PHENOLOGICAL PATTERNS OF TERRESTRIAL PLANTS

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Article:

INTRODUCTION

"From March to November each month brings a new prospect in field and forest and each edition [of flower life] seems thoroughly to harmonize with its own peculiar season."

H. L. Clark (47)

The term phenology is derived from the Greek word *phaino* meaning to show or to appear. Hence, phenology is defined as the study of the seasonal timing of life cycle events. For plants the seasonal timing of such events can be critical to survival and reproduction. In agriculture the most common failure of introduced crops is the inability to adjust to the seasons imposed by the new, environment (68). In the past few years, interest in the ecology and evolution of timing of life cycle events has grown. Here we review the literature on phenological patterns of germination, flowering, and fruiting (including dispersal).

The phenological pattern of any life cycle event can be quantitatively defined as a statistical distribution characterized by such parameters as time of occurrence (onset, mean, mode), duration (range), synchrony (variance), and skewness. For each life cycle event we discuss each parameter for which data are available. Because parameters at one level can contribute to parameters at higher levels, parameters are sometimes related. For example, the degree of synchrony within and among individuals can determine duration at the population level. Therefore, we discuss phenological patterns at the levels of individuals, populations, species, and communities. Also, we use the word phenology in its strict sense of seasonal timing within years; and we address variation among years only when it pertains to the discussion of within-year patterns.

The purpose of this review is to present hypotheses about possible evolutionary causes and consequences of different phenological patterns and to discuss the evidence for each hypothesis. We also briefly summarize information about the environmental and genetic controls of timing because these are the proximate factors that can influence the evolution of phenological patterns. We divide our review into four sections. The first three address germination, flowering, and fruiting separately. Each section covers possible selective factors, proximate environmental cues, and genetic determinants of different phenological parameters. The last section focuses on the relationships of germination, flowering, and fruiting, to the whole life cycle of the plant. Here we address possible ecological and evolutionary constraints that may direct the evolution of all life cycle events.

Space prevents an exhaustive literature review, particularly of descriptive studies, so we mention representative studies and reviews that provide the reader access to additional literature. We do not address phenological patterns of leaf production (43, 146) or the specific methodologies for collecting and analyzing phenological data (151, 194, 20 1).

GERMINATION

The seedling stage is the most vulnerable time in the life cycle of a plant (10 1). Mortality is often severe because small seedlings have minimal capacity for homeostatic responses or physiological retrenchment in the

face of unfavorable abiotic or biotic conditions (10). Therefore, the timing of germination should be under strong selection to occur when conditions will continue to be favorable for seedling establishment.

Selective Factors

TIME OF OCCURRENCE Several studies indicate that abiotic factors favor germinating as early as possible to gain resources for reproduction, but not so early that survival to time of reproduction is unlikely. Generally, in temperate herbs individual seeds that germinate unusually early in the season have lower probabilities of survival than do those germinating later, but the few that do survive have much higher reproductive success because of the longer growing season (13, 20, 95, 158, 255). These effects can be attributed to abiotic factors. By artificially watering areas in the desert during the summer, Tevis (255) produced abnormally early germination of Abronia. However, only one of many individuals survived the subsequent dry summer, but this individual produced copious seeds the following winter, when most other individuals germinated. Summer-germinating seedlings of *Leavenworthia stylosa* in cedar glades suffered four times the mortality of autumn-germinating seedlings because of drought, but summer seedlings produced eight times as many seeds (20). These studies indicate that time of germination reflects a trade-off between selection for high seed set and selection for high survivorship.

Biotic factors like interspecific competition may also influence seasonal timing of germination. Evidence comes from observations and manipulations of species in natural habitats. Winter annuals can strongly suppress the growth of spring-germinating annuals (210). An early-spring emerging annual, *Ambrosia trifida*, increased mortality and reduced the seed set of neighboring late-spring germinating annuals (4). The annual, *Impatiens capensis*, preempts space from established perennials by germinating early in the spring before perennial growth has begun (289). Garwood (85) suggests that, because of intense competition, rapid emergence is critical for successful establishment in light gaps in tropical rain forests. In these cases interspecific competition favors early germination.

Intraspecific competition also favors early germination. Many greenhouse experiments show that early-emerging individuals within cohorts preempt biological space and gain competitive advantage over late-emerging individuals (e.g. 29, 218). Ross & Harper (218) demonstrated that the increased fitness of early emergers is not solely due to increased growing time; early emergers grow more quickly and continually increase their ability to acquire resources at the expense of later emergers. Several studies of natural pop-ulations show that late-emerging individuals suffer higher mortality and/or reduced seed set (53, 181, 120), but these studies do not distinguish between competitive effects and effects produced by seasonal changes in the microenvironment. Weaver & Cavers (279) separated emergence order from seasonal changes by sowing *Rumex* seeds at different times into natural habi-tats. They found that the emergence order within cohorts was more influential than the emergence date in determining seedling success (279). Abul-Fatih & Bazzaz (4) observed similar results when examining the effects of germination time of *A. trifida* on the success of other weeds.

Seasonally restricted predators or pathogens could select for timing of germination. Predators and pathogens are major causes of seed and seedling mortality (17, 10 1). In some cases pathogenic potential changes over a season (102). Late planting of crops can decrease some diseases (e.g. loose smut of wheat, *Ustilago tritici*) and increase others (e.g. wheat bunt, *Tilletia caries*) (19). Predation of dispersed seeds should select for rapid germination after release from the parent (124), but the only support for this hypothesis comes from observations of red and white oaks (77). Squirrels prefer white oak over red oak acorns. White oak acorns germinate soon after dispersal in autumn, whereas the less preferred red oak acorns germinate the following spring. Germination timing may reflect a compromise between the probabilities of predator or pathogen attack at the seed stage and the seedling stage. However, at present we know too little about the seasonal activities of such predators or pathogens to evaluate this idea.

SYNCHRONY AND DURATION The same abiotic and biotic factors that determine when seeds germinate may also control the degree of germination synchrony within and among species. Correlations between seasonal

changes in the physical environment and the simultaneous germination of many species within plant communities suggest that species respond to similar abiotic environmental conditions. In temperate climates most herbs germinate as temperatures rise in the spring, although they may exhibit more than one pulse of germination, e.g. during the summer (132) or in spring and autumn (22). In climates with hot, dry summers and cold, humid winters, herbs usually germi-nate in the autumn and early winter (132). In deserts many species germinate just after rains (25, 281). In seasonal tropical forests in Panama, 75% of the woody species germinate early in the rainy season (85). Abiotic factors probably produce this synchronous germination among and within species, and habitats that provide only a short time for seedling establishment, vegetative growth, and reproduction should increase this synchrony. Competition may intensify synchrony indirectly by selecting for germination at the earliest possible time in the growing season to gain competitive advantage.

Asynchronous germination (and extended duration) is likely to be favored in habitats where times suitable for seedling establishment are either long or unpredictable. Several temperate herbs exhibit two pulses of germination--in autumn and in spring. However, seedlings often establish during only one germination pulse for any given year (13, 139, 156). In *Ludwigia leptocarpa*, which has only one germination pulse, early-emerging individuals surpass late emergers in survivorship, growth, or seed set only in some years (60). For tree species germinating in the shaded understory of tropical forests in Panama, the risk of mortality is unpredictable for the duration of the rainy season; and many tree species extend germination throughout this season (85). In aseasonal tropical forests of Malaysia, tree species germinate throughout the year (182).

In unpredictable environments the production of offspring that differ in germination requirements could spread the risk of mortality and represent a bet-hedging strategy (101). Annual species more commonly produce seeds with variable germination requirements than do perennials, perhaps because they risk complete reproductive failure during a single unfavorable period (101). Theoretical studies examining the relationship between environmental unpredictability and fractional germination (e.g. 49, 267) have considered germination among years, however, rather than within years.

Environmental Cues

The initiation of germination is caused by a remarkable diversity of factors including temperature, moisture, light intensity, light quality, photoperiod, carbon dioxide, and minerals (10, 113, 132, 136, 160, 287). Some factors that directly stimulate germination also directly influence seedling survival, e.g. soil moisture in deserts (97, 255, 282). Other factors that stimulate germination do not affect the seedling directly but are correlated with factors that do. For example, some desert seeds germinate in response to reduced soil salinity, which occurs only after heavy rains that ensure establishment. Seeds will not germinate after light rains, which may be followed by drought (97). Many species require a combination of specific conditions to initiate germination. For example, some desert perennials respond to moisture only if temperatures are cool or moderate (10, 255, 281).

Successful seedling establishment depends on the prevention of germination during conditions unfavorable for growth, and this is achieved through a number of dormancy mechanisms. Harper (101) succinctly summarized these: "Some seeds are born dormant, some achieve dormancy and some have dormancy thrust upon them." These three types of dormancy are termed innate, induced, and enforced dormancy, respectively (101). *Innate dormancy* is established during seed maturation, and it prevents seeds from germinating even when placed into favorable conditions until some cue releases dormancy. Induced dormancy is acquired after dispersal and also prevents seeds from germinating even when conditions are favorable. Seeds with *enforced dormancy* will germinate as soon as they are placed in a favorable environment. Both induced and enforced dormancy permit opportunistic germination during un-predictable environmental conditions (10). After innate dormancy is broken by some factor, a seed may remain in enforced dormancy. Seeds of some species go through pulses of induced dormancy, which prevent germination during seasons hostile for seedling establishment (22, 216). Factors inducing dormancy may have direct effects or may act as predictors of unfavorable conditions. For example, induced dormancy in many grassland species is caused by a decreased ratio of red to far-red light that occurs beneath leaf canopies; this light quality is correlated with established vegetation and a competitive environment (229).

Changes in environmental factors can alter the germination responses of seeds as they mature on the parent plant (61, 98, 132, 231). This environmental pre-conditioning can cause the proportion of progeny with a specific germination requirement to vary within sibship. Maternal effects can also produce variable progeny (see Ecological and Evolutionary Constraints section, below).

Genetics

Because germination time is strongly influenced by environmental conditions, the genetic component of germination timing has been difficult to determine (215, 286). Variation in germination times of seeds collected from different geographic regions is often ascribed to genetic differences, but environmental preconditioning has seldom been eliminated in germination tests, and most results are equivocal (21, 219). Growing plants under constant conditions and then examining the germination of the subsequent generation of seeds can reduce environmental effects, but this technique has seldom been used in studies of natural populations (21, 206). Ecotypic variation in germination responses is best documented for a few weedy species (167, 258). For example, seeds of *Silene dioica* are summer-dormant in southern Europe where winter rains occur, whereas seeds from northern Europe are winter-dormant (258). In contrast, many weed species from the continental climate of central Europe show no ecotypic variation and germinate over a wide range of conditions (258). Seeds from cool-climate populations of *Typha* (165) and *Trifolium subterraneum* (172) show greater dormancy at low temperatures than do seeds from warm-climate populations. In cool climates, low temperatures are more often correlated with even lower temperatures that cause seedling mortality. Time required for germination is shorter in more northern populations of *Vaccinium* and *Cyanococcus* (58).

Most available information on the genetic basis of germination timing comes from agricultural studies. Genetic crosses show that germination timing is a polygenic trait, and that maternal, paternal, and additive effects can be significant (103, 205, 232, 286). Artificial selection has produced changes in seed dormancy (232) and germination phenology (290). Although genetic differences in emergence times of crop varieties may be significant, often they are not as great as environmental effects (286). The genetic basis of germination timing in natural plant populations is less well known. In both *Papaver dubium* and *P. rhoeas*, artificial selection reduced dormancy (13). Germination timing shows low heritability in *P. dubium* (13) and *Geranium carolinianum* (214).

Summary

Although numerous specific case studies of dormancy and germination require-ments exist, few have characterized the genetic component of these requirements. Germination asynchrony observed within natural populations could result from microenvironmental heterogeneity, genotypic differences among individuals, or phenotypic plasticity. The possible adaptive nature of phenotypic plasticity in producing variable progeny in either flexible or fixed proportions, as well as the simple genetic control of germination requirements, needs to be explored (34, 130). No studies of germination time that we found focused on the duration of germination, e. g. the length of time from breaking of the seed coat to seedling emergence. Selection for rapid germination rate should be strong but may vary over habitats or species.

The effects of the abiotic and biotic environment and their interaction need to be examined further in manipulative experiments. The extent to which inter- or intra-specific competition determines the fitness of seedlings in natural populations is still poorly known. Even less is known about the seasonal occur-rences of predators or pathogens and their effects on seed and seedling survival.

FLOWERING

Flowering includes floral bud initiation and development, blooming (anthesis), and floral persistence (32, 67, 142). Here we generally limit our discussion to the blooming period, which is the time for pollination. We use the term flowering in this context unless we indicate otherwise.

Selective Factors

TIME OF OCCURRENCE Abiotic factors are often correlated with flowering times. In temperate regions frost in spring and autumn may limit the flowering season, although some wind-pollinated and alpine plants flower either during freezing weather or under snow. In the seasonal neotropics, most herbs and shrubs flower in the rainy season (57, 171), but twice as many tree species flower in the dry season as in the rainy season (79). In contrast, in aseasonal tropical forests, no flowering peaks occur and many species flower more than once a year (57, 187, 203). Abiotic factors may limit flowering seasons either directly by affecting the ability to produce flowers or indirectly by affecting pollen vectors. These effects are seldom separated in studies.

The seasonal availability of conditions favorable for pollen transfer may account for the seasonal flowering of some wind-pollinated species. In temperate areas wind-pollinated trees commonly flower before leaf emergence in early spring (47, 91 , 217) when pollen dispersal is least impeded. In the tropics many wind-pollinated tree species flower in the dry season (57, 75, 79), when the tradewinds are strongest and when some trees have lost their leaves (75).

The seasonal availability of pollinators may select for flowering times of animal-pollinated species, but this poses the "chicken and egg" paradox: Is the availability of seasonal pollinators a cause or an effect of flowering? Many studies show seasonal correlations between pollinator populations and flowering (175, 217, 253). However, only a few studies show that pollinator presence is determined independently of flowering time. For example, migration times of hummingbirds, which are correlated with the flowering times of humming-bird-pollinated plants, may be seasonally restricted by other factors (36, 92, 274, 276). Waser (274) found that seed set per flower in ocotillo (*Fouquieria splendens*), a hummingbird-pollinated shrub, was greater for plants flowering coincidentally with the presence of hummingbirds than for plants flowering after hummingbirds had migrated. The seasonal appearance of lepidopterans coincides with a relative increase in the number of moth-pollinated species that are flowering (79, 122). The appearance of these lepidopterans also coincides with the flush of new foliage necessary for larval development. Schemske et al (226) observed that seed set was commonly limited in many temperate wood-land herbs. They attributed this to the variance in the seasonal availability of insect pollinators. A lack of reliable environmental cues that accurately predict pollinator presence may make perfect timing impossible (226).

Seasonal pollinator presence is probably more commonly an effect of flowering. Many pollinators (e.g. tropical birds and bats) are highly opportunistic and disperse locally to areas of abundant floral resources (72, 74, lO7, 204). Other pollinators (e.g. multivoltine or social bees) can extend their life span or reproductive period if the flowering season is extended (87). A dramatic example of a population response to flowering is seen in thrips, which are the major pollinators of the Malaysian dipterocarps that flower together every 7-10 years (44). Thrips populations increase more than a thousand-fold on the first species that flowers and are thus available for subsequently flowering species.

SYNCHRONY AMONG SPECIES Aggregated flowering of different species could be advantageous if facilitation occurs, i. e. if the presence of one species increases the visitation rates and seed set of another species (208, 260, 262, 275). Although aggregated flowering is common, little evidence suggests that facilitation currently occurs. In controlled-density experiments with two woodland herb species the presence of heterospecific neighbors increased visits but also increased interspecific pollen transfer (176, 177). In several other species, positive but weak correlations have been reported between the presence of one plant species and visitation rates or seed set of another plant species (260, 262).

Coincidental flowering of species with visually similar flowers has been considered mimicry in which one or all species benefit from increased pollinator visits (36, 197, 224). Only Bierzychudek (28) has done the critical tests of floral mimicry (288), and she found no evidence for the mimicry hypothesis in her examination of three tropical herbs with visually similar flowers. The similarity in flowers and timing for various purported mimics could simply reflect response to selection by the same pollinators; more tests, however, are needed.

Asynchrony or divergence of flowering times among species could arise in two ways. First, interspecific competition for pollinator visits could favor divergence because reduced visitation can decrease pollen donation and seed set. No strong evidence supports this as a primary cause of divergence (208, 275). Second, interspecific pollen transfer could favor divergence because this transfer could reduce pollen donation, reduce seed set, and produce less fit hybrids. Two studies provide strong evidence that divergence in flowering times has been caused by interspecific pollen transfer. Waser (275) found that sympatric populations of *Delphinium nelsonii* and *Ipomopsis aggregata* always flower sequentially and that they differ in the order of flowering in different geographic localities; this suggests that they have diverged differently in local populations in response to each other. To determine the possible cause of divergence, Waser (272) artificially created coincidentally flowering pop-ulations and demonstrated that interspecific pollen transfer by shared hummingbird pollinators significantly reduced seed set of *D. nelsonii*. The most likely cause of the reduced seed set appears to be stigma clogging by interspecific pollen (273). McNeilly & Antonovics (166) showed that sympatric, heavy-metal-tolerant and -intolerant populations of both *Anthoxanthum* and *Agrostis* have recently evolved differences in flowering times. The most likely cause appears to be selection against gene flow and hybridization. Competition for pollinators could not be the cause because these species are wind pollinated. Other possible cases of character divergence in flowering times (161, 208, 275) need further examination.

Interspecific divergence in flowering within plant communities is rarely found. Most statistical tests of flowering dispersion within seasons have shown flowering to be aggregated (9, 189, 196, 208, 260) or indistinguishable from a random pattern (207, 283). Random models with different assumptions, however, can give different results (208). For example, phenological displacements reported for two plant assemblages (52, 88, 193, 250) have under a different analysis (196, 260) been reported to be aggregated. Thus, the results and interpretations based on random models remain controversial, and results should be viewed cautiously.

Divergence of flowering times may be rare because flowering time is just one of several pre-mating isolation mechanisms that can reduce interspecific gene flow (149). Flowering time may be the easiest mechanism to alter given the evidence for simple genetic control (178, 190), but because flowering time seems to be such a phenotypically plastic character, divergence in flowering time may not prevent hybridization as effectively as would changes in such other plant characters as floral morphology. The absence of evidence for flowering divergence at the community level may reflect such alternative solutions for reproductive isolation. Many closely related species are separated by habitat rather than by flowering time (121, 217, 249).

Evidence that competition for pollinators currently occurs in natural plant populations is sparse. Competitive effects on seed set have seldom been found either because pollinators are very abundant (41, 71, 176, 208, 275) or because plants produce persistent flowers (176) or are selfing or apomictic (133, 223). Current competition has been detected in artificial or disturbed situations. In hybrid seed gardens, competition for honeybee visits commonly reduces seed set among crop varieties (65, 66, 8 1). In old fields in Michigan, introduced honeybees visit *Solidago graminifolia* only after other plant species have ceased flowering; consequently, early flowering clones set fewer seeds (96). In natural populations, traits other than flowering times may lessen potential competitive effects.

Divergence may also be uncommon because competition among plant species is inconsistent and nondirectional over time. Consistent flowering se-quences between years have been reported in a few studies (44, 253, 266), but the degree of flowering overlap often varies. In other studies (75, 252), flowering times vary greatly and independently between years. For tropical trees that flower in response to rainfall, local rains can cause highly patchy and asynchronous flowering between species and within a species (16, 32). Interspecific interactions are unlikely to cause directional selection on flowering times in these cases. Interspecific interactions are also likely to vary over a species' geographic range as other potential competitors and pollinators change. These different interactions would select for unique flowering times that are initiated by different environmental conditions. Some species show ecotypic variation in flowering (112, 143), but the influence of interspecific interactions is unknown. However, the ability to predict flowering times in many temperate woody species over wide latitudes

using cumulative day-degrees (212, 235, 266) suggests that local interspecific interactions have not influenced flowering times. Anomalous populations should be sought and examined.

DURATION, SYNCHRONY, AND SKEWNESS WITHIN SPECIES Flowering duration within populations can last from a single day to the entire year for different species (24, 78). Gentry (86) first categorized flowering patterns for species based upon duration: species with short durations commonly produce masses of flowers in a synchronous display (mass flowering) whereas species with extended durations commonly produce a few flowers a day over long periods (steady-state flowering). In tropical forests, mass flowering is common among trees that flower during the dry season whereas steady-state flowering is found in most understory species (14, 24, 79, 86, 122, 187). Variations exist between these two extremes.

Within individuals, extended duration of flowering may be advantageous for spreading the risk of uncertain pollination. Obligate outcrossing species tend to flower longer than autogamous or self-compatible species (24, 195), and this may reflect the greater uncertainty of pollination. Extended duration could also allow individuals to track and accumulate resources needed for seed maturation in environments where resources are either temporally unpredictable or sparse (24). Extended flowering is more common in aseasonal environments and occurs in most understory species in tropical forests (79); this may reflect unpredictable or sparse resources. Alternatively, this extended duration may reflect a lack of seasonal differences in resource or pollinator availability.

Synchrony at both the population and individual levels affects floral density. Increased synchrony can be either advantageous or disadvantageous depending upon density-dependent interactions with other organisms. Increasing synchrony may increase the attractiveness of a floral display, or it could satiate pollinators or predators (208). To test the effects of synchrony on pollinators and seed predators, Augspurger (15) experimentally created asynchronous flowering within populations of a tropical shrub, *Hybanthus prunifolius*; she found that individuals flowering synchronously with the population attracted more pollinators, set more seed, and suffered less seed predation than did individuals flowering asynchronously with the population. These effects appeared to be caused by the different densities of synchronous and asynchronous individuals. In contrast, Zimmerman (293, 294) found that individuals of *Polemonium foliosissimum* that flowered when floral density was high, attracted fewer bees, produced less seed and suffered more seed predation. The conflicting results from these two species suggest that trade-offs between pollination and predation depend upon the relative densities of pollinators, seed predators, and flowers.

Asynchrony may be favored in a number of situations. Although some degree of flowering synchrony within populations obviously is necessary for outcrossing among individuals, slight asynchrony would promote outcrossing if it forced pollinators to move between individuals (80). Asynchrony within populations could also reduce intraspecific competition for pollinators, reduce effective population size (23, 200), and increase the number of mates as temporal neighbors change (24). These effects have not been examined. Additionally, in monoecious species with temporally separate male and female flowers, asynchrony of the male and female phases within the population is necessary; synchrony of each phase would preclude any chance for reproduction. In *Cupania guatemalensis*, a monoecious tropical shrub, asynchrony between the sexual phases is assured because individuals start with different phases and each sexual phase has a variable duration (23).

Asynchronous flowering within individuals of hermaphroditic species can reduce geitonogamy and promote outcrossing by forcing pollinators to move between plants (24, 152, 227, 246). In monoecious species the sexes are often asynchronous within an individual plant and so reduce geitonogamy (23, 37). The most extreme example of asynchronous flowering both within and among individuals is seen in *Ficus* (125, 170). Within an individual plant the female phase may be separated from the male phase by a month or longer. The pollinating wasps enter a receptive syconium, deposit pollen, oviposit, and die. Individuals of the next generation develop over several weeks and collect pollen while exiting from the syconium which is now in the male phase. Wasps must fly to another tree with receptive syconia to deposit pollen and oviposit. Individual fig trees flower at irregular intervals, and this may maximize the probability that one will be female while another individual is

male in the population (125). Such asynchrony within fig populations has the additional benefit of maintaining a population of pollinating wasps, dependent upon figs and apparently short-lived.

Sudden, synchronous onset or cessation of flowering by many individuals produces a skewed flowering distribution within a population. Many species have right or positively skewed flowering distributions, i.e. flowering begins abruptly and then tails off (207, 227, 261). Thomson (261) hypothesized that right skewing could increase detectability and attractiveness to pollinators, which would then continue to visit these known plants even as flowering declined. However, the same pattern is observed in wind-pollinated plants (207) and in an autogamous species (227). Synchronous onset of flowering probably reflects similar responses to a uniform and unambiguous environmental cue (124, 227).

Environmental Cues

Only three major physical environmental factors have been identified as cues that initiate onset of flowering: photoperiod, temperature, and moisture (67, 142, 228). Photoperiodic control has been reported primarily for short-lived herbs (67, 142). Most temperate woody species (151, 212, 235) and some perennial herbs (266) flower in response to temperature, which usually acts through cumulative heatsums above some threshold level. In seasonal tropical forests, flowering is often induced by rainfall (8, 16, 73, 115, 186). Heavier rains increase synchrony of flowering within populations of some tropical trees (16, 17). Bochert (3 2) has shown that flowering in some tropical trees occurs in response to decreased water stress which may be stimulated by either leaf loss or rainfall. In deserts the drying soil, which indicates the end of the growing period, causes annuals to flower (28 2, 255). A number of environmental factors may interact to determine flowering onset. In some plants floral buds are produced only after a sequence of environmental cues that may occur several months apart (6 7, 142). For example, low temperature may induce biochemical changes in the seed that later permit the vegetative plant to flower in response to a second cue such as short nights (105). The timing of bud initiation and development and the cues involved are little known (211).

Genetics

Ecotypic differentiation in seasonal flowering times between natural pop-ulations has been found in uniform garden experiments (112, 143). In general, populations from higher latitudes flower earlier than do populations from lower latitudes when planted at low latitudes. Stages of flowering that occur late in the growing season, such as flower bud formation, tend to show greater interlatitudinal variation than stages occurring early in the growing season (211).

Evidence for the genetic basis of flowering timing is stronger than that for germination timing. Genetic variation within natural plant populations is high in a few species (3, 6, 127, 128). Distinct early and late flowering genotypes have been found within populations of *Melandrium*, *Arabidopsis*, and several cereal crops (5, 145, 163, 282a). Artificially produced polyploids flower later then their diploid progenitors (84). Agricultural studies, involving selection and crossing of different lines, have demonstrated for many herbaceous species that only one or a few genes determine flowering onset (178, 272). Genotype-environment interactions are strong in some species (e.g. 173). Selection for flowering time in several species has produced significant changes within a few generations (40, 190).

Summary

Phenotypic variation in patterns of flowering in natural populations may reflect heterogeneous environmental factors, differences among genotypes, or phenotypic plasticity. The causes of this variation need further study. Correla-tions between flowering time and seed set (14, 96, 226, 227, 272, 273, 293, 295, 296) are consistent with the assumption that flowering time affects fitness. However, the causal relationship remains to be demonstrated. Both maternal and paternal contributions to fitness must be measured.

In general, there are many more hypotheses about ultimate factors that may mold flowering times than there are thorough studies that permit testing them. Thus, at this time it is difficult to evaluate the hypotheses. Experimental studies are needed to clarify the role of pollinators as selective forces in the evolution of

flowering times. Plants and pollinators may coevolve and increase their phenological matching, but evidence that variance in seasonal flowering times affects pollinator fitness is lacking. Other biotic factors, such as parasitism (106), can influence flowering time, but these effects have received little attention. We also have little information about the direct effects of seasonal timing on the ability to produce or maintain flowers or to mature seeds. Schmitt (227) suggests that early drying of serpentine soils has selected for earlier flowering in two *Linanthus* species. Schemske (225) has strong evidence that herbivory in mid- and late-summer has selected for early-summer flowering in some *Impatiens* populations. These examples indicate that it may be necessary to study the entire life history in order to understand the selective forces that influence flowering times. We hope that we will not need to extend studies over twelve centuries as the Japanese have done in their observations of the blooming dates of Kyoto cherry trees (12).

FRUITING

Fruiting includes initiation, growth, and ripening of fruit and the presentation of fruit to dispersers, as well as the eventual dispersal of fruits from the parent plant. Here we discuss only the timing of fruit (or seed) ripening and dispersal. A ripe seed has severed its attachment to the parent. A ripe fruit has developed characteristic properties, like color and flavors that attract dispersers or effect dispersal. Usually fruits ripen before they are successfully dispersed; however, the fruits of some species, e.g. avocado and durian, develop their attractive properties only after they have fallen from the parent plant (184).

Selective Factors

TIME OF OCCURRENCE Abiotic factors may limit ripening times, but few studies address this relationship. In temperate regions, late frosts in spring and high temperatures in summer occasionally cause significant fruit mortality (245). Pecan clones that develop late in the season produce smaller fruits than do early-ripening clones because the nut is filling while conditions are poor (259). Daucus carota seeds dispersed late usually have low viability (139). In the tropics, fruits of Hybanthus shrubs atypically produced during the dry season are often abnormally small and contain nonviable seeds (14).

The time of fruit ripening should reflect timing of conditions that influence dispersal success. Offspring movement away from the parent is usually assumed to be advantageous (119). Evidence for this comes from correlations between times of fruit ripening and abiotic conditions favoring dispersal in wind-dispersed species. In seasonal tropical forests most wind-dispersed species ripen and release fruits near the end of the dry season when the trade winds are strong and when many leaves have fallen (56, 75, 119, 122, 150, 182, 203, 236). This dispersal timing also minimizes the time that seeds will lie on the ground before germinating at the beginning of the rainy season (85).

Availability of animal dispersers should also select for ripening times in animal-dispersed species. In temperate areas most species with fleshy fruits ripen their fruits during autumn bird migrations (109, 111, 174, 238, 243, 248, 257). In aseasonal tropical forests in Malaysia, where animal dispersers may be available throughout the year, fruiting occurs all year and no fruiting peaks are evident (203). In Panamanian forests, a slightly greater proportion of species ripen fruits in autumn when birds arrive from northern areas than at other times of the year (75, 122, 131). In more seasonal, tropical forests, the number of species with animal-dispersed fruit show a peak of fruit ripening during the rainy season (75, 76, 122, 131, 150, 254). Many correlations between ripening times and presence of dispersers exist, but the conclusions that may be drawn from these correlations are limited. Dispersal success is logistically difficult to measure and is seldom known. Ultimately, one must follow individual off-spring and quantify their fitness.

Although disperser availability should select for ripening times, the problem of circularity arises again as with flowering and pollinators: Is seasonality of disperser availability a cause or an effect of fruiting time? Migrating birds have been hypothesized to select for autumn fruit ripening in temperate plants, but this hypothesis rests on at least two assumptions. One is that birds would not migrate earlier if fruits were available earlier. No studies address this assumption. The second is that dispersal is more successful during migrations than earlier or later in the season. Thompson & Willson (257) found that removal rates were faster for species with autumn-ripening

fruits than for species with summer-ripening fruits. During the spring and summer, the local, territorial birds are sparse and feed primarily on insects-high-protein food that birds require for reproduction. Birds may switch to fruits in autumn because they need high energy for migration (248). Temperate woodland herbs that ripen fruits in spring are often ant-dispersed, whereas bird-dispersed herbs ripen fruits in late summer (256). The fate of dispersed seeds, however, has not been followed.

Seed mortality caused by seasonal predators or pathogens could also in-fluence times of ripening and dispersal. Most evidence comes from interspecific comparisons rather than from studies of individuals within populations. Several studies of temperate herbs show how species that ripen seeds during summer suffer higher predation than congeners that ripen seeds earlier in the spring (35, 93, 99). In several temperate shrubs, fruit damage by pests is more severe for species with summer-ripening fruit than for species with fall- or winter-ripening fruit (109, 257). Pre-dispersal predators or pathogens can destroy seeds, making fruit less attractive to dispersers (124, 248).

SYNCHRONY AMONG SPECIES Facilitation could select for aggregated fruiting times among species by increasing the number of dispersers or by increasing the movement of frugivores between species (284). Dispersal away from conspecifics, it is hypothesized, increases seedling survival (119, 284). Seedlings of *Casearea nitida* survived better under unrelated perch trees used by bird dispersers than under con specifics (118). Synchronous fruiting would be necessary for a mimic and its model (164), but the mimicry hypothesis has never been tested for fruits.

Interspecific competition for animal dispersers should select for phenological asynchrony or divergence among species (164, 236, 237). Snow proposed that competition caused staggered fruiting times of bird-dispersed *Miconia* species in Trinidad (237). However, this staggered pattern has been shown to be statistically indistinguishable from a random pattern (88). In general, fruiting times of animal-dispersed species tend to be aggregated or random rather than displaced (75, 79, 88, 109, 110, 111, 25 7, 283). Current interspecific competition among plants for dispersers has not been studied. Occasional anecdotal reports of undispersed fruits suggest that competition may occur at times (108, 119, 164), but other environmental factors could produce similar results.

If interspecific interactions are to select for divergence or convergence in fruiting times, fruiting sequences should be fairly consistent between years. Few long-term descriptions of fruiting patterns exist. For tropical trees fruiting times can be inconsistent within and between years (75). In aseasonal forests in Malaysia, intervals between fruiting were often irregular both within and between species (203). Individuals of many tropical trees may skip fruiting in some years (121, 124, 169); this would eliminate or change any interactive effects among or within plant species for dispersers.

DURATION AND SYNCHRONY WITHIN SPECIES Duration of individual fruits must be separated into potential duration (or persistence ability) and observed duration determined by removal rates. Mortality of ripe fruits and seeds on the parent could select for rapid release or removal after ripening (124) and for short potential and observed duration times. In temperate regions, bird-dispersed fruits in summer have been found to rot or dry rapidly whereas autumn fruits can remain attractive for weeks or months (248). Stiles (248) hypothesized that the short potential duration times of summer fruits reflect rapid removal rates caused by territorial birds that learn the locations of fruits (257). Autumn-ripening fruits last longer because they must be discovered by migrating birds that are unfamiliar with plant locations. Since conditions are less favorable for microbial and pest attack on fruits during the autumn, ripe fruits can persist longer. Morphological or chemical mechanisms may also deter pests (234).

Within an individual plant, extended duration of dispersal may represent a bet-hedging strategy against uncertainty in colonization opportunities (24, 139). In the neotropics early successional trees have longer fruiting times than do forest trees, which may increase the probability that their seeds will reach gaps, which are formed throughout the year (186). Extended ripening could also reflect the seasonal unpredictability or scarcity

of resources needed for fruit development (24). Extended fruiting is more common among understory plants than among canopy trees (79), and resources may be more limited for understory plants. Colonizing weedy herbs commonly have long periods of seed release (102). In *D. carota*, extended duration of seed release; partially controlled by the parent (138), probably increases dispersal distance (139). Extended duration for a species could be caused by asynchronous fruiting within individuals and/or among individuals, and these have not often been separated in species surveys.

Increased fruiting synchrony both within and among individuals may facilitate dispersal if increases in fruit density cause the attraction of relatively more dispersers. In temperate areas, synchrony is greater for shrub species that ripen fruits in autumn than for species that ripen fruits in summer (257). The consequently larger displays may attract migrant birds unfamiliar with the locations of specific plants (174, 257). These larger displays could also satiate dispersers; however, this is less likely during autumn migrations (257). Researchers have hypothesized that the degree of fruit specialization by the dispersers selects for sychrony in fruiting within individual plants (117, 164). Because specialized frugivores are locally sparse, they are likely to be satiated by large, synchronous fruit crops; hence, asynchronous, small fruit crops should be favored. In contrast, because nonspecialized, opportunistic dispersers are abundant, dispersal success should increase with larger fruiting displays and greater synchrony (117). Most studies do not support this hypothesis. Removal rates of fruits are usually highly variable and unrelated to either fruit crop size or disperser specialization (119).

Within an individual, synchronous fruiting could be disadvantageous if dispersers spend long times at one tree and therefore drop most seeds under the parent tree. This effect could be eliminated if predation on dispersers forces dispersers to move frequently (116). Pratt & Stiles (198) show that cryptic birds, which should be less susceptible to predation, have longer linger times in fruiting trees than do noncryptic birds. Effects on fruit dispersal success were not measured.

Synchronous fruiting both within and among individuals may satiate seed predators. Augspurger (15) artificially created asynchrony among individuals of *Hybanthus prunifolius*, a tropical shrub, and showed that individuals fruiting asynchronously with the population experienced higher seed predation than did individuals fruiting. synchronously. Janzen (123, 124) proposed that predator satiation has selected for mast fruiting in trees whose nutrient-rich seeds are dispersed by the major seed predator. In several mast-fruiting species, seedling establishment occurs only during the mast year. Individuals fruiting asynchronously with the population, i.e. in a non mast year, leave no offspring (33, 234, 240, 24 1). No studies have examined similar effects within years. Synchrony both within and among individuals may be limited to species where seeds are wind-dispersed and satiation is unimportant (27) or where the predator and the disperser are the same species and satiation is advantageous.

If predators differ from dispersers, then the degree of synchrony within and among individuals will likely reflect a balance between attracting dispersers and satiating either dispersers or predators (27). In limber pine, the cones ripen synchronously within a tree but asynchronously within a population (27). This appears to allow nutcrackers, the major disperser, to harvest seeds more effectively than can squirrels, the major predator. Because ripening is synchronous within individual trees, many nutcrackers can find a ripening tree and remove seeds more quickly than can squirrels. Because ripening is asynchronous within the population, satiation of nutcrackers is prevented.

Asynchronous ripening may reduce competition for dispersers, but spatial aggregation may alter this effect (157). In nutmegs (*Virola surinamensis*) individual trees within clumps appear to attract relatively more dispersers than do isolated trees, but they compete among themselves for these collectively gained dispersers (157). Isolated trees attract fewer dispersers but do not satiate dispersers. The advantages of aggregation in attracting dispersers may need to be balanced with the disadvantages of competing for dispersers. In nutmegs, intraspecific competition may be the stronger force and may have selected for asynchronous fruiting (157).

Environmental Cues

Environmental cues seldom stimulate the onset of fruit ripening. Rather, onset is determined primarily by internal factors that control the rate of fruit development (e.g. 55, 144). Environmental factors may secondarily influence ripening rates by influencing metabolism. For example, lower light intensity reduces the percent of berries ripe at harvest date in *Vaccinium angustifolium* (2). Higher temperatures decrease fruit development time in sour cherry (264). External environmental conditions can directly influence fruit dehiscence, abscission, and dispersal (138, 265). Extreme drought or fire initiates cone dehiscence in many pines. Relative humidity controls the rate of seed dispersal in a number of species (138, 265).

Genetics

Evidence for genetic control of the time of fruit ripening comes from studies of domesticated species. Genetic variability in development time is common among clones and sibs in pecans (259). Artificial selection has significantly changed ripening times in several species, usually by changing development time (flower-to-fruit interval) (18, 82, 268). In several species fruit development time is a polygenic trait (18, 82, 268), and in peaches heritability of development time is quite high (.73-.98) (268). Crosses within some cultivated fruit species have demonstrated strong paternal control of the time of ripening (55, 185, 191). The pollen source can determine the number of seeds, fruit size and hence ripening time (59, 62, 63). Paternal control of ripening time was discovered even before scientists understood the mechanism of fertilization in plants (180).

Although mechanisms that control the time of seed dispersal have been lost with plant domestication in a number of species (244, 285), little is known about the genetic control of dispersal timing. In *Lactuca seriola* the opening of involucal bracts, permitting dispersal, occurs only in wild populations and is controlled by a single gene (285).

Summary

Of the three life history events considered in this review, temporal fruiting patterns have received the least attention. The effects of both external and internal environments on fruiting patterns and the nature of genetic control of fruiting are poorly known. Few experimental studies have addressed the hypotheses about the selective forces acting upon fruiting, probably in part because of the difficulty in measuring offspring dispersal success.

ECOLOGICAL AND EVOLUTIONARY CONSTRAINTS

Studies addressing the ecology and evolution of phenological patterns have usually considered the timing of each life cycle event in isolation from the rest of the life cycle. Focusing on one event permits an examination of the selective pressures acting directly upon that event. Natural selection, however, acts upon an entire organism, and so considering each event alone can be misleading (30). Phenological patterns are likely to be constrained by plant morphology, physiology, and more generally the genetic and epigenetic background of each individual. In this section we explore the possible constraints that the rest of the life cycle may place upon temporal germination, flowering, and fruiting patterns. We define a constraint in the broad sense as any trait that indirectly limits the power of a selective force to change a phenological pattern. Constraints may affect one or all phenological traits. Phenological traits themselves may con-strain each other. Few studies have specifically addressed these constraints or their genetic basis, and so we hope that drawing attention to these studies will stimulate further research in this area.

Effects of Resource Limitation

Flowering, fruiting, and even germination require an input of energy and nutrients. Therefore, resource abundance and a plant's ability to assimilate and allocate these resources may influence phenological patterns. Floral bud initiation is often associated with some "ripeness-to-flower" factor (e.g. 114, 142, 144). Plants of some species flower only after they have accumulated a threshold level of resources, often measured by plant size. In annuals, large plants that have accumulated resources quickly often flower earlier in the growing season than do small plants (26, 127, 128). In some indeterminately growing crop plants, the production of many fruits stops further flowering (148). Resource levels can also influence duration of flowering. In some annuals, large

plants produce more flowers over a longer time than do small plants (39, 227). In some perennials, large plants flower longer (e.g. 14, 200, 223, 292).

Plants that require more resources for reproduction should flower later and/or for a shorter time. In dioecious species, females often begin flowering later than do males. This delay may allow females time to accumulate more resources that are needed for fruit and seed development (154), although early flowering by males may have resulted from competition among males for pollinators (24). Males often produce more flowers and flower for a longer time as in *Jacaratia dolichaula* (37), presumably because of the lower cost of producing pollen. Also, females flower less often than do males within (38) and among years (168). Janzen (124) argued that for many hermaphroditic tree species, individuals may flower more often than they set fruit, thus, acting as males more often than as females, because pollen production is less costly than fruit production. This hypothesis has yet to be tested.

The impact of resource limitation on flowering time may depend upon the absolute time interval between floral bud initiation and anthesis. In annuals, flowering immediately follows bud initiation, and therefore the time of attainment of threshold size influences the time both of bud initiation and of anthesis. Perennial herbs may resemble annuals when they flower after vegetative growth has occurred early in the growing season. However, if several months separate bud initiation and anthesis as in many trees and shrubs, resource accumulation likely influences only time of bud formation. Reader (211) found that seasonal resource accumulation determined when floral buds were formed in three ericaceous shrub species but that flowering was initiated by a more predictable external environmental cue. Presumably, subsequent fruit development uses resources accumulated in the previous year rather than in the current year. However, the relative use of stored versus current assimilates for fruit maturation is poorly known (245, 278).

Resource limitation and the limited time for growth and reproduction in annuals (104, 122) have motivated the development of theoretical models that predict when and how an annual plant should switch from vegetative to reproductive growth. Cohen (50, 5 1) proposed that for annuals growing in a habitat where length of the growing season is predictable, flowering should be delayed to maximize resource accumulation but not so delayed that there is insufficient time to mature seeds. Plants should switch sharply from vegetative to reproductive growth. For annuals growing in habitats where length of the growing season is unpredictable, flowering should begin earlier and span a longer time to insure some seed production even in years when the growing season is cut short. Resource allocation to reproductive growth should gradually increase with time. Other studies extend Cohen's model to predict the optimal time of onset of flowering when plants are subject to vegetative and reproductive losses, e. g. via herbivory (e. g. 45, 13 4, 188), competition (221), or seasonal variation in photosynthesis and storage potential (45, 222). Of the two models (45, 134) tested with data from natural populations, the King and Roughgarden (134) model accurately predicted time of onset of flowering. In general, most models have predicted a sharp transition from vegetative to reproductive growth. Sharp transitions have been found in *Lupinus nanus* (192), some annual grasses growing in the Mediterranean region, and in crops (101) that grow in highly predictable environments. However, other empirical data indicate that biomass allocated to reproduction increases gradually in annuals (26, 45, 46, 135, 251) and that vegetative growth and fruit development compete for resources once flowering has begun (144, 184). Thus, most empirical evidence shows a gradual transition to reproduction.

Few studies have characterized the seasonal switch in resource allocation from vegetative to reproductive growth in perennials. Many studies show proportional changes in biomass allocation through the growing season but do not indicate whether vegetative growth continues or ceases with onset of flowering or fruiting. Carbohydrate accumulation in the meristem may induce flower bud formation and inhibit vegetative growth (32), producing a sharp switch from shoot expansion to flowering. However, some tropical trees such as coconut palms, mangoes, and bananas simultaneously grow vegetatively, flower, and fruit (144). Root expansion continues after flowering begins in *Lupinus variicolor*, an herbaceous perennial (192), and vegetative growth occurs before, during, and after reproduction in wild strawberry (129).

The life history of a species may influence seasonal resource allocation patterns. *Lupinus nanus*, an annual, switches to reproductive growth earlier in the summer than does *L. variicolor*, a perennial (192). Likewise, annual species of *Lolium* (48) and *Plantago* (199) flower before perennials. In *Lolium*, annuals are induced to flower by longer nights (48). Selection may favor this flowering delay in perennials because the delay provides more time for vegetative growth, which could enhance subsequent survival (199). Also, because there is less pressure for a perennial to produce seeds within any one growing season, perennials can risk flowering at a later date.

Conditions that affect resource allocation to offspring can affect fruit size (81, 201, 292) and ripening times within an individual. Competition among fruits for resources may delay ripening. Larger fruit crops ripen later than small crops in *Vaccinium* (155). Fruits with more seeds may produce more auxin, accumulate resources faster, and grow larger (184). In *Vaccinium angustifolium*, many-seeded fruits ripen earlier than fruits with fewer seeds (1). However, species that produce large fruits tend to develop fruit more slowly than do species that produce small fruits (201).

Resource allocation may influence temporal germination patterns as well as fruiting patterns. When plants are grown under the same environmental conditions, maternal effects often associated with seed position on the mother can produce progeny that vary in their germination requirements (42, 97, 282). In many Compositae, ray and disc flowers produce seeds that differ in time of germination (267). In *Xanthium*, seeds are borne in pairs, with one seed usually germinating 12 months after the other (101).

Maternal effects may influence subsequent germination times by regulating seed size (e.g. 95, 220, 231). In two species of *Rumex*, large seeds, borne on the proximal portion of inflorescences, germinate more slowly than do small seeds borne on the distal end (42). Other studies show similar germination patterns (286). In contrast, large seeds germinate earlier than do small seeds *in Mirabilis hirsuta* (280) and at the same time in *Latium perenne* (179) and *Raphanus raphanistrum* (242).

Rates of resource accumulation are likely to be controlled genetically as well as environmentally. Size components like height and weight, which estimate resource accumulation, show strong genetic control in several species (3, 83, 270, 271). Other data indicate that height itself has been subject to natural selection (3, 270, 271). Gottlieb's (89) study of *Stephenomeria* and Solbrig's (239) study of violets (*Viola* spp.) point out, however, that in some cases size may be completely environmentally determined.

Selective pressures and mutations that alter resource assimilation or allocation patterns could affect the evolution of phenological patterns. A mutation that increases assimilation and growth rate may cause plants to flower earlier, and this exposes them to an effective pollinator whose presence did not previously overlap with flowering time. Environmentally induced reductions in resource accumulation could eliminate late-flowering genotypes from a population because these genotypes can no longer set seed before the end of the growing season. Mutations that accelerate fruit maturation and/or dispersal could allow seeds lacking dormancy to germinate in autumn and grow large enough in autumn to produce mature seeds. The above are hypothetical examples, but they illustrate how selection might alter a phenological trait not only directly but also indirectly through changes in assimilation rates and allocation patterns. These changes occur independently of any selective pressure acting directly on timing.

Morphological Constraints
Developmental patterns that determine plant shape may also influence phenological patterns. For example, selection for reduced height could produce either a reduction in number of leaves and internodes on the flowering stalk or a reduction in internode length. A reduction in leaf number could reduce photosynthesis and consequently delay flowering if the plant now requires more time to reach a threshold resource level for flowering. In contrast, shortening internodes would reduce photosynthesis only if leaves shade each other, e.g. if leaves are oppositely arranged. A little leaf overlap should not reduce photo-synthesis and therefore should not change flowering time.

The few studies that have actually examined the relationship between phenological and morphological patterns have focused primarily on temporal differences in flowering associated with determinate versus indeterminate growth. In plants with determinate growth, the terminal meristem of a shoot differentiates into an inflorescence after producing new vegetative tissue. The separation between vegetative and reproductive growth is sharp, and lateral buds subtending the inflorescence resume vegetative growth the following season. In plants with indeterminate growth, the terminal meristem grows only vegetatively and inflorescences are produced from lateral meristem, i. e. on side shoots. This growth pattern permits simultaneous vegetative and reproductive growth. In the seasonal tropics, determinate growth patterns of trees may restrict flowering to the dry season, whereas indeterminate growth patterns may permit flowering throughout the year (32). In temperate habitats where length of the growing season is predictable, e.g. agricultural fields, determinate growth habits are common. The determinate growth habit in some annuals may allow them to delay flowering and yet still set seed before the end of the growing season (101). In habitats where the length of the growing season is unpredictable, indeterminate growth patterns are more common; this growth pattern permits "opportunists" to grow vegetatively from the terminal meristem while producing flowers from lateral meristems (101). Evolutionary change in growth patterns has occurred rapidly in crop plants. For example, one locus determines the growth habit in lima beans, the determinate habit having recently evolved from the indeterminate habit, which predominates in wild populations (7).

Most information about morphological constraints comes from descriptive community studies. Within plant communities different life forms flower at different times. In Great Britain, peak time for tree flowering is May; for shrubs-June; for herbaceous perennials, annuals, and biennials-July; and for bulbs and corms-April-May and September (91). Herbs commonly flower during or at the end of the active growth, most often in summer (32, 47, 91,94). In the seasonal tropics herbs and shrubs tend to flower in the wet season (57, 171), but trees flower in both wet and dry season (57, 79, 171). Different life forms may also germinate at different times. For example, in Californian deserts many annual species germinate only after light but extended winter rains that occur during most years, whereas most perennial shrubs germinate only after short but heavy summer storms that occur only once every 5-20 years (281). Went (281) argues that annuals can mature successfully on a single winter rain period but perennial shrubs require both summer rains and subsequent predictable winter rains for seedling establishment. These documented patterns of temporal germination and flowering may or may not reflect large-scale differences in development that make each life form unique. In either case, the observations illustrate that we still have much to learn about the ecology and evolution of developmental patterns in plants (cf 31).

Gould (90) among others has proposed that changes in the timing of developmental processes strongly direct the evolution of size and shape. It seems possible that size and shape also direct the evolution of the timing of development. The modular nature of plant growth (10 1) may permit different parts of a plant to behave as independent physiological units (278). Each unit, e.g. a ramet of a clonal plant, may control its own resource assimilation and allocation. The degree of control may vary among species. We therefore predict that increased autonomy of modules and increased environmental sampling by the modules will produce increased variation in onset and duration of flowering and fruiting within an individual plant and may produce increased variation in temporal germination patterns of offspring.

Phenological Correlations
The sequence of germination, flowering, and fruiting seems developmentally fixed within the life cycle of an individual; at least no one has yet found a species in which individuals flower before they germinate (cf 64)! However, an unanswered question is: "Do phenological events follow each other after fixed time intervals, or are they independently controlled by different environmental cues?" (233). Time of flowering and fruiting may be completely canalized (*sensu* 269) once germination occurs, so that minor environmental changes will not alter their time of occurrence. Alternatively, time of flowering and fruiting may be completely controlled by external environmental cues. Flowering and fruiting times of seven chaparral annuals appeared to be partially canalized although the effects of plant size were not considered (233). During this six-year study (233)

germination time varied greatly in response to rainfall, and flowering and fruiting times were more strongly correlated with elapsed time from germination than with any of the measured environmental variables.

Other studies have shown correlations among germination, flowering, and/ or fruiting times. Early spring-germinating *Thlaspi arvense* individuals flower before late spring-germinating individuals (163). Males of *Silene* species both germinate and flower earlier than do females, and *Asparagus officinalis* females germinate earlier but flower later than do males (154). Onset of seed dispersal follows onset of flowering after a predictably fixed time in *Daucus carota* (139). Such correlations may reflect the canalization of events following germination. Bamboos exhibit the most striking example of canalization of flowering time, even though the time scale spans years, rather than months or days within years. Individual clones flower only once every 5-120 years after germination, and cuttings of individual clones flower synchronously regardless of where in the world the cuttings are grown (124). Not all studies show correlations, however. Early- and late-germinating individuals of *Veronica peregrina* (153) and *Teesdalia nudicaulis* (181) flower at the same time. Phenological correlations have been detected in a few species; additional work is needed to determine the extent and cause of such correlations.

If phenological events are canalized, then to consider the evolutionary consequences of a phenological event in isolation from other events may lead to erroneous conclusions. For example, early-flowering plants produce more than three times the number of fruits as do late-flowering plants of *Papaver dubium* (13). However, plants flower early because they germinate early. Thus, selection may be favoring early germination rather than early flowering (13, 69). Alternatively, each may independently affect an individual's fitness and be subject to direct selective pressure (cf 140).

Even if phenological events are not canalized, the timing of one event may be altered by selection because that event interacts with a second phenological event. For example, temporal dispersal patterns may determine temporal germination patterns. In *Daucus Carota*, the seed dispersal season overlaps and extends beyond the autumn germination season. Dispersal time influences offspring fate because only seed dispersed before or during the autumn germination season can germinate that autumn (139, 140). In contrast, in *Geranium carolinianum*, dispersal finishes before the germination season and does not affect germination time (214). Ritland (213) has postulated that in annuals flowering time and seed dormancy may be jointly altered by selection. His optimality models suggest, for example, that variation in flowering time depends more on mean value of germination time than on the mean value of flowering time. Though Ritland's argument focuses on the variation in germination over years, one could probably apply the models to within-year variation in germination as well.

Genetic Correlations
Mather (159) and Wright (29 1) among others have argued that natural selection acts upon the phenotype of integrated gene systems rather than upon individual components comprising the systems. For example, in many weed species, one plant may produce several types of seeds; a unique shape, size, and set of germination requirements characterizes each type (101). Selection may act upon this whole suite of seed traits, rather than upon each trait individually, because the whole suite permits each parent to exploit more than one habitat through its offspring (100). Genetic correlations among traits constituting an integrated phenotype prevent the independent evolution of the component traits (141).

A few studies have shown that traits associated with time of flowering are genetically correlated to components of plant size (11, 83), reproductive effort (202), and frost tolerance (48). Crop studies show genetic linkage of genes controlling germination and flowering times in cucumbers (286). Thus, flowering and germination times may represent one component of an integrated gene complex in some species. Flowering time is not genetically correlated with components of reproductive output in Lalium (54) germination in rice (286), or self fertility or zinc tolerance in Anthaxanthum (11). Therefore, in other species selection may act upon each trait individually as it has in Anthaxanthum populations growing along metal mine tailings (11). In peaches, the time between flowering and fruit ripening is genetically fixed in one variety but not in another (18).

Genetic correlations between nonphenological traits may also influence the evolution of phenological traits. In *Vufpia jascicufata*, early emerging plants produce many spikelets but few seeds per spikelet; late emergers produce few spikelets but many seeds per spikelet (277). If the correlation between spikelet number and seed number per spikelet is genetically based, as are reproductive traits in other plant species, (e.g. 202) then altering germination time will alter reproductive components of fitness but will not change net fitness because reproductive components are negatively correlated. Negative genetic correla-tions can weaken directional or stabilizing selection acting upon a phenological pattern. In general, the degree to which a phenological pattern may evolve in response to a selective pressure will depend on the number, strength, and direction of genetic correlations and on the genetic control of correlated traits. Correlations that are easily broken, that manifest themselves only in extreme environments seldom encountered by a species, or that involve traits under simple Mendelian control should not constrain the timing of developmental events for long. Alternatively, correlations that are difficult to break, that contribute strongly to individual fitness or that involve polygenic traits may strongly determine the degree and direction of evolutionary change in phenological patterns.

CONCLUSIONS

An environmental pressure may precipitate one of several alternative evolutionary responses within populations, and these responses may or may not be phenological. For example, spatially and temporally heterogeneous environments may select either for increased seed dormancy or for increased dispersibility (10, 101). In some cases plants have evolved dimorphic seeds, which increase both offspring dormancy and dispersibility, albeit in different seeds (267). Seed predation may select for an increase in toxic compounds in seeds, a change in seasonal fruiting or germination pattern, and/or the development of mast fruiting. Seedling competition could select for either accelerated germination or larger seed size (230). It is time to acknowledge these alternative pathways in evolutionary studies of phenological responses.

Future studies need to address all levels of complexity of phenological patterns. We need to examine the trade-offs engendered by countervailing selective pressures acting directly upon each phenological event. We also need to examine the constraints that other aspects of an organisms's life cycle may place upon potential phenological changes. Future phenological studies need to consider both why an organism responds to a particular environment by changing its phenological pattern rather than by changing some other attribute and how the genetic and the epigenetic background constrain the direction and degree of adaptation.

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