Editor's Note

Seed banks can significantly influence the demography and genetic structure of plant populations, but are rarely studied empirically. Evans and Cabin ask whether seed dormancy can affect the evolution of post-germination traits leading to potentially adaptive syndromes. The authors use a population of the mustard, Lesquerella fendleri, to test whether selection may generate these syndromes. Providing the first empirical data supporting this hypothesis, they emphasize the necessity of more field evidence. They acknowledge the difficulty of studying seed banks, particularly the genetic aspects, and point out a number of new empirical approaches that may be used to study these adaptive syndromes. Ultimately, explorations may include the ecological and genetic mechanisms underlying such correlations between germination and post-germination traits.

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CAN DORMANCY AFFECT THE EVOLUTION OF POST-GERMINATION TRAITS? THE CASE OF LESQUERELLA FENDLERI

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Abstract

Seed dormancy, which is thought to have evolved in response to unpredictable environmental variability, has led to the existence of seed banks—populations of dormant, viable seeds in the soil. Seed banks are theoretically important to both the demography and genetic structure of plant populations. The presence of seed dormancy can also affect the evolution of traits not directly associated with dormancy and germination.

Theoretical models have suggested that the existence of dormancy can influence the rate of evolution of post-germination traits. The eventual outcome (e.g., allele frequencies) may be influenced as well, leading to adaptive syndromes of germination and post-germination traits. Seeds that germinate in different conditions may experience different selective regimes for post-germination traits. If there are trade-offs between the fitness of post-germination traits in different environments, then seeds that germinate in the environment to which their post-germination traits are adapted will be at a selective advantage. If differences in germination and post-germination traits are genetically based, then potentially adaptive genetic correlations between germination and post-germination traits may evolve. We feel that investigating the ecological and evolutionary importance of these correlations requires an empirical approach. As a first step, here we ask whether the conditions necessary for such syndromes to arise exist in a particular plant population.

We show that conditions favoring the joint evolution of dormancy and post-germination traits leading to adaptive syndromes exist in the mustard, Lesquerella fendleri, in central New Mexico. First, Lesquerella experiences the sort of variation in environmental conditions that would be expected to lead to adaptive trade-offs in the expression of post-germination traits for individuals that differ in germination traits. Annual precipitation varies greatly from year to year so that germination in drier years would be expected to select for more xerophytic traits. Within a year, microenvironmental spatial variation exists. Lesquerella growth and

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reproduction are sensitive to both year-to-year and microenvironmental variation. Second, the seed bank can affect both the demographic and genetic structure of the population. Dormant seeds remain viable for at least 3 yr and can mitigate the negative demographic effects of reproductive failure. Allozyme differences exist between seeds that germinate in the field and seeds that remain dormant, suggesting that the evolutionary potential of the aboveground population is influenced by dormancy. Finally, the necessary genetic and environmental variation is present. Both germination percentage and post-germination traits (e.g., leaf morphology) vary among and within populations as well as among environmental treatments. Thus, the potential exists for *Lesquerella* to respond to selective differences between different temporal or spatial environments.

We suggest experimental approaches for assessing the extent to which seed dormancy has affected or will affect the evolution of post-germination traits. The consequences of past evolution could be explored by asking "What genetic and phenotypic differences exist between individuals that germinate and those that remain dormant?", while controlling for factors that influence germination (maternal genotype, maternal environment, and germination environment). Exploring whether evolution is currently occurring would require an assessment of natural selection and the genetic potential for response to selection. Given the difficulty of such studies, a reasonable first step would be to explore how evolution can occur by performing an artificial selection experiment on dormancy or germination percentage. Then, correlated responses of post-germination traits could be examined.

Empirical studies such as these are necessary in order to better understand the role of seed banks in plant ecology and evolution. Then, once associations that can be interpreted as adaptive syndromes are documented, questions about the ecological mechanisms (e.g., necessary frequencies of different year types) and genetic mechanisms (e.g., linkage disequilibrium vs. pleiotropy) can be explored. We hope to draw attention to seed dormancy, which is an often-ignored stage in the life history of plants, and to encourage empirical work, which lags far behind theory.

**Key words:** creosote shrubland; dormant seeds; leaf morphology; microenvironmental variation; reproductive success; southwestern North America.

**Introduction**

Seed dormancy in higher plants is a means of avoiding unfavorable environmental conditions by arresting growth and development. Many other diverse organisms have similar dormant stages (e.g., encysting in dinoflagellates, Binder and Anderson 1990; egg dormancy in copepods, DeStasio 1989). All such forms of dormancy are thought to have evolved in response to environmental variability and uncertainty. With respect to seeds, there are two types of dormancy. Within a year, dormancy serves to delay germination until a time more favorable for seedling establishment and growth, while between-year dormancy may balance the risk of local extinction from germination in unfavorable years with the risk of missing good years by remaining dormant (Silvertown 1988). The widespread occurrence of between-year dormancy has led to the existence of seed banks—large populations of dormant, viable seeds in the soil—in most of the world’s major ecosystems (for reviews see Leck et al. 1989, Thompson 1992).

While a few recent studies have begun to empirically demonstrate the ecological and evolutionary importance of seed banks (Kalisz and McPeek 1992, McGraw 1993, Tonsor et al. 1993), much of our conceptual understanding remains based on mathematical models and theoretical predictions (e.g., Cohen 1966, 1967, Templeton and Levin 1979, Venable and Lawlor 1980, Venable and Brown 1988). Theoretically, via dispersal through time, a seed bank can (1) reduce the probability of extinction over the long term, (2) add age-structure, and (3) change the genetic structure of a population. A seed bank reduces the probability of extinction by providing temporal migration. Age structure is added because a seed bank introduces overlapping generations. A seed bank can change the genetic structure of a population by acting as a genetic memory (since the seed bank contains seeds produced in different years and therefore under different environmental and selection regimes). Seed dormancy also has the potential to affect the evolution of traits not directly associated with dormancy and germination through genetic correlation due to linkage and/or pleiotropy. Again, there are numerous theoretical treatments of this issue (e.g., Templeton and Levin 1979, Venable and Lawlor 1980, Ritland 1983, Brown and Venable 1986, Klinkhamer et al. 1987, Venable and Brown 1988, Venable 1989), but few empirical studies.

Before focusing on how dormancy might affect the evolution of post-germination traits, we briefly review how variable dormancy might evolve. Theoretical considerations assume that maternal plants can reduce the risk of reproductive failure of their seed crops by spreading germination over time (reducing the variance in fitness among years). Seeds can evolve to "predict" favorable germination periods if there are environmental cues that are correlated with favorable growth and establishment conditions and if plants can evolve to use those cues to break dormancy (reviewed by Mayer and Poljakoff-Mayber 1975, Baskin and Baskin 1989). As the ability to predict favorable pe-
rions increases, uncertainty is reduced, and germination behavior is expected to become less variable (Cohen 1967). If environmental conditions could be perfectly predicted, we might expect either complete dormancy or complete germination within a population experiencing a given germination environment (Silvertown 1988). Yet environmental conditions typically vary considerably in time and space, both between and within habitats. Thus, it is plausible that seeds within a population, as well as different populations of a given species, have evolved different germination requirements based on their particular environmental and evolutionary history.

How might the existence of dormancy affect the evolution of post-germination traits? Models by Templeton and Levin (1979) suggest that for traits whose fitness varies with the environment, the existence of a seed bank influences the rate of evolution: traits that confer fitness in good environments evolve faster than traits that confer fitness in poor environments. Similar models by Brown and Venable (1986) suggest that the evolution of germination and post-germination traits will have a damping effect on one another. Since they are viewed as alternative means of decreasing variance in fitness among years. These models emphasize that a seed bank can permit a population to escape the need to respond adaptively to selection for post-germination traits in poor years by specializing on good years. We wish to consider adaptation to both good and poor years and suggest that the joint evolution of dormancy and post-germination traits may lead to adaptive combinations of germination and post-germination responses (“syndromes.” Venable 1989).

The scenario we imagine can be illustrated as follows. In desert habitats, the amount of precipitation varies considerably from year to year. Seeds that germinate in different conditions experience different selective regimes for post-germination traits. In relatively dry years, individuals with more xerophytic traits (e.g., greater water-use efficiency) should have greater reproductive success, while, in relatively wet years, individuals with more mesophytic traits (e.g., lower water-use efficiency due to spending water more profligately) should have greater reproductive success. Thus, a trade-off exists in the expression of a trait that confers adaptation to environments that differ in water availability. Given trade-offs between the fitness of post-germination traits in different environments, seeds that germinate in the environment to which their post-germination traits are adapted will be at a selective advantage. If differences in germination and post-germination traits are genetically based, then different syndromes of germination and post-germination traits that are adaptive in different environments can potentially come about through the evolution of increased genetic correlations between germination and post-germination traits. Thus, we might expect plants with xerophytic adult traits to require less water to break dormancy.

An example of an adaptive syndrome involving dormancy is the desert annual Heterotheca latifolia. Disc achenes of this composite species were more successful (in terms of survival and biomass accumulation) than ray achenes when grown under a regular watering regime (Venable 1985). However, ray achenes ultimately achieved greater success under simulated drought conditions by exhibiting greater dormancy during the drought periods. Venable and Levin (1985) also found that only ray achenes formed a between-year seed bank. This is an example of a species-level somatic seed polymorphism: all individuals produce both seed morphs. Such polymorphisms are widespread, and generally have been regarded as a form of bet-hedging by maternal plants (Silvertown 1984, Venable 1985).

While the existence of somatic seed syndromes is interesting in itself, we wish to focus on whether genetic syndromes occur. It is not clear whether intraspecific germination differences among seeds without obvious polymorphisms (i.e., with continuous variation) are due to genetic factors, environmental maturation effects, or interactions of these and other forces. Determining to what extent these differences are adaptive can be tested empirically, although to date no studies have examined continuously varying post-germination traits (e.g., water-use efficiency) that have presumed adaptive significance in particular environments (but see Ritland and Jain 1984 for a comparison between two species).

A first step in determining the importance of seed dormancy in the evolution of other traits is to ask what conditions could favor joint evolution of dormancy and post-germination traits that leads to syndromes. First, environmental variation must be of the sort that would be expected to lead to trade-offs in the expression of post-germination traits. As illustrated by the models of Templeton and Levin (1979), unless fitness varies across environments, the existence of a seed bank will affect only the rate of evolution of a post-germination trait, and not its equilibrium frequency. Both spatial and temporal variability should be important in the joint evolution of dormancy and post-germination traits (Venable 1989). Second, a persistent seed bank must exist that has the potential to significantly affect the demography and genetic structure of the aboveground population. While even one seed remaining viable in the soil between years could conceivably rescue a population from extinction, the evo-
lution of adaptive syndromes is more likely in populations in which the seed bank is known to be persistent and to play a role in demographic security. Evidence that seeds with different germination requirements differ genetically would suggest that dormancy influences the evolutionary potential of the aboveground population, since the aboveground population that is subject to selection on post-germination traits in the current environment is not a random subsample of all available seeds. Third, there must be genetic and environmental variation for dormancy and post-germination traits. Traits must be environmentally sensitive (plastic) in order for selection to act on trade-offs, and must be genetically variable in order for an evolutionary response to selection to occur. Here we explore these conditions in the desert mustard, Lesquerella fendleri, and discuss how the potential for dormancy to affect the evolution of post-germination traits might be tested empirically.

Methods

The study system

Lesquerella fendleri (Brassicaceae) is a self-incompatible, short-lived perennial native to southwestern North America. It ranges from western Texas through New Mexico and eastern Arizona into northern Mexico at elevations between 600 and 1800 m in calcareous, sandy soils (Rollins and Shaw 1973). Germination occurs primarily in the late winter to early spring (February to March), but a second flush of germination may occur in the fall if rainfall is sufficient. Flowering usually occurs between March and April and may also occur following suitable rains in the fall. Plants may produce up to several hundred fruits, with up to 30 seeds per fruit.

We have been studying Lesquerella at the Sevilleta National Wildlife Refuge (NWR), 80 km south of Albuquerque in central New Mexico. The Sevilleta NWR, a Long-term Ecological Research site, is one of the few large areas in the Southwest protected from human disturbances; cattle grazing and human uses other than research have been prohibited for almost 20 yr. At the Sevilleta, Lesquerella occurs in ecologically diverse habitats, including creosote (Larrea tridentata) shrublands, grasslands, and more open, sandy washes. Our main study site (Five Points) is dominated by creosote shrubs and largely open, barren patches in the interspaces between the shrubs.

Spatial and temporal environmental variation

To evaluate the potential for dormancy to affect the evolution of post-germination traits, we employed a number of observational and manipulative studies. To assess temporal environmental variation, we used monthly records of precipitation for 64 yr from Albuquerque and for 2 yr (1991 and 1992) from a weather station = 3 km from the Five Points study site.

To assess spatial variation created by the mosaic of shrub canopies and open spaces, light intensity and soil temperature, moisture, and organic matter were measured. Light and temperature data were taken from 19 creosote sub-canopies and adjacent interspace locations at the Five Points study site on 5 August 1992. Photosynthetically active radiation was measured using a light meter (Model LI-6200, LI-COR, Lincoln, Nebraska, USA) at 10 cm above the soil surface, which corresponds to average Lesquerella height in this population. Soil temperatures were measured at the surface and at 10 cm depth, since we have observed that the bulk of Lesquerella roots are typically within 10 cm of the soil surface. Soil samples for moisture and organic matter were taken at the surface and at 10 cm depth under 20 creosote canopies and adjacent open interspaces on 25 June 1993 at Five Points. Soil moisture was calculated as the percentage difference in mass between fresh and dried samples. Percentage organic matter was calculated from fresh and combusted dry masses. The surface samples include litter as well as soil organic matter.

The importance of spatial and temporal environmental variation for Lesquerella performance was evaluated by measuring several demographic parameters beneath creosote canopies and in the interspaces between the shrubs in 1991 and 1992. For the sub-canopy microhabitat, 25 1-m² plots, each centered on a creosote shrub, were sampled. For the interspace microhabitat, sampling was done along a 50-m transect through the study site. Along this transect, 1-m² quadrats on both sides of the line were sampled using only 1-m² positions with <10% shrub cover, for a total of 38 1-m² plots. The density of Lesquerella plants and the mean number of Lesquerella seeds produced per square metre were also estimated.

Lesquerella seed bank

To investigate the importance of the Lesquerella seed bank, we assessed the density and longevity of the seed bank, and compared the genetic structure of the seed bank with that of the seedling population. Previous work has shown that there are significantly more Lesquerella seeds in the soil under creosote canopies than in the interspaces (R. Cabin, unpublished data). We subsequently focused our attention on the more dense seed bank under creosote canopies and collected 10 soil samples (10 × 10 × 2 cm) randomly from a 1-m² plot under each of 30 creosote shrubs prior to Lesquerella seed maturation in 1991. These 300 samples were sieved and searched under a dis-
secting microscope for any Lesquerella seeds from previous years.

To discover whether seeds that germinate in the field differ genetically from seeds that remain dormant under the same environmental conditions, Lesquerella genotypes were characterized by employing starch gel electrophoresis. All seedlings that germinated in the field within 30 1-m² plots under creosote in the fall of 1991 were collected for electrophoresis using five enzyme systems and seven polymorphic loci. Once germination in the field had ceased, 10 soil samples (10 × 10 × 2 cm) were collected from each of the same plots, spread in a thin layer over potting mix in the greenhouse and treated with a 0.1 g/kg gibberellic acid solution known to break dormancy (Sharir and Gelmond 1971, R. Cabin and R. Mitchell, unpublished data). All emerging Lesquerella seedlings from these samples were collected for electrophoresis as above. We are confident that this technique recovers most of the viable dormant Lesquerella seeds, since the number of seeds recovered via germination does not differ significantly from the number recovered by searching under the microscope (R. Cabin, unpublished data).

**Genetic and environmental variation for germination and post-germination traits**

To assess the degree of genetic and environmental variation for dormancy and post-germination traits, we used three experiments, one of which explored inter-population variation, and the other two of which estimated intrapopulation variation. First, interpopulation variation in germination and post-germination traits was measured by exposing populations to different environmental treatments in the greenhouse. Second, intrapopulation variation in germination behavior was assessed among maternal plants. Third, intrapopulation variation in post-germination traits (including maternal, paternal, and environmental sources) was evaluated.

Interpopulation variation was evaluated in the following manner. Seeds from five populations representing the range of habitats at the Sevilleta NWR were exposed to five germination treatments in the greenhouse to simulate the range of environmental conditions experienced by Lesquerella plants in the field. For each population, 54 seeds were planted in sand in the greenhouse in each of the following treatments: control (ad libitum watering), low water (watering reduced by half), creosote (creosote litter on the soil surface and control water), low water and creosote litter, and shade (light intensity reduced by half with shade cloth and control water). We did not measure soil moisture but, as expected, creosote litter and shade appeared to reduce evaporation. Germination percentage was quantified, and maximum plant diameter, and width and length of the most recent fully expanded leaf were measured with digital calipers (Series 550, Mitutoyo Corporation, Tokyo, Japan). These measurements were made 9 wk after planting, when the plants were still in the seedling stage.

To assess within-population variation in germination percentage, field-collected sibships from seven maternal plants were used. Because we do not know the paternity of these seeds, we cannot tease apart maternal and embryonic controls on germination (see Discussion). For each of the seven sibships, 90 seeds were scored for germination percentage under ambient conditions in the greenhouse.

Finally, maternal, paternal, and environmental sources of variation within a population in post-germination traits were evaluated as follows. Pollinations were performed on plants grown from field-collected seeds (from a different population and year than above) as parents utilizing a 7 × 7 diallel breeding design without self-polllinations. Progeny were treated with gibberellic acid, germinated in a common environment, and four plants per family were grown in each of two watering treatments. Plants in the low watering treatment were watered half as frequently as plants in the high watering treatment. Plant diameter, leaf length, and leaf width were measured as above, but at a later stage in ontogeny (4 mo after planting, just prior to flowering). Because gibberellic acid was used to germinate progeny in a common environment, we cannot examine correlations between germination percentage and post-germination traits in different environments.

**Results**

**Spatial and temporal environmental variation**

The influence of the global El Niño–Southern Oscillation weather pattern on precipitation in central New Mexico is well-documented: in El Niño years, winter and spring precipitation is greater than average, while in La Niña years, it is lower than average (Ropelewski and Halpert 1986, 1990, Molles et al. 1993). Thus, while average precipitation for the primary growing season of Lesquerella is low, certain years can be categorized as relatively wet or dry (Fig. 1a). The years 1991 and 1992 exemplify La Niña and El Niño conditions, respectively (Fig. 1b).

Within a year, the microenvironments beneath creosote shrubs and in the spaces between shrubs differ considerably. The lower light intensity (Fig. 2) and soil temperature (Fig. 3), and the greater surface organic matter (Table 1) under creosote canopies likely lead to slower evaporation of soil moisture than in the
Lesquerella shows genetic variation for dormancy. In one experiment, seeds from five populations were tested for germination in five environments. Germination percentage differed among populations (log-linear ANOVA: \( \chi^2 = 177.15, P < 0.0001 \)) and environments (log-linear ANOVA: \( \chi^2 = 272.99, P < 0.0001 \)). There was also a significant population-by-environment interaction (log-linear ANOVA: \( \chi^2 = 109.71, P < 0.0001 \)), indicating population differentiation for plasticity of germination (Fig. 4).

In another experiment, 90 seeds from each of seven maternal plants were tested for germination in the greenhouse. Germination percentage varied from 3 to 97%. (Values for the other five families: 84, 8, 53, 67, 97, and 31 mm). Monthly precipitation in central New Mexico (March through May) and near the Five Points study site, 1991 and 1992 (Table 2). Lesquerella appears to be sensitive to microenvironmental variation (Table 2). Winter-spring precipitation was greater in 1992 (108 mm) than in 1991 (31 mm), and both plant abundance and seed production were significantly greater in 1992. Lesquerella also appears to be more successful under creosote canopies; plants are more abundant and produce more seeds under creosote sub-canopies than in the interspaces between shrubs (Table 2).

Lesquerella seed bank

The Lesquerella seed bank at the Five Points site appears to be persistent. While only 51 ± 20 new Lesquerella seeds/m² (mean ± SE) were produced beneath creosote in 1990, 247 ± 38 seeds/m² were found in the soil prior to fruiting in 1991. Since essentially no fruiting was observed in 1989 in this or any other nearby population, a significant portion of the seeds in the soil in 1991 must have been at least 3 yr old.

Electrophoretic data show genetic differentiation between dormant seeds and seedlings. Allele frequencies of seeds and seedlings are highly significantly different at four loci and marginally different at two of the remaining three loci examined (Table 3). Thus, Lesquerella seeds that germinate in the field differ genetically from seeds that remain dormant under the same environmental conditions.

**Fig. 1.** Winter–spring precipitation in central New Mexico. (a) Monthly averages from Albuquerque, 1920–1984. Averages for medial (n = 48), El Niño (n = 5) and La Niña (n = 12) years. Adapted from Molles et al. 1992. (b) Monthly precipitation near the Five Points study site, 1991 and 1992.

**Fig. 2.** Microhabitat variation for Lesquerella in intensity of PAR. Each point = mean ± 1 SE (n = 19).
and 51%). Hence, variation for germination exists among maternal sibships within a population.

Environmental and genetic variation also exists for post-germination traits in Lesquerella. Plant diameter and leaf length and width varied among populations and/or germination and growth environments and showed population-by-environment interaction (Table 4). These post-germination traits also showed within-population genetic variation (Table 5). Plant diameter and leaf length differed significantly among sires and dams and leaf width differed significantly among dams.

Discussion

The Lesquerella case

The potential exists for dormancy to affect the evolution of post-germination traits in Lesquerella fendleri at the Sevilleta NWR in central New Mexico. First, Lesquerella experiences the sort of variation in environmental conditions that would be expected to lead to trade-offs in the expression of post-germination traits for individuals that differ in germination traits. Certain years are wetter or drier than average. Germination in drier years would be expected to select for individuals with more xerophytic traits (e.g., greater water-use efficiency, higher root: shoot ratio). The sensitivity of Lesquerella to environmental variation is illustrated by microhabitat differences in growth and reproduction as well as by year-to-year variation. Indeed, it is conceivable that within a year, environmental differences between microhabitats result in differences in natural selection.

Second, the seed bank is persistent and can affect the demographic and genetic structure of the population. Seeds remain viable in the field for at least 3 yr. and likely longer, since seeds stored in the laboratory have been shown to remain viable for at least 7 yr (Sharir and Gelmond 1971). Thus, the presence of the seed bank can mitigate the negative demographic effects of reproductive failure. The seed bank can also affect the genetic structure of the surface population, since allozyme frequencies differed between seeds that germinated in the field and seeds that re-

### Table 1. Microhabitat variation in soil water content and organic matter. Data are reported as mean ± 1 SE.

<table>
<thead>
<tr>
<th>Soil water content (%)</th>
<th>Organic matter (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Surface</td>
</tr>
<tr>
<td>Sub-canopy</td>
<td>0.20 ± 0.06</td>
</tr>
<tr>
<td>Interspace</td>
<td>0.15 ± 0.06</td>
</tr>
</tbody>
</table>

### Table 2. Year-to-year and microenvironmental variation in Lesquerella abundance and reproduction. Values are mean number per m² ± 1 SE.

<table>
<thead>
<tr>
<th></th>
<th>Sub-canopy</th>
<th>Interspace</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer 1991</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult plants</td>
<td>4.08 ± 0.89</td>
<td>1.32 ± 0.17</td>
</tr>
<tr>
<td>Seed production</td>
<td>14.41 ± 3.64</td>
<td>1.71 ± 0.35</td>
</tr>
<tr>
<td>Summer 1992</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult plants</td>
<td>13.08 ± 1.68</td>
<td>1.92 ± 0.16</td>
</tr>
<tr>
<td>Seed production</td>
<td>2428.77 ± 349.37</td>
<td>143.08 ± 14.70</td>
</tr>
</tbody>
</table>
mained dormant under the same environmental conditions. Thus, the genotypes of seeds that germinated were probably not a random subset of all available seeds, which suggests that the evolutionary potential of the aboveground population is influenced by the expression of dormancy and the existence of the seed bank.

However, this genetic interpretation is possibly biased by details of the sampling scheme. Allele frequency data for seeds and seedlings in this study were pooled across all 30 plots. Therefore, allelic differences between these two stages could also be attributed to spatial environmental differences that resulted in differential germination rates among the plots. If there is spatial genetic structure in the Lesquerella population, pooling across plots would overestimate genetic differences between dormant and dormant seeds (i.e., differences between dormant vs. germinating seeds would be due at least partially to spatial environmental factors). While performing plot-by-plot comparisons should take care of this problem, our sample sizes per plot are too small and variable, particularly in the case of the seed bank, whose density is notoriously variable and cannot be assessed a priori.

Finally, genetic and environmental variation exists for both germination and post-germination traits. The propensity of seeds to germinate varied among populations as well as among maternal plants from a single population. Variation among maternal plants may be due to maternal effects and/or variation among paternal parents (additive genetic variation), both of which may be relevant to the evolution of germination requirements. However, as we suggest below, the most reasonable demonstration of a genetic basis for the observed variation would be a response to family selection on dormancy. There was significant variation among populations in the plasticity of germination percentage in different environments. In addition, there was genetic and/or environmental variation for size and leaf morphology both between and within populations, and evidence of interactions between genetic and environmental effects. Thus, the potential exists for some Lesquerella traits to respond to selective differences between different spatial or temporal environments.

Some of our information about the evolutionary potential of Lesquerella, especially for environmental plasticity in dormancy and post-germination traits, comes from population comparisons. Intrapopulation information, which we are currently working on obtaining, would be better since we are interested primarily in microevolutionary processes. However, the same evolutionary processes that occur within populations can lead to population differentiation. Furthermore, desert plants and their seed banks are notoriously patchy in space and time (reviewed by Kemp 1989). It therefore seems reasonable to use variation between populations as an initial indicator of variation within populations. Thus, we interpret the interpopulation variation we observed, along with the intrapopulation data, as supportive of the idea that Lesquerella has the sort of genetic and environmental variation favoring the evolution of adaptive syndromes of germination and post-germination traits within populations.

### Further empirical approaches

While these results indicate that dormancy can affect the evolution of post-germination traits in Lesquerella, the extent to which the seed bank has affected or will affect the evolution of post-germination traits...
must be assessed through other means. If the joint evolution of dormancy and post-germination traits has led to adaptive syndromes, we would expect to see differences in the expression of post-germination traits for individuals with different dormancy-breaking requirements. Hence, the consequences of past evolution could be documented by asking, "What genetic and phenotypic differences exist between individuals that germinate and those that remain dormant?" Such an approach would involve a comparison of seeds that germinate in a given environment with individuals that remain viable but dormant. Dormant seeds would have to be forced to germinate, which could be accomplished by the application of gibberellic acid. The possibility that gibberellic acid may influence the expression of traits would have to be explored, but studies with other species suggest that any differences due to gibberellic acid treatment would be insignificant (Baskin and Baskin 1973; G. Fox, A. Evans, and C. Keefer, unpublished data).

The relationship between dormancy and post-germination traits is complicated by the factors that regulate germination. Hence, the controls on variation in seed germination must first be understood. Heritable genetic variation (especially maternal variation) and the maternal environment, as well as the germination environment, can contribute to diversified germination behavior within a population.

### Table 4. Variation among populations and environments in three post-germination traits at 9 wk. ANOVA was performed on measurements of the same plants for which germination data are reported in Fig. 4. However, due to mortality-induced reductions in sample size, data from one population and the low water and control treatments were omitted from this analysis. Both treatment and population are considered to be fixed effects.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Source of variation</th>
<th>df</th>
<th>MS*</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant diameter</td>
<td>Environment</td>
<td>2</td>
<td>320.63</td>
<td>3.80</td>
<td>0.03</td>
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<tr>
<td></td>
<td>Population</td>
<td>3</td>
<td>193.23</td>
<td>2.24</td>
<td>0.09</td>
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<tr>
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<td>Environment × population</td>
<td>6</td>
<td>261.28</td>
<td>3.09</td>
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</tr>
<tr>
<td></td>
<td>Error</td>
<td>93</td>
<td>84.45</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf length</td>
<td>Environment</td>
<td>2</td>
<td>102.42</td>
<td>3.74</td>
<td>0.03</td>
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<tr>
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<td>3</td>
<td>21.07</td>
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<tr>
<td></td>
<td>Environment × population</td>
<td>6</td>
<td>70.24</td>
<td>2.57</td>
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<tr>
<td></td>
<td>Error</td>
<td>93</td>
<td>27.37</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf width</td>
<td>Environment</td>
<td>2</td>
<td>4.82</td>
<td>17.51</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Population</td>
<td>3</td>
<td>0.33</td>
<td>1.20</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>Environment × population</td>
<td>6</td>
<td>0.27</td>
<td>0.98</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>93</td>
<td>0.28</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Type III sums of squares were used to calculate mean squares.

### Table 5. Within-population genetic and environmental variation in three post-germination traits. The ANOVA is based on a mixed model; treatment is fixed while sires and dams are random.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Source of variation</th>
<th>df</th>
<th>MS*</th>
<th>F</th>
<th>P</th>
</tr>
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<tbody>
<tr>
<td>Plant diameter</td>
<td>Environment</td>
<td>1</td>
<td>502.65</td>
<td>1.16</td>
<td>&gt;0.5</td>
</tr>
<tr>
<td></td>
<td>Sire</td>
<td>6</td>
<td>618.16</td>
<td>4.99</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Dam</td>
<td>6</td>
<td>643.07</td>
<td>5.20</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Environment × sire</td>
<td>6</td>
<td>176.25</td>
<td>1.42</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>Environment × dam</td>
<td>6</td>
<td>134.23</td>
<td>1.09</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>288</td>
<td>123.78</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf length</td>
<td>Environment</td>
<td>1</td>
<td>79.12</td>
<td>0.53</td>
<td>&gt;0.5</td>
</tr>
<tr>
<td></td>
<td>Sire</td>
<td>6</td>
<td>176.94</td>
<td>4.81</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Dam</td>
<td>6</td>
<td>188.96</td>
<td>5.13</td>
<td>0.0001</td>
</tr>
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<td></td>
<td>Environment × sire</td>
<td>6</td>
<td>66.15</td>
<td>1.80</td>
<td>0.1</td>
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<tr>
<td></td>
<td>Environment × dam</td>
<td>6</td>
<td>46.97</td>
<td>1.28</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>288</td>
<td>36.81</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf width</td>
<td>Environment</td>
<td>1</td>
<td>25.79</td>
<td>9.00</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>Sire</td>
<td>6</td>
<td>0.42</td>
<td>0.60</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>Dam</td>
<td>6</td>
<td>1.19</td>
<td>3.15</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>Environment × sire</td>
<td>6</td>
<td>1.09</td>
<td>1.57</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>Environment × dam</td>
<td>6</td>
<td>1.08</td>
<td>1.56</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>288</td>
<td>0.69</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Type III sums of squares were used to calculate mean squares. Random effects were tested over error ms, while treatment was tested over pooled ms (since interactions were not significant; Sokal and Rohlf 1981).
We have shown that *Lesquerella* populations at the Sevilleta NWR respond differently to different germination environments. Similar results have also been found for other species. For example, for three Chihuahuan Desert annuals, germination increased with the amount of precipitation (Freas and Kemp 1983). Venable and Lawlor (1980) referred to this environmental sensitivity or plasticity of germination as "predictive germination," suggesting that seeds have evolved to predict favorable germination periods based on environmental cues. Genetic variation for environmental sensitivity may be considerable. In Saskatchewan (Amelanchier alnifolia), population-by-year interaction (indicating population variation for plasticity) accounted for almost 20% of the variation in germination among 27 populations tested in 3 yr (Acharya et al. 1989).

However, it is not clear to what extent intrapopulational germination variation is genetically based. That is, for seeds within a population, are there heritable differences in the environmental variables required to break dormancy? There is considerable evidence that seed dormancy is under some degree of heritable genetic control (see Garbutt and Witcomb 1986 for a review). The seed is composed of up to three tissues (the maternal seed coat, the diploid embryo, and the endosperm, which may be of variable ploidy, or absent, as in the Brassicaceae); hence, genetic regulation can be quite complex. Of these three tissues, the maternal genotype is usually the most important in determining dormancy (e.g., Garbutt and Witcomb 1986, Biere 1991, Platenkamp and Shaw 1993), as seed coat characteristics are usually involved in the proximate regulation of dormancy. However, an embryonic component may also be involved (e.g., Garbutt and Witcomb 1986). A response to artificial selection on dormancy as a maternal family trait, as has been demonstrated for several species (e.g., Hilu and de Wet 1980, Garbutt and Witcomb 1986), illustrates the evolutionary potential of maternal genetic effects.

As is the case for seed size and other early performance traits (Roach and Wulff 1987), the environmental conditions experienced by the maternal plant during seed development can influence germination in the offspring (e.g., Koller 1962, Gutterman 1981, 1992). Some suggest removing such "preconditioning" effects by growing maternal plants in a common environment and thus removing any confounding of maternal environmental and maternal genetic variation (Baskin and Baskin 1973, Quinn 1977). However, preconditioning itself may be genotype dependent (Westoby 1981), and, in nature, the maternal environment may well be an important regulatory factor. To date, the degree to which maternal environment affects germination behavior is poorly understood.

It is clear that heritable variation (usually maternal genotype), maternal environment, and germination environment can all contribute to variable germination behavior. However, studies of the relative contributions of these factors are few (e.g., Biere 1991, Schmitt et al. 1992, Platenkamp and Shaw 1993). The factors regulating germination must be documented in order to understand how dormancy affects the evolution of post-germination traits. Consequently, we suggest asking how the influences of maternal genotype, maternal environment, and germination environment are related to variation in post-germination traits.

What post-germination traits should be studied? Aside from seed traits associated with heterocarpy and dispersal, few post-germination traits have been considered in conjunction with dormancy. Obviously, the traits must be ecologically relevant to the species. For example, Platenkamp and Shaw (1993) emphasized the role of interspecific competition on dormancy and post-germination success in the annual *Nemophila menziesii*. For *Lesquerella*, water availability is clearly of major importance. A number of post-germination traits associated with water use might be expected to involve an adaptive trade-off between relatively wet and dry environments. For example, as noted earlier, greater water-use efficiency should be more adaptive when water availability is more limiting. Several aspects of leaf morphology (e.g., leaf area, stomatal density) may be related through gas exchange with water-use efficiency (Zangerl 1978, Bhagsari and Brown 1986, Geber and Dawson 1990). For example, the photosynthetic cost of smaller leaf area commonly found in arid environments might be offset by greater stomatal density. Root-to-shoot ratio is another trait for which optimal expression is expected to differ between wet and dry environments; as water becomes more available, less investment in root tissue is required so that more shoot biomass can be allocated to growth and reproduction (Schulze 1986). Studying ecologically relevant traits that are expected to show trade-offs in different germination and growth environments will provide the best test of whether germination and post-germination traits have evolved adaptive syndromes.

The approaches outlined above can be used to determine whether past evolution has led to syndromes of germination requirements and post-germination traits. To determine whether evolution is currently acting requires an assessment of natural selection and of the genetic potential for response to selection. Given the difficulty of such studies, especially for dormancy, a reasonable first step would be to explore how evo-
lution can act by performing an artificial selection experiment on dormancy or germination. Then correlated responses of post-germination traits, which may not necessarily be adaptive (Johnson et al. 1992), can be examined.

Additional considerations

We have emphasized an empirical approach to the study of how dormancy might affect the evolution of post-germination traits. Observing adaptive syndromes as outlined above would certainly support the idea that the existence of dormancy can influence the evolution of post-germination traits. But several other questions must also be addressed before we can incorporate into our ecological-evolutionary perspective the often-ignored life stage of dormant seeds.

Why ask how dormancy affects the evolution of post-germination traits rather than the other way around? Recently, mathematical models have addressed how post-germination traits, such as adult longevity, can influence the evolution of dormancy (Rees 1994). We have chosen to emphasize dormancy as the phase influencing others. Because dormancy is difficult to study empirically and hence has often been ignored, we wish to highlight its importance in order to provoke discussion and research.

What are the genetic mechanisms through which adaptive syndromes might arise? We expect phenotypic correlations between germination requirements and post-germination traits to be driven, to some extent, by genetic correlations (as opposed to being driven solely by plastic responses). Such genetic correlations can arise in two main ways. First, through pleiotropy—the same genes influencing the expression of different traits. Second, through linkage disequilibrium—nonrandom associations among alleles. In general, pleiotropy is the more common cause (Falconer 1989). However, the relative roles of pleiotropy and linkage as genetic mechanisms may depend on the ecological mechanisms through which dormancy affects the evolution of other traits.

Linkage disequilibrium is more likely to be important if reproductive isolation comes into play (see Hedrick et al. 1978 for a review of multilocus evolution). Variation in germination itself could lead to partial temporal reproductive isolation. However, the age structure introduced by a seed bank would tend to counter the effect of reproductive isolation. The sort of linkage disequilibrium brought about by reproductive isolation would not, at least at first, necessarily be adaptive (Spiess 1989). We envision an evolutionary-ecological mechanism driven not just by reproductive isolation but by natural selection acting within each year. Seeds that germinate in the environment to which their post-germination traits are adapted will be at a selective advantage. Hence, evolution will favor certain genetic correlations, whether due to pleiotropy or linkage.

We have suggested conditions necessary for certain correlations to be favored. Whether these conditions are sufficient remains to be seen, and should be explored in more than one system (species or population). We believe the question of sufficiency is largely empirical, since a natural system may not be adequately described by theoretical models. However, theoretical models have pointed out several factors that we have not yet addressed.

One important consideration is the nature of predictive germination. Discussions of predictive germination—plasticity in dormancy—usually implicitly assume that adaptive "decisions" are made. Presumably, seeds evolve to use environmental cues that are informative about the probability of future reproductive success. The classic example is that germination should increase with rainfall. But just documenting an increase in germination with water availability does not demonstrate adaptiveness, since seeds imbibe more water when more water is available. Therefore, we need to untangle adaptive decisions from unavoidable physiological responses. In Lesquerella, predictive germination may be uncoupled from unavoidable physiological responses, since germination does not always increase with water availability. Some populations did not show greater germination under wetter conditions. Whether the lack of increase in germination with water availability is adaptive remains to be tested.

As has already been pointed out from theoretical models, the frequency of different year types is also important since, by definition, most seeds will be produced in good years. The scenario we propose is more likely in the sort of environment we are studying—one in which good years are rare (dry years are the norm) so that selection for dry-adapted traits is not swamped by selection for wet-adapted traits. Modeling efforts, using data derived from natural populations (as has recently been done with regard to extinction dynamics by Kalisz and McPeek [1993]), would help clarify the effect of different patterns of good vs. poor years on the evolution of adaptive syndromes of germination and post-germination traits.

The strength of selection necessary (and sufficient) is also unclear. We suggest that trade-offs in the expression of germination and post-germination traits in different environments are necessary. However, this does not necessarily imply that more dormant genotypes should perform worse under good conditions than under poor conditions. The sort of selection we
envision could be quite weak. Thus, we do not think it would be necessary for, say, dry-adapted plants to perform better in dry than wet years—only that they perform better than wet-adapted plants in dry years. However, we have not yet evaluated this idea.

A final topic that has not received much theoretical work is maternal environmental effects on germination. As we point out above, such preconditioning may be an important component of the natural variation in germination; to evaluate this possibility will require experimentally teasing apart maternal environmental and genetic effects. Maternal effects can evolve adaptively (Kirkpatrick and Lande 1989). Thus, maternal effects may play a significant role in the joint evolution of dormancy and post-germination traits.

Seed banks are thought to have evolved as a response to unpredictable environmental variability (Cohen 1966, 1967, McDonald and Watkinson 1981, Freas and Kemp 1983, Schmidt and Lawlor 1983). Theoretical models have suggested that seed dormancy can influence the evolution of traits not directly associated with dormancy and germination (Templeton and Levin 1979, Venable and Lawlor 1980, Ritland 1983, Brown and Venable 1986, Klinkhamer et al. 1987, Venable and Brown 1988, Venable 1989). We suggest that a possible outcome may be the evolution of adaptive syndromes of germination and post-germination traits. Because of the complicated genetic and phenotypic relationships among traits, we advocate empirical approaches for exploring the extent to which the seed bank has affected or will affect the evolution of post-germination traits.

Acknowledgments

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