of genetic diversity of these traits is that selection fluctuates across environments: phenotypes favored in one environment are disfavored in another, and the environment varies over space and time (Via and Lande 1985; Gillespie and Turelli 1989; Whitlock 1996; Vogler and others 1999; but see Sasaki and Ellner 1997).

Evidence of local adaptation of different plant populations in response to different environments has been shown in several studies (Stratton 1994, 1995; Boose 1997; Sugiyma and Bazzaaz 1997; Wu and Stettler 1997; Roy and others 1999). However, studies of local adaptation in plant–herbivore systems are rare and usually tested the effect of plant genotypes on herbivore performance (Diawara and others 1994; Orians and Fritz 1996; Fritz and others 1997; Kause and others 1999) rather than effects of herbivory on plant genotypes. Only a few studies have estimated the effects of herbivory and other environmental factors on plant performance (Delph and others 1997; Fornoni and Nuñez-Farfán 2000; Juenger and Bergelson 2000).

Models of the evolution of plant resistance assume a cost, which reduces fitness in the absence of natural enemies (Mauricio and Rausher 1997; Mauricio 1998). Resource availability interacts with selection exerted by herbivores to result in fitness trade-offs associated with different environments (Herms and Mattson 1992). Therefore, different levels of herbivory in different plant populations create environmental heterogeneity and this in turn may select for local adaptation (Ward and Saltz 1994). Genotype × Environment (G × E) interactions can maintain genetic variation if the relative fitness of a plant genotype changes in different environments (Mitchell-Olfs 1992). Thus, herbivores may directly select for local adaptation for 2 components of fitness, namely, investment in defense and growth.

In this study, we determine the relative importance of environmental and genetic factors and the interaction between them on the expression of an avoidance strategy of the desert lily *Pancratium sickenbergeri* (Amaryllidaceae), a hysteranthous geophyte commonly found in sand dunes of the Negev.
Desert. The dorcas gazelle (*Gazella dorcas*) is the major herbivore on this lily (Ward and Saltz 1994) and may exert strong selection on the development of antitherbivore strategies (Ruiz and others 2002a, 2002b). It is known that bulbs of the desert lily grow deeper in soft-sand dune habitats than in compact, loess—sand habitats (Saltz and Ward 2000). This difference may be purely phenotypic (i.e., it is easier to grow down into soft sand) or it may be due to genotypic differentiation caused by the considerably greater level of herbivory in dune habitats, due to the lower cost of digging in soft sand for the gazelle. Ward and Saltz (1994) found a positive correlation between the depth of the bulb and the number of leaves produced, which indicates that deeper growth (to escape being eaten by gazelles) has a positive effect on the number of leaves that the plant produces the following winter. In addition, they found a negative correlation between the amount of bulb that is consumed and whether or not it produces leaves in the following winter (Saltz and Ward 2000). Furthermore, partly consumed bulbs had fewer, smaller leaves in the following winter than unconsumed bulbs. These correlations suggest that, at least in the short term, there is an effect of herbivory of the bulb on plant fitness.

The hypothesis that depth of the bulb in the desert lily is an avoidance strategy selected by herbivory (Saltz and Ward 2000) raises the following question: do bulbs from populations with high levels of herbivory grow deeper into the sand than lilies from populations without herbivory? If there is only a phenotypic constraint to bulb depth, that is, sand compaction constrains bulb depth, then we can predict that individuals from different sources planted in the same habitat will grow to the same depth. In loose sand, bulbs will grow deeper than in compact sand because it is easier for the bulb to grow down in the loose sand. In this case, the depth of the bulb is independent of the source (population) of the plant and its level of herbivory.

If herbivory selects plants to grow deeper to minimize consumption, then we predict that bulbs from populations with a high level of herbivory from the loose sand will grow to a greater depth than bulbs from populations with a low level of herbivory regardless of whether they are growing in loose or compact sand. That is, if the plant is exposed to different levels of herbivory, the bulb with a genotype from populations without herbivory (A) will not grow deep because there has been no selection for such a trait, whereas the genotype from populations with herbivory (B) will grow deeper, independent of the type of sand. Consequently, the negative impact of herbivory on fitness would be greater on genotype A. Clearly, if both factors are at play, bulbs will grow deepest in soft sand with herbivory and shallowest in hard sand without herbivory.

**Materials and Methods**

**Study Area**

The study was conducted in different populations in 2 erosion cirques in the Negev Desert of Israel, Makhtesh Katan and Makhtesh Ramon. Makhtesh Katan is a small (30.6 km²), oval-shaped cirque surrounded by steep walls. This area is characterized by an arid to extremely arid climate, vegetation cover is scarce and confined to the stream channels, and soil substrate is composed mainly of limestone. Makhtesh Ramon is an anticlinal 200-km² erosion cirque on the southern boundary of the Negev highlands (see Saltz and others 1999). Makhtesh Ramon is characterized by low rainfall (40–90 mm/year) and a variety of soil substrates (e.g., sandstone, gypsum, limestone, dolomite, and various clays). The strong environmental changes (rainfall and temperature) are reflected in the vegetation (Ward and Olsvig-Whittaker 1993; Ward and others 1993, 2001; Saltz and others 1999). The sand dunes (Ardon and Machmal) support unique plant communities, with one perennial plant species, the desert lily *P. sickenbergeri*, common to both dunes (Ward and Olsvig-Whittaker 1993; Ward and others 1993).

In Makhtesh Ramon, we concentrated this study in 2 isolated, eastern lobes of this cirque, known as Ardon and Machmal valleys, located about 6 km apart at its eastern end and separated by a large hill. The predominantly western winds have created large sand deposits along the eastern walls of these valleys (Ward and others 1997). Loose sands can support dense populations of lilies (up to 2 m⁻²), and they are attraction points for the dorcas gazelles (Ward and Saltz 1994; Saltz and Ward 2000). Away from the dunes the sands are more compact and mixed with loess. Compact sand habitats occur in the lower regions on the peripheries of the loose sand of Ardon and Machmal valleys (Ward and Saltz 1994). These compact sands are marginal habitats because of high water runoff and characterized by lower densities (approximately 0.1 m⁻²) of smaller lilies with shallower bulbs and fewer leaves and flowers (Saltz and Ward 2000). In addition, we included a lily population from Neqarot canyon, which is separated from the other 2 populations by 7–10 km (Ward and others 1997). Lilies in this population grow in a loose sand (dune) habitat and have no gazelle herbivory (Saltz and Ward 2000). Gazelles never enter canyons, presumably because of the presence of a major predator, the leopard, *Panthera pardus* (Saltz and Ward 2000). There is a dense population of lilies in this canyon (approximately 1.4 m⁻²). We can classify the different lily populations into those enduring high and low herbivory with a high degree of certainty based on 10 years of observations (see Ward and Saltz 1994; Ward and others 1997, 2000; Saltz and Ward 2000). Machmal dune lilies suffer the highest level of herbivory followed by Ardon dune, Machmal compact sand, and Ardon compact sand lilies. Neqarot lilies showed the lowest level of herbivory. In Makhtesh Katan, the population of lilies grows in a small sandy valley and is exposed to a very low level of herbivory. Neqarot and Makhtesh Katan lilies do not suffer bulb or leaf herbivory, but they are exposed to flower herbivory sporadically (during drought years).

**Study System**

Gazelles consume lilies during each of the lilies’ phenological stages (Saltz and Ward 2000). Lily leaves appear on the surface after the winter rains in late November and December.
(i.e., after the flowers have wilted). In spring, all the leaves dry up and fall off, leaving no aboveground material (Saltz and Ward 2000). During winter, gazelles eat the leaf tip (±1 cm), and up to 100% of the plants may be affected. Calcium oxalate in the leaves is an effective deterrent to this herbivore (Ward and Saltz 1994; Ward and others 1997; Saltz and Ward 2000), and the tip is the only part of the leaf not defended by it (Ward and others 1997). Lilies in habitats with high levels of herbivory produce more calcium oxalate crystals in their leaves than plants in populations with little herbivory (Ward and others 1997). The leaves have a basal meristem (Bold and others 1987) and gazelle herbivory does not affect the growing point of the leaves. Thus, leaf herbivory has only a minor impact on the lilies (Ward and Saltz 1994).

Summer foraging by gazelles has a negative impact on the desert lily especially in loose sands. In the summer, gazelles dig for underground parts of lilies and may consume all or part of the bulb, which contains most of the plant's volume (Ward and Saltz 1994). During this time, 50–88% of the lilies have their underground parts partially consumed and up to 10% are completely consumed (Saltz and Ward 2000). Within populations, all morphological characteristics are allometrically scaled to one another. There are significant positive correlations between depth of the bulb, vault volume, shaft diameter, leaf diameter, leaf number, and plant wet mass (Ward and Saltz 1994). The greatest impact the gazelles have on the lily populations in sand dunes is the consumption of flowers. A lily flower on this sand dune has less than a 0.0001 probability of surviving to the seed-producing stage (Saltz and Ward 2000).

The dorcas gazelle is a small herbivore native to the deserts of the Middle East (Lawes and Nanni 1993). Gazelles show a number of behavioral characteristics that are consistent with a long period of coadaptation with the lily. They concentrate their activity in areas of high lily density, take the biggest plants with the most leaves in the winter, avoid those parts of the leaf defended by calcium oxalate, and in the summer dig for those plants that maximize the benefit–cost ratio of foraging (Ward and Saltz 1994; Ward and others 2000). Gazelles prefer to feed on the lilies in loose sands presumably due to a lower energetic cost of digging in compact sands and/or to the high density of lilies. As sand compaction increases, the proportion of lilies that is dug up by gazelles decreases (Ward and Saltz 1994). Gazelles also dig deeper in the loose sand, removing more of the bulb of each plant. In addition, in the compacted-sand areas, the probability of a flowering lily reaching the seed-producing stage is considerably higher than that in the loose sands (0.026 vs. <0.0001—Saltz and Ward 2000). Thus, although compact sands provide a poorer growing substrate, the level of herbivory is less.

Common Garden Experiment

Lily bulbs are able to move downward to reach a safe position in the sand as a result of root contraction (Putz 1996a, 1996b). Previous studies had established that deeper bulbs were not simply the result of differential growth rates or greater covering of plants by shifting sand in soft-sand populations (Ward and Saltz 1994); however, it could not be determined whether, in the soft sand, bulbs were deeper due to increased herbivory or simply due to low sand compaction. To test whether the depth of the bulb is related to sand compaction or to herbivory, we conducted a common garden experiment. We took seeds from 6 populations with different levels of bulb herbivory: Katan-soft sand (without), Neqarot-soft sand (very low), Ardon-hard sand (low), Ardon-soft sand (very high), Machmal-hard sand (low), Machmal-soft sand (very high). Seeds were planted in 6 hard-sand and 6 soft-sand plots in the open at the Institute for Desert Research at Sede Boquer, approximately in the geographic center of the study populations. Twelve 6 × 4-m plots that were carved out of the surrounding loess substrate to a depth of 50 cm and filled with either hard or soft sand from the vicinity that was similar to that in the study populations. Sand was allowed to settle for 6 months before the onset of the experiments.

To avoid the effects of sand compaction on germination, seeds were planted in trays with sand and germinated seedlings were transplanted into the experimental plots, 1 seedling/cell. Lily seedlings were planted at the same depth (3 cm) in 6 compact sand and 6 loose sand plots (6 × 4 m) in a randomized block design. Each plot was divided into cells of 20 × 20 cm. We used 50 plants/population, 24 seeds/plant, and 2 seeds/plant/treatment/plot. We used maternal families (the plants are self-incompatible—Ruiz 2000) to reduce variance within populations. After 2 years, bulb depth, bulb length, bulb diameter, leaf length, and leaf width of the plant were measured. The experimental design was unbalanced and used only 2292 plants because of the low number of fruits in some populations (Ardon hard, Machmal hard, and Neqarot) and low percentage of germination (Ardon soft, Machmal soft, and Katan).

Because lilies reach reproductive stage only after several years, we could not compare fitness in terms of current reproduction, that is, number of fruits and seeds, for all the populations in each type of sand. We compared bulb depth as a component of fitness because the deeper the bulb the higher the probability of survival and reproduction in the next flowering season where herbivores are present (Saltz and Ward 2000).

The bulb depth results were transformed (log10), and we used a mixed-model approach (SAS PROC MIXED procedure, SAS Inc., 1995) to analyze this complex, unbalanced design with a mixture of fixed and random effects and using a restricted maximum likelihood (REML) approach to compare full and reduced models. A number of authors (Henderson 1985; Shaw 1987; Lynch and Walsh 1998) have shown that REML estimators, unlike analysis of variance (ANOVA) estimates of variance components, do not place any special demands on the design and balance of data. REML estimators are suitable for the unbalanced designs that frequently arise in quantitative genetics (Lynch and Walsh 1998).

Population and sand compaction (“Environment”) were the main factors, and log10 bulb width was used as a covariate to account for ontogenetic bulb size variation. Because
families were nested within populations, the Population effect was tested against the Family(Population) mean square. Family is treated as a random effect. The “Environment” term estimates the mean phenotypic plasticity. The “Genotype” term may either estimate variation among genotypes in the “average” environment or estimate the covariance of the genotypic values across environments. The Population × “Environment” interaction term estimates the genetic variation in response to the environment (Van Noordwijk 1989; Stearns 1992; Via 1993). Specifically, in this analysis, the Population × Sand interaction measures population differences in plasticity related to history of herbivory, whereas Family (Population) × Sand interaction measures the heritable component of plasticity. We compared the $-2 \times \log$ Likelihood value for the full model with that of reduced models. The difference between these values is distributed as $\chi^2$. A significant difference between the full model and a full model reduced by one of the variables, or interactions, indicates that the particular variable/interaction contributes significantly to the full model.

To determine whether there were changes in genotypic rank among populations (beyond that shown by the ANOVA), we graphically constructed the norms of reaction, the set of phenotypes produced by a single genotype across a range of environment conditions (Thompson 1991; Stearns 1992; Scheiner 1993). That is, we plotted the mean phenotype for each population in the 2 types of sand. In addition, for every population independently, we constructed the norms of reaction with the mean phenotype of each family in the 2 types of sand.

In the character state approach, norms of reaction can be viewed as genetic correlations (Via and Lande 1985). We consider the phenotypes that a genotype expresses in 2 environments as 2 characters: $z_1$ in environment 1 and $z_2$ in environment 2 (Via and Lande 1985; Via 1994; Futuyma 1998). Thus, plots of reaction norms were transformed into plots of each genotype’s phenotypes in hard sand versus soft sand. In this way, we assess the genetic independence between the character states expressed in 2 environments as a minimal requirement for the evolution of a new reaction norm.

### Results

Most of the variation in bulb depth was explained in the MIXED analysis by the main factors and not by the interactions (Table 1). In addition, progeny derived from different populations varied considerably in mean bulb depth, indicating genotypic population differentiation. The significant effect of sand compaction demonstrated that there is variation in the phenotypic response to the environments or environmental plasticity. A positive effect of the size of the plant on bulb depth (measured as bulb width) exists in this lily ($r = 0.68$).

When we compared the full and reduced models using the REML approach, there was a significant difference between the $-2 \times \log$ Likelihood values for the full model and the reduced model with Family (Population) × Sand ($\chi^2 = 9120 - 8363 = 756$, df = 1993 - 1748 = 245, $P < 0.001$) removed only. This means that, in addition to the significant effect of soil, population, and bulb width, there is a significant effect of Family (Population) × Sand, that is, a significant heritable component of plasticity.

It was significantly more costly for plants to grow in hard sand than in soft sand: plants grown in soft sand had significantly larger bulbs (the storage organ) ($F = 239.322$, $P < 0.001$, df = 1), longer leaves ($F = 13.834$, $P < 0.001$, df = 1), and more leaves ($F = 23.259$, $P < 0.001$, df = 1) than plants grown in hard sand. Costs should also be expressed as a reduction in fitness, or one of its components, of resistance genotypes relative to susceptible genotypes in the absence of herbivores (Mauricio 1998; Elle and others 1999). To test this, we compared bulb size in plants from populations with the highest level of herbivory (Ardon soft, Machmal soft) and plants from populations with low or no herbivory (Ardon hard, Machmal soft, Neqarot soft, and Katon soft). Bulb size should be a reliable measure of fitness in these geophytes because it is the storage organ and there is strong positive correlation between bulb size and various other components of fitness (leaf size and number, fruit production—Saltz and Ward 2000). Plants from populations with high herbivory grew deeper in the sand than populations with low or no herbivory ($F = 12.571$, $P = 0.0004$, error df = 2278; mean ± SE bulb depth for plants from populations with high herbivory = 4.219 ± 0.045 cm, low herbivory = 4.013 ± 0.036 cm). We then tested whether the greater bulb depth of plants from high-herbivory populations resulted in a significant cost in terms of bulb size—bulb size was significantly smaller in plants from high herbivory populations ($F = 10.262$, $P = 0.0014$, error df = 2278). Thus, there is evidence from differences in bulb size that there is a significant cost to the resistant genotype.

### Table 1. The full model using REML approach (in SAS PROC MIXED) for log10 Bulb Depth against population, sand type, and family nested within population and interaction effects. Interpretation indicates the meaning of a significant result for that factor

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>F</th>
<th>P</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>log10 Bulb Depth</td>
<td>1</td>
<td>158.6</td>
<td>&lt;0.001</td>
<td>Ontogenetic effect</td>
</tr>
<tr>
<td>Population</td>
<td>7</td>
<td>5.58</td>
<td>&lt;0.001</td>
<td>Genotypic population differentiation</td>
</tr>
<tr>
<td>Sand</td>
<td>1</td>
<td>41.49</td>
<td>&lt;0.001</td>
<td>Environmental plasticity</td>
</tr>
<tr>
<td>Family (Population)</td>
<td>276</td>
<td>1.09</td>
<td>0.109</td>
<td>Genetic determination</td>
</tr>
<tr>
<td>Population × Sand</td>
<td>5</td>
<td>1.15</td>
<td>0.331</td>
<td>Population differences in plasticity</td>
</tr>
<tr>
<td>Family (Population) × Sand</td>
<td>245</td>
<td>0.92</td>
<td>0.799</td>
<td>Heritable component of plasticity</td>
</tr>
<tr>
<td>Error</td>
<td>1748</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
The plot of the reaction norms of each genotype ("Population") for the response of bulb depth to the 2 environments ("Sand") indicates that bulbs in soft sand grow deeper than those in hard sand for all the populations (Figure 1). Differences in elevation of the reaction norms denote genetic variation, whereas nonparallel reaction norms indicate a Population \times Environment interaction. Families from populations with higher levels of herbivory grew deeper than families from populations with lower or no bulb herbivory. These reaction norms show that families from the population without bulb herbivory (Katan soft) had the shallowest bulbs in both hard and soft sands. Comparing populations with herbivory with different strengths of selection, families from Ardon soft and Ardon hard grew deeper than families from Machmal soft and Machmal hard in hard sand. However, in soft sand, families from Machmal grew deeper than families from Ardon. That is, there appears to be no optimal genotype in all the environments, and a certain level of genetic specialization is expressed.

The analysis of the reaction norms of each family mean for every population (Figure 2) showed that there is variability in bulb depth among families in each population. The genotypic rank for each family in soft sand cannot be predicted by knowing the rank in hard sand. Populations from hard sand and low herbivory have much less variability either in hard sand (i.e., Ardon hard) or soft sand (i.e., Machmal hard). In contrast, genotypes from soft sand with high herbivory (Ardon soft and Machmal soft) have the highest variability in both hard and soft sands.

The plot of the character states among populations, phenotypes in hard sand versus soft sand (Figure 3), showed a partial genetic independence of the character states in the 2 environments. Via and Lande (1985) showed that any genetic correlation between characters expressed in different environments that is less than 1 translates into a significant genotype–environment interaction. In our study, the genetic

**Figure 1.** Means of log_{10} Bulb Depth for each population on the 2 different types of sand (hard, soft). MS, Machmal-soft sand; AS, Ardon-soft sand; MH, Machmal-hard sand; AH, Ardon-hard sand; N, Neqarot-soft sand; K, Katan-soft sand.

**Figure 2.** Means of log_{10} Bulb Depth for each half-sib family on the 2 different types of sand (hard, soft) for every population. They are shown according to the level of herbivory in the source population, from high to low: (A) Machmal-soft sand; (B) Ardon-soft sand; (C) Machmal-hard sand; (D) Ardon-hard sand; (E) Neqarot-soft sand; (F) Katan-soft sand.
Figure 3. Genetic correlation between character states expressed in each environment. Each point corresponds to the mean phenotype that a given genotype expresses in each of 2 environments. \( Z_h \) is the phenotypic value of the character state that is expressed in hard sand; \( Z_s \) is the phenotypic value of the character state that is expressed in soft sand. The adaptively optimal character state is shown by a. Index of genetic correlation, \( r = 0.63 \).

correlation \( r = 0.63 \) [the upper 95% confidence limit from 1000 bootstrap resamples of \( r \) was 0.73 (i.e., considerably less than 1)]. Selection in each of the 2 environments favors a joint optimum. This optimum value is given by the optimum reaction norm. In our case, the value corresponds to an optimal phenotype that minimizes physiological cost in hard sand and minimizes the cost of herbivory in soft sand. The way that this optimum is approached by the populations depends where it lies relative to the correlated distribution of the 2 characters.

**Discussion**

Resource availability interacts with selection exerted by herbivores to result in fitness trade-offs associated with different environments (Herms and Mattson 1992). Different levels of herbivory in different plant populations create environmental heterogeneity and this, in turn, may select for local adaptation (Ward and Saltz 1994; Ward and others 1997). \( G \times E \) interactions maintain genetic variation in natural populations if no single genotype produces the optimal phenotype in all environments (Gillespie and Turelli 1989; Mitchell-Olids 1992). Thus, herbivores may directly select for \( G \times E \) interaction for 2 components of fitness, namely, investment in defense and growth.

The main aim of this research was to establish whether bulb depth is determined by environmental constraints only or is due to genetic variability created by herbivores (i.e., \( G \times E \) interaction). The strong effect of sand compaction on bulb depth (phenotypic plasticity) is due to constraints on plant underground movements that are important for reaching a suitable position in the sand. If soil conditions (e.g., temperature, water) are more stable at depth, then deep geophytes are less likely to dry out during the dormancy period (Putz 1996a, 1996b). For this movement, a geophyte can produce contractile roots, which create a pulling force, pushing the soil away laterally and forming a soil channel in which movement is made easier (Putz 1996b). Thus, the physiological cost of growing down is higher for plants in hard sand than for plants in soft sand as a consequence of the aforementioned growth pattern. The high physiological cost of growing in hard sand was expressed in this study in the production of smaller bulbs and fewer, smaller leaves in hard sand and is likely to be demonstrated in greater allocation of resources in contractile roots and the future cost of production of vegetative and reproductive stems (cf. Saltz and Ward 2000). Consequently, plants from different populations experiencing different sand conditions are likely to grow to different depths. In addition to this environmental effect, we also detected interpopulation differences in bulb depth that are related to the level of herbivory that mothers in each population experienced (see also Ward and others 1997). That is, offspring from mothers growing in high-herbivory populations grow deeper than offspring from mothers from low-herbivory populations, which indicates genetic variation for this character that is affected by the level of herbivory on the population. This result is supported by the REML analyses that indicated that there is a significant heritable component of plasticity.

**Costs of Resistance**

Is herbivory more costly to a desert lily than sand compaction? It is expected that natural selection acts to minimize costs where they occur (Elle and others 1999). Even though growing down in hard sand had a high physiological cost for the plant (bulbs were smaller and fewer, smaller leaves were produced), lilies subject to herbivory are selected to grow deeper because this decreases the probability of consumption and increases survival. Bulbs that can avoid being eaten during the summer will produce more leaves, and they will store more nutrients and may invest more in reproduction (Saltz and Ward 2000). Thus, bulb depth is an important component of fitness. Costs are expressed as a reduction in fitness, or one of its components, of resistance genotypes relative to susceptible genotypes in the absence of herbivores (Mauricio 1998; Elle and others 1999). The cost of this avoidance strategy for lily bulbs was shown in the fact that plants from populations with the highest level of herbivory (Arden soft, Machmal soft), and which had deeper bulbs than plants from low-herbivory populations, had smaller storage organs than plants from populations without herbivory, independent of sand compaction. That is, bulb size of resistance genotypes (Arden soft, Machmal soft) decreased in the absence of herbivory. Further studies will be needed to ascertain whether additional costs (e.g., flower and seed production or long-term bulb storage) are incurred and how they affect growth strategies over the lifetime of the plant.
Population **×** Environment Interactions and Heritable Plasticity

The REML analysis indicated that there was a significant interaction effect of Family (nested in Population) and Sand type, that is, that there is a significant heritable component of plasticity that is determined by both genotype and environment. The reaction norms and the character state approach also indicated the independent effects of the 2 main factors (sand type and population) on bulb depth. This independence is necessary because, if there is no genetic independence of the character states in the different environments, a change in the norm of reaction cannot evolve (Via and Lande 1985; Via 1993). The norm of reaction showed that the direction of the interaction is the same for all the genotypes (positive from hard to soft sand) but that the slope was lower for genotypes from populations without herbivory than for genotypes with herbivory (see Katan soft vs. Machmal soft; Figure 1). In addition, the reaction norms showed that much more variation exists in family mean phenotypes within populations (Figure 2) than among populations (Figure 1). Thus, growing the bulb down deeper into the sand constitutes an avoidance strategy selected by herbivory. We suggest that the herbivores select for this avoidance strategy, which maintains the observed genetic variability between plant populations.

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