

SPECIAL PAPER

DROUGHT AND THE EVOLUTION OF FLOWERING TIME IN DESERT ANNUALS¹

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Drought is often thought to stimulate flowering in desert, and sometimes in mesic, annuals. I review experimental studies of the effect of drought on flowering time in both desert and mesic annuals. No convincing experimental evidence presently exists that drought stimulates flowering in any annual plant; some experimental results suggest the opposite. The design and analysis of flowering time studies are also reviewed; most extant studies have serious flaws. Thus, a convincing demonstration of drought-stimulated flowering will require carefully designed and analyzed experiments.

In light of these results, I examine several ways in which drought may affect the ecology and evolution of flowering time in desert annuals, and suggest directions for research. Several mechanisms probably contribute to phenotypic variation in flowering time and size, including water and nutrient limitation, competition, and variation in seed size and germination time. Phenotypic effects of seed traits suggest that seed and flowering time traits may not evolve independently of one another. Water stress during reproduction can influence seed traits; such maternal effects can influence the outcome of selection both on seed traits and on flowering time. The multivariate character of flowering time evolution suggests that genetic and phenotypic correlations among these traits may present important constraints on the evolution of flowering time.

Annual plants in hot deserts have been noted (Went, 1949; Shreve, 1951; Rathcke and Lacey, 1985; Lacey, 1986; Fox, 1989, 1990a) to display considerable variation in flowering time and size. While there is variation for these traits in most plant populations, a number of researchers have suggested that desert annuals display an unusual degree of phenotypic plasticity in flowering time and size, and that this plasticity may be adaptive (Went, 1948; Evnari, Sharon, and Tadmor, 1971; Lacey, 1986).

In particular, it is widely held that flowering time in desert annuals is strongly influenced by an adaptive phenotypic plasticity, in which onset of flowering is stimulated by drought. This claim may have originated with Went's (1948) statement that "after heavy rains the plants remain vegetative for some time, and start to flower only after a considerable size is reached. After the lightest rain which just allows germination, the plants almost immediately change over to the reproductive stage, and thus remain diminutive." Went's view has

been influential; while Koller (1969) and Mott (1979) found no evidence for this relationship between rainfall and phenology, it is cited in such places as a widely used plant development textbook (Leopold and Kriedemann, 1975), a review on the effect of drought on pasture plants (Turner and Begg, 1978), and a review of plant phenology (Rathcke and Lacey, 1985).

Drought-stimulated flowering is thought of as a means by which desert annuals can maximize their size at flowering, but still assure that they "almost always" set seed before season's end (Solbrig et al., 1977; Rathcke and Lacey, 1985). A consequence of this flowering time plasticity, according to several authors (Went, 1949; Shreve, 1951; Lacey, 1986) is that natural selection is likely to act primarily on this plasticity and on germination responses, limiting the potential for local adaptation of desert annuals in flowering time and size.

There are at least two reasons to question this view of desert annual life histories. First, recent studies (Aronson, 1989; Fox, 1989, 1990a) suggest that adaptation in flowering size and time does occur in local populations of desert annuals. Second, evidence that few plants die before flowering comes only from anecdotes by Went and his associates; these authors do not always distinguish between seed set by species and seed set by individuals (Went, 1948,

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1949, 1955; Went and Westergaard, 1949; Juhren, Went, and Phillips, 1956). Numerous other studies have reported that while probability of survival to maturity varies considerably, in most years a large fraction (often a majority) of individuals die without setting seed (Shreve, 1951; Tevis, 1958a, b; Klickoff, 1966; Beatley, 1967; Loria and Noy-Meir, 1979–80; Inouye, 1980; Burk, 1982; Fox, 1989; D. L. Venable, unpublished data).

Furthermore, it is not clear that drought actually does stimulate flowering in desert annuals. Evidence cited by Went (1949) was purely anecdotal. On the other hand, other workers (e.g., Bernier and Sachs, 1979; Bernier, Kinet, and Sachs, 1981) have suggested that water stress may generally act among most plants to stimulate flowering. If this generality is true, drought-stimulated flowering would not be a special adaptation to desert conditions, regardless of its present significance (Gould and Vrba, 1982).

Does drought stimulate flowering in either desert or mesic annuals? After introducing some experimental and statistical problems that arise in examining this issue, I review experimental studies on the effect of water stress on flowering in both desert and mesic annuals. I conclude from this literature review that there is presently no convincing evidence that drought stimulates flowering in any annual plant. I then examine ways in which drought may affect the ecology and evolution of flowering time in desert annuals.

METHODS AND STATISTICS IN FLOWERING TIME STUDIES

Experimental methods—Experimental manipulations of water availability are necessary to evaluate the hypothesis that drought stimulates flowering. However, such studies can address this hypothesis only in an ecological sense; they can test whether plants given less water tend to flower earlier than others, but cannot usually assess the independent physiological consequences of drought stress. This limitation results from the correlations among plant water status, tissue temperature, and nutrient status.

A number of techniques have been used to impose water stress. A number of researchers have used hydroponic approaches, imposing drought stress either by manipulating the osmotic properties of the growth medium—usually by adding polyethylene glycol (PEG) (Husain and Aspinall, 1970; Aspinall and Husain, 1970; King and Evans, 1977; Frank, Bauer,

and Black, 1987)—or by removing plants from the growth medium for varying lengths of time (Boot, Raynal, and Grime, 1986). Hydroponic techniques are attractive because they allow quantitative control over treatments. However, this advantage would seem to be more than offset by the clear disadvantage of hydroponic approaches: they may lack ecological and physiological relevance. It is not clear that the osmotic stress imposed by PEG treatments is really analogous to the drought stress experienced by plants growing in soil outdoors, and PEG can have undesirable effects on the plants (references in Snow and Tingey, 1985). Moreover, hydroponic approaches assume that roots and their environment are important only as a means of getting water and nutrients to the rest of the plant. If accurate quantitative control of treatments is necessary, the approach of Snow and Tingey (1985)—which allows plants to be grown in soil—seems preferable to osmotic treatments.

While growth chambers have been used by some researchers (Nicholls and May, 1963; Husain and Aspinall, 1970; Aspinall and Husain, 1970; Marc and Palmer, 1976; King and Evans, 1977; Frank, Bauer, and Black, 1987), they do not seem to present any particular advantage in most cases, because soil water potentials cannot be controlled by growth chambers. Growth chamber experiments are likely to impose limits on sample sizes. Furthermore, conditions in growth chambers are often less ecologically meaningful than those in greenhouses or gardens. On the other hand, growth chambers can be useful in examining the interaction of water stress and factors such as temperature or photoperiod.

Plants can be grown in gardens or outdoor containers if rain shelters are available, or in greenhouses. Soil water potentials may be difficult to control in a garden. Moreover, differences in experimental treatments are likely to lead to differences in plant growth, which can cause garden experiments to be confounded by differences in the intensity of competition within treatment groups. On the other hand, growth conditions in gardens are likely to be more realistic ecologically. Soil in containers can dry much more quickly than natural soil, leading to droughts more severe than those encountered by natural populations, or to sharp swings in soil moisture potentials. This can also lead to considerable mortality and thus a need for very large samples.

Statistical analyses—Distributions of flowering times are likely to depart significantly from normality. This non-normality is gen-

erally inherent in "event-time" data (i.e., data defined as "time until an event occurs") so that transforming the data usually will not normalize them (Kalbfleisch and Prentice, 1980; Lee, 1980; Lawless, 1982). The distributions are partly a consequence of the nature of the experiments—the start of an experiment establishes a sharp cutoff date for the first event. As a result, event-times are often well described by lognormal, gamma, exponential, or Weibull distributions, but only rarely by normal distributions.

This non-normality invalidates statistical approaches that simply compare means and variances of treatment groups. Unless data are known to be approximately normal (e.g., as shown by a Kolmogorov-Smirnov test), means and their standard errors are not adequate to describe results, and statistical tests that assume normality (e.g., analysis of variance (ANOVA) and *t*-tests) can be quite biased.

In most experiments, event-times for some individuals will not be recorded because the plant dies or the experiment is terminated before flowering occurs in some individuals. In statistical jargon such data points are "right-censored": it is known that a response did not occur by some time, but after that time no information is available. Clearly, ignoring right-censored data points leads one to eliminate useful data. Ignoring right-censored points can also seriously bias significance tests, especially if experimental treatments cause more right censorship in one group than in others (e.g., if plants given less water are more likely to die than plants given more). In the presence of right censorship, ANOVAs and *t*-tests can therefore be biased even if the data are approximately normally distributed.

Fortunately there are several powerful, conceptually straightforward, and easy-to-use approaches to the analysis of event-time data, that do not assume normality and can properly use right-censored data. These include failure time and Cox (also called "proportional hazard") models, and life tables (Kalbfleisch and Prentice, 1980; Lee, 1980; Lawless, 1982; Manly, 1985). Failure time and Cox models are similar in many respects; one first estimates a "survival function" (probability of an event occurring at each time) for a failure time model or a "hazard function" (probability of an event occurring at each time given that it has not yet occurred) for a Cox model. Then one asks how covariates such as treatment group shift the survival or hazard function in time. Life table models are a nonparametric approach, through which one compares the median "survival" times of different treatment groups (Lee, 1980;

Pyke and Thompson, 1986). Each of these approaches can be used with at least one of several widely used statistical packages (Dixon, 1981; SAS Institute, 1988; SPSS, 1988). Recent applications of these approaches to ecological and evolutionary problems are shown in Muncheow (1986), Pyke and Thompson (1986), and Fox (1989, 1990a, b).

Some researchers have used as a response variable the time to some macroscopic event such as anthesis or first flower bud; others have examined shoot apices to measure their length or assess their morphology in order to estimate the timing of apical conversion to reproductive growth. Either type of response variable may be useful, depending on the hypotheses under consideration. However, use of apical characters raises a design problem if apices must be harvested for measurement. Such sampling does not kill plants but may have other effects; consequently, individual plants should not be sampled more than once. This kind of experimental design thus introduces considerable right censorship into a data set, which can increase necessary sample sizes. Alternatively, one can use ANOVA to analyze apical length data by including a harvest time factor in the model. Scores on indices of apical morphology should be treated as categorical data.

EMPIRICAL EVIDENCE

Studies reviewed are restricted to experimental whole-plant studies on the effect of water stress on flowering time in annual plants. I searched the AGRICOLA (National Agricultural Library, U.S. Department of Agriculture, Beltsville, MD) and BIOSIS (Biosis, Philadelphia, PA) data bases for experimental studies published after 1973. Earlier papers were found through the exhaustive review of Salter and Goode (1967) or through citations in papers found by either of these methods. A total of 18 empirical studies, using eight species of desert annuals, two species of native mesic annuals, and nine species of domesticated and weedy mesic annuals, are reviewed.

Desert annuals—Only four studies have examined the influence of water stress on flowering in desert annuals. In a garden experiment with the Sonoran Desert annual *Plantago insularis* (Plantaginaceae), Klickoff (1966) varied both the frequency of irrigation and plant density. Unfortunately, he used as response variables the date of first flowering of any individual within each treatment and a subjectively determined date of maximum flowering within each treatment. Klickoff con-

cluded that “earliest flowering and fruiting were at medium water stress,” but his choice of response variables and lack of statistical analysis make it difficult to draw any conclusion from his data.

In a greenhouse experiment, Mott (Mott and McComb, 1975a; Mott, 1979) studied three Australian desert annuals: the composites *Helipterum craspedioides* and *Helichrysum cassianum*, and the grass *Aristida contorta*. High, medium, and low water treatment groups consisted of plants grown at field capacity, at 8%–10% and at 4%–7% moisture contents, respectively. Mott reported significant delays in anthesis between the medium and low treatments for *Helipterum* and *Aristida*; no other pairwise comparisons were significant. This study involved small samples; each treatment group consisted of ten plants per species. The extent of right censorship was not reported by Mott, nor is it clear how Mott analyzed his data; he reported only “least significant differences” for pairwise comparisons, which may reflect multiple *t*-tests or pairwise comparisons following ANOVA. Both methods assume normality and an absence of right-censorship, but multiple *t*-tests also use an inappropriate number of degrees of freedom. Aside from these statistical problems, a methodological problem is suggested by Mott’s (1979) observation that *Aristida* “does not grow well at the moisture levels near field capacity maintained in the unstressed controls.” This observation suggests that growing in saturated soil may be stressful for some desert annuals; maintaining a treatment group at field capacity can help to generate differences among treatment groups, but these differences may not always address the hypotheses of interest.

In two greenhouse experiments, Fox (1990a) studied the Sonoran and Chihuahuan Desert annual *Eriogonum abertianum* (Polygonaceae). In the drought experiment, plants were watered weekly except during scheduled droughts lasting 0, 2, 4, or 6 weeks. In the watering experiment, plants were watered either weekly or every 2 weeks from establishment until death. In both experiments reduced water availability significantly delayed flowering; the delay monotonically increased with the length of drought treatments in the drought experiment. These effects did not vary among population of origin, despite the consistently earlier flowering of Sonoran relative to Chihuahuan plants. Due to the severity of the drought treatments there was substantial mortality in the drought, but not the watering, experiment. However, the use of failure time models to analyze the data made statistical

inference possible. These experimental results appeared to be consistent with field demographic studies (Fox, 1989).

Aronson (1989) grew plants of three Israeli species in pots in an open-air nursery provided with rain guards. The crucifer *Erucaria hispanica*, and two grasses, *Bromus fasciculatus* and *Brachypodium distachyon*, were compared in a factorial design in which population of origin (desert vs. Mediterranean sites) and watering treatments were varied. The three watering treatments were: 1) soil held at field capacity (31.6% moisture content); 2) soil at roughly 30% moisture content; and 3) plants not watered for 3–5 days or until wilting, then returned to field capacity for 1–3 days. Aronson recorded the number of days until the first reproductive shoot or tiller was observed for all three species, and days to anthesis for *Erucaria* and *Brachypodium*; the cleistogamous flowers of *Bromus* made it impossible to examine this variable. Within populations, Aronson reported no significant differences among treatment groups for days to first reproductive shoot or tiller for *Erucaria* or *Bromus*, but for *Brachypodium* he reported that plants maintained at field capacity showed first reproductive growth significantly later than the other two treatment groups. Time to anthesis did not differ significantly among treatment groups for the desert *Brachypodium* population or for either *Erucaria* population. For the Mediterranean *Brachypodium* population, anthesis was reported to be significantly later for plants maintained at field capacity. For all species, Mediterranean populations were reported to flower significantly later than desert populations. Aronson suggested that “very low” mortality among experimental plants made ANOVA an acceptable significance test, but it is not clear whether the data were approximately normally distributed. Statistical issues aside, it is difficult to be certain that differences that might exist among treatment groups were caused by water stress in treatment groups 2 or 3, and not by the stress caused by growing group 1 in saturated soil.

Mesic annuals — native plants — Newman (1965) conducted greenhouse experiments with the English winter annual *Teesdalia nudicaulis*. Drought conditions were imposed at the time of onset of flowering and somewhat later in the flowering season. Plants subjected to droughts matured fewer inflorescences and flowers, as shown by ANOVA. Newman interpreted this as evidence that drought delays bud maturation. This conclusion is consistent with the results.

Boot, Raynal, and Grime (1986) studied the annual nettle, *Urtica urens* (Urticaceae) in a hydroponic setting. Droughts were imposed by removing plants from the culture medium for varying periods. Although no statistical analysis was performed, the data appear to show that drought generally delayed anthesis, at least when treatments were initiated before all flowering began. There was considerable mortality associated with prolonged drying, but it seems likely that inclusion of these right-censored data points in a statistical analysis would strengthen the case that drought inhibited flowering in this experiment. The experimental design in this case may be more ecologically realistic than it appears at first glance, as the study species often inhabits the floodplains of rivers.

Mesic annuals—domesticated and weedy species—A large number of studies concern domesticated and weedy species in mesic environments; these are summarized in Table 1. Almost all of these studies reported that water stress significantly delayed flowering. However, there are important design or analysis problems in most of these studies. Many of these studies used osmotic stress as a treatment. One study (Frank, Bauer, and Black, 1987) allowed competition between plants within treatment groups. In several cases no statistical analyses were conducted; in others it is impossible to tell whether ANOVA or multiple *t*-tests were used. Several authors inappropriately applied these statistical tests to indices of apical morphology. In several of the studies using such indices, apices were harvested at various times, but the statistical analyses did not include harvest time as a factor; other investigators used apical characters without harvesting apices. No study reported on mortality or other sources of right censorship. Thus, these studies provide little conclusive evidence of an effect of drought on flowering time.

DISCUSSION

Few experimental studies have been conducted on the effect of water stress on flowering time in annual plants. Most extant studies are seriously flawed in their methods, their statistical analyses, or both. Given these limitations, however, this literature provides little support for the widely held view that drought generally induces flowering in either desert or mesic annuals. A convincing demonstration that drought does stimulate flowering will require careful attention to experimental and statistical issues.

Clearly, drought hastens completion of the life cycle in annuals by causing rosette and leaf senescence, and sometimes by speeding the maturation of previously set fruit (Newman, 1965; Gates, 1968; Aronson, 1989; Fox, 1990a). Such early maturation of fruit could potentially result in a net fitness gain for a plant dying of water stress. However, this mechanism is different from the drought-stimulated flowering often claimed for desert annuals. No studies have examined the fitness consequences of accelerated maturation of fruit as a response to drought.

Flowering time is a trait of considerable selective importance. It is likely that drought affects flowering time and its evolution both directly and indirectly. Seasonal drought directly affects the evolution of flowering time by acting as a selective agent. Moreover, reduced availability of water can delay flowering in some species (Fox, 1990a), contributing to the phenotypic variance in flowering time and plant size. Drought is likely to have important indirect effects on the evolution of flowering time because water stress during reproduction can strongly affect seed characteristics. These and related issues are discussed below.

Models of optimal flowering time—The evolution of flowering time in annual plants has attracted considerable theoretical attention for some 20 years (e.g., Cohen, 1971; Paltridge and Denholm, 1974; Gadgil and Gadgil, 1975; Schaffer, 1977; Mirmirani and Oster, 1978; Vincent and Pulliam, 1980; King and Roughgarden, 1982a, b; Schaffer, Inouye, and Whittam, 1982; Chiariello and Roughgarden, 1984; Fox, unpublished data). These models address a number of topics, but most treat flowering time as a fixed trait expressed in a predictable environment. Because flowering in desert annuals appears to be influenced by both photoperiod (see "Photoperiod and flowering in desert annuals" below) and the availability of water (Fox, 1990a), such models have mainly heuristic uses at present.

Season length was treated as a random variable in two models (Cohen, 1971; King and Roughgarden, 1982b), but flowering time was regarded as a fixed trait in these models as well; the optimum depended on the expected length of the season, but the process of flowering itself was assumed not to be influenced by environmental conditions. Such models are likely to be difficult to test if variable environmental conditions, such as water stress, have important effects on flowering time. Development of more realistic models may depend on information from empirical studies on the envi-

TABLE 1. Summary of studies on the effect of moisture limitation on flowering time in annual crops and weeds

Author	Setting	Response variables	Methods*	Reported results	Statistics
<i>Corchorus olitorius</i> (jute)					
Johansen, Wa-seque, and Begum, 1985	Greenhouse	Days to flower	Withheld water on a schedule	Drought delayed flowering	ANOVA
<i>Helianthus annuus</i> (sunflower)					
Marc and Palmer, 1976	Growth chamber	Mean of an index of apical morphology	Watering to constant Ψ_1	Drought retarded apical growth	None
<i>Hordeum vulgare</i> (barley)					
Nicholls and May, 1963	Growth chamber	Mean of an index of apical morphology; apical length	Water withheld to constant soil pressure	Drought retarded apical growth	None
Husain and Aspinall, 1970	Growth chamber	Index of apical morphology	Water withheld on a schedule; scheduled osmotic treatments	Drought retarded apical growth	ANOVA or multiple <i>t</i> -tests
<i>Lolium temulentum</i> (Darnel ryegrass)					
Aspinall and Husain, 1970	Growth chamber	Index of apical morphology; apical length	Scheduled osmotic treatments	Drought retarded apical growth	ANOVA or multiple <i>t</i> -tests
King and Evans, 1977	Growth chamber	Index of apical morphology; apical length	Osmotic treatment during light induction	Drought retarded apical growth	SE of apical length
<i>Pennisetum americanum</i> (pearl millet)					
Mahalakshmi and Bidinger, 1985a	Garden	Days to anthesis	Water withheld on a schedule \times photoperiod	Drought delayed flowering or had no effect, depending on photoperiod	ANOVA
Mahalakshmi and Bidinger, 1985b	Garden	Days to panicle initiation and anthesis	Water withheld on a schedule	Drought delayed anthesis, not panicle initiation	ANOVA
Bidinger, Mahalakshmi, and Rao, 1987	Garden	Days to 50% flowering	Water withheld on a schedule	Drought delayed 50% flowering	ANOVA
<i>Pharbitis (Ipomea) nil</i> (morning glory)					
Aspinall and Husain, 1970	Growth chamber	Index of apical morphology; apical length	Schedule of osmotic treatments	Drought caused complete suppression of flowering	ANOVA or multiple <i>t</i> -tests
<i>Sorghum vulgare</i> (sorghum)					
Whiteman and Wilson, 1965	Greenhouse	Days to 50% flowering	Water withheld on a schedule	Drought delayed 50% flowering	None
<i>Triticum aestivum</i> (wheat)					
Angus and Mancur, 1977	Greenhouse	Days to anthesis	Water withheld to constant Ψ_1	Drought delayed flowering	SE for each plant
Frank, Bauer, and Black, 1987	Growth chamber	Days to double ridge on apex	Osmotic treatments	No significant effect	ANOVA for "average of two runs" of experiment
<i>Xanthium strumarium</i> (cocklebur)					
Aspinall and Husain, 1970	Growth chamber	Index of apical morphology	Water withheld on a schedule	Drought during or after induction delayed flowering; no preinduction effect	ANOVA or multiple <i>t</i> -tests

* Ψ_1 = Predawn leaf water potential.

ronmental sources of variation in flowering time and their demographic significance.

The economics of drought as a cue—What sorts of environmental stimuli or “cues” for flowering should we expect to see in different environments? Theoretical treatments of this issue have not yet been attempted. Discussion of the evolution of cues necessarily involves two issues: the reliability of a cue and the cost of “perceiving” and using it. Meaningful theoretical treatments thus require knowledge of the mechanistic details; the literature reviewed above suggests that many of these mechanistic details are not yet well understood and deserve further empirical study.

Seed number and seed size are reduced by water stress during flowering and fruiting in virtually every plant species studied (Salter and Goode, 1967; Slatyer, 1973; Fischer, 1973; Fischer and Turner, 1978). Drought significantly reduced seed number, seed mass, and germinability in all three species of Australian desert annuals studied by Mott (Mott and McComb, 1975a). In Delph's (1986) demonstration of moisture limitation of fruit and seed set in the Sonoran Desert annual *Lesquerella gordonii*, flowers produced at the end of the season failed to set fruit.

Carbohydrate sources are severely limited during drought, since drought inhibits both new assimilation (Gates, 1968; Yoshida, 1972; Slatyer, 1973) and translocation of carbohydrates (Wardlaw, 1968). Translocation of nutrients is reduced, proteolysis increased, and protein synthesis inhibited during drought (Crafts, 1968; Gates, 1968; Wardlaw, 1968). Moreover, drought inhibits microsporogenesis, pollen grain germination, and fertilization (Slatyer, 1973; Fischer and Turner, 1978). These sequelae to water stress do not render drought-stimulated flowering impossible for an annual. They do restrict the circumstances in which the benefits of such a mechanism might actually outweigh its costs. Moreover, they may affect the way in which flowering time evolves (see “Interaction between flowering time and seed traits” below).

The costs of drought as a flowering cue are likely to be related to the speed with which soils dry and water stress begins to limit the plants' reproductive output. It seems reasonable to speculate that this process may be particularly rapid in hot deserts (Shmida and Burgess, 1988). If so, one is more likely to find drought-stimulated flowering among annuals in milder climates (e.g., Mediterranean regions) than in deserts.

Water stress is unlikely to be a good predictor

of the end of the growing season in most desert environments. In these settings rainfall is highly unpredictable at all times of year, and droughts occur regularly even during “rainy” seasons (Bryson, 1957). Autocorrelation in rainfall is very low in deserts; presence or absence of rainfall at a given time does not generally predict subsequent rainfall patterns (McDonald, 1956; Sellers and Hill, 1974; Ezcurra and Rodrigues, 1986). Time of year is probably a better predictor of the probability of rainfall in most desert regions than is current soil water potential. Desert annuals, especially in regions with two rainy seasons, may thus be more likely to use photoperiod than water status as a flowering cue. Again, this contrasts strongly with Mediterranean climates, which have highly predictable, temporally autocorrelated, and strongly unimodal rainfall patterns (Shmida and Burgess, 1988). A search for drought-stimulated flowering seems more likely to be successful among Mediterranean annuals or those from desert regions with a single rainy season (Shmida and Burgess, 1988).

Photoperiod and flowering in desert annuals—Mott and McComb (1975b) grew three species under varied photoperiod and temperature conditions. They reported that mean time to anthesis and initiation of reproductive structures varied significantly among both kinds of treatments. This conclusion must be interpreted cautiously because it is based on a statistical analysis consisting of either ANOVA or multiple *t*-tests.

Evenari and Gutterman (1965) grew 20 Israeli desert annual species under both short- and long-day treatments, both in a greenhouse and outdoors. They reported that in almost all species there were strong effects of both photoperiod and growing site on the mean number of days from germination to appearance of the first flower bud. Variable responses among photoperiodic treatments were interpreted as evidence for two life history syndromes among the species studied. For some species, germination and growth under long-day treatments hastened all life history events: the plants flowered and fruited earlier and at smaller size than when grown under short days, and death was earlier as well. For other species, long-day conditions led to earlier flowering but not to earlier death—flowering continued while conditions suitable for growth were maintained. Some caution is necessary in interpreting these data because Evenari and Gutterman reported only the means and standard errors of time to the first flower bud. Additionally, their data sug-

gest that there may have been significant interactions between photoperiod and location.

Flowering time and germination characteristics—The interpretation given by Evenari and Gutterman (1965) is intriguing and suggests future studies on the effect of varied germination time on flowering and other life history events. For several Sonoran Desert winter annuals studied by Venable and his students, fitness consequences of germination time are substantial but vary among years (D. L. Venable, personal communication). Evolutionary insight will require data on several problems. How are germination time and subsequent life history traits coupled phenotypically and genetically? If distinct syndromes exist (Evenari and Gutterman, 1965), are they consequences of basic plant morphology (e.g., determinate vs. indeterminate flowering) or might they be independently selected? Under what circumstances should we expect later germination to accelerate all, some, or no subsequent life history events?

Since flowering and germination are both influenced by environmental conditions, studies of their relationship will need to examine not only average responses but also their variability. Ritland (1983) examined the phenotypic optima of a flowering trait (percent early- vs. late-flowering) and a germination trait (percent germinating each year) in a randomly varying environment. His results showed that the optimum for each trait was strongly dependent on the variance of the other trait.

Ritland's optimization model might lead one to expect the evolution of strong genetic correlations between these traits. However, Ritland (1983) also analyzed a two-locus genetic model that showed that, in a variable environment and in the absence of epistasis, these characters may not tightly coevolve; simulations showed that the gene frequencies at loci for each trait became uncorrelated with one another over time. Empirical studies are needed to examine the genetic architecture of these traits in multiple populations.

Interaction between flowering time and seed traits—The maternal environment may affect seed size and germinability, and therefore may indirectly affect flowering time and size (Roach and Wulff, 1987). In *Lupinus texensis*, an annual of central Texas, Schaal (1984) demonstrated that age-specific survivorships and fecundities were strongly affected by seed size, which in turn was affected by the maternal environment. It seems likely that water stress during reproduction may lead to important

maternal effects in desert annuals. Mott and McComb (1975a) presented evidence that water stress can affect both seed size and germinability in three Australian desert annual species. Gutterman (1980–81) reviewed evidence for a number of other maternal effects on germinability in desert annuals. In one of Fox's (1990a) greenhouse experiments the resemblance between parents and offspring in flowering time and size depended on the length of drought treatments given maternal plants. These results suggest that maternal effects may be an important component of phenotypic variability in life history characters in desert annuals, and for this reason alone deserve study. Genetic studies may also require attention to maternal effects, because quantitative genetic parameters can be badly misestimated if maternal effects are ignored (Roach and Wulff, 1987).

These maternal effects may influence the course of evolution of flowering time. Maternal effects can either magnify or retard the responses of populations to selections (Kirkpatrick and Lande, 1989). Maternal effects can also cause traits to change in a direction opposite to that favored by selection, as demonstrated in a selection experiment on litter size in mice (Falconer, 1965) and examined theoretically by Kirkpatrick and Lande (1989). Moreover, time lags introduced by maternal effects can cause trait means to continue to change after selection is relaxed (Kirkpatrick and Lande, 1989). Thus, maternal effects may be important not only because they contribute to phenotypic variation or because they complicate genetic studies; they may considerably complicate the evolution of flowering time. Carefully designed empirical studies (review, Roach and Wulff 1987) are needed to examine the nature and magnitude of these effects.

Phenotypic plasticity—Are desert annuals more plastic than other plants? Several authors have suggested that this is so (Went, 1948; Evenari, Sharon, and Tadmor 1971; Lacey, 1986), but there are no data available to evaluate this hypothesis. Flowering time and size may vary more within desert annual than within mesic annual populations, but this could be a consequence of greater plasticity or of greater environmental variability in deserts.

To examine the hypothesis that desert annuals show more phenotypic plasticity than other plants, common-environment experiments are necessary. Aronson (1989) showed that for a number of traits there was actually more phenotypic variability among Mediterranean than desert populations of three species

of Israeli plants, although his design (Scheiner and Goodnight, 1984; Schlichting, 1986) does not exclude the possibility that this reflects differences in genetic variance rather than phenotypic plasticity. Studies that measure both plasticity and genetic variance in both desert and non-desert populations of several species would be particularly useful.

Variation in water (Fox, 1990a) and nutrient (Mott, 1979) availability have been suggested as causes of plasticity in time and size at flowering; given the heterogeneous nature of desert soils, both kinds of explanations seem plausible. Since larger plants generally have deeper roots and therefore access to more water and nutrients, size distributions within populations are likely to become increasingly skewed over time. Variation in germination time and in growth rates can generate similarly skewed size distributions.

Competition—especially for water—may also be an important source of phenotypic variation. Competition is well known to lead to marked size hierarchies among mesic plants (Gates, 1982; Westoby, 1982; Hara, 1984; Weiner, 1985; Weiner and Thomas, 1986). Although Went asserted (1948, 1949, 1955) that competition does not occur among desert annuals, he presented no supporting evidence. A recent study of Sonoran Desert winter annuals (Pantastico, 1990) demonstrated that competition is an important factor in the population dynamics of some species, suggesting that it could be an important source of intrapopulation variation in flowering time and size.

There is good reason to expect flowering time to be under strong selective pressure in populations of desert annuals. There are a large number of ecological models of optimal flowering time, but these have limited applicability to desert annual populations because flowering can be strongly influenced by variable environmental conditions. Theoretical progress will likely require an improved empirical understanding of the mechanisms affecting flowering. The evolution of flowering time may be strongly affected by such factors as maternal effects on seed traits and genetic and phenotypic correlations among life history traits. These factors can affect not only the speed with which populations respond to selection, but even the direction of the response. Populations of desert annuals thus present numerous opportunities to gain insight into evolutionary processes and to test and improve ecological and evolutionary models.

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