Phenotypic Variety in Seed Germination Behavior: The Ontogeny and Evolution of Somatic Polymorphism in Seeds

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PHENOTYPIC VARIETY IN SEED GERMINATION BEHAVIOR: THE ONTOGENY AND EVOLUTION OF SOMATIC POLYMORPHISM IN SEEDS

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Germination polymorphism seems to be an extremely common phenomenon but it is usually overlooked or ignored when not associated with a polymorphism of seed shape or size. A single type of treatment to a bulked seed sample very rarely produces germination of all the viable seeds it contains. A variety of sequentially applied treatments is often required to achieve the maximum germination response (e.g., Palmblad 1969; Grime et al. 1981). This widespread phenotypic variety in germination behavior can arise in two ways: (1) from bulking seeds obtained from plants with different genotypes; or (2) from somatic variation between the seeds of individual mother plants. In this paper a season's seed production from one plant will be called a "clutch."

An unknown but probably large amount of variety within bulked seed samples results from somatic polymorphism within individual clutches (Palmblad 1969). This view is difficult to support unequivocally from the literature because few studies have examined the source of germination polymorphism in noncrop plants. However, it is remarkable that germination polymorphisms in crop plants in which genetic polymorphism is limited by controlled breeding are often still significant (e.g., *Daucus carota*, Gray [1979]; *Triticum vulgare*, Wellington [1956]; *Trifolium subterraneum*, Grant Lipp and Ballard [1964]). When within-clutch variation has been examined for wild plants, it has often proved to be a major source of germination polymorphism (e.g., *Rumex crispus*, Cavers and Harper [1966], Maun and Cavers [1971a, 1971b]; *Phleum arenarium*, Ernst [1981]; *Plantago coronopus*, Dowling [1933], Schat [1981]).

Germination polymorphism is an important phenomenon both to applied biologists who wish to eradicate it and to physiologists and ecologists who wish to explain it. From either point of view there are two relevant questions, How does germination polymorphism originate and why does it persist?

Here I present a simple but general model of somatic polymorphism and attempt to answer these two questions for the case of variation within clutches. First we examine the relationship between seed development and within-clutch variation.

SEED DEVELOPMENT AND SOMATIC POLYMORPHISM:
SOME EXAMPLES FROM THE LEGUMINOSAE

Occurrence, Ontogeny, and Heritability of Dormancy

A somatic polymorphism in germination behavior occurs in a very wide range of legume species. Nondormant seed morphs imbibe water rapidly in standard germination tests and have "soft" testas, while dormant morphs may remain impermeable to water for several years before their "hard" coats break down and permit imbibition and germination. The dormancy of hard seeds can usually be broken by scratching the seed coat. The polymorphism for hard seededness occurs in many annuals, in herbaceous perennials (e.g., *Alysicarpus monlifer,* Maurya and Ambasht [1973]) and even in legume trees (e.g., *Leucaena leucocephala, Acacia tortilis, Robinia pseudoacacia;* Pathak et al. [1974, 1978, 1980]). The polymorphism occurs in a number of legume crops and pasture species in which it has been extensively studied. The proportion of hard seed produced within a plant's clutch is often reported as a varietal character and in some populations has been shown to be heritable (review Quinlivan 1971*b*).

Seed development and the parallel development of dormancy have been studied in a number of herbaceous legumes (e.g., Hyde et al. 1959; Sidhu and Cavers 1977; Quinlivan 1971*b*). The pattern of hard seed development in *Trifolium repens* and *T. pratense* appears to be typical. In these two species seeds achieve 90% viability as soon as 12 days after pollination. At this stage the seed coat is permeable to water and the seeds are nondormant. Seeds then begin to lose water and as this proceeds, the testa gradually becomes impermeable and hard, producing a dormant condition in the seed (Hyde et al. 1959).

The chemical and anatomical changes which cause the change in the permeability of the seed coat are not fully understood but two important factors influence the dormancy state of the seed when it is dispersed: the relative maturity of the seed, and the level of humidity during seed maturation (Quinlivan 1971*b*). The length of the nondormant phase which precedes the development of a hard coat varies between species and dormancy develops faster in drier environments.

Source of Within-Clutch Variety in Germination Behavior

Because the occurrence of this kind of seed coat dormancy depends upon the relative timing of seed development and seed dispersal, somatic polymorphism may easily appear within a clutch. Seeds which initiated development at different times but which are harvested or dispersed together, seeds which developed at different rates and are consequently at different stages of maturity when shed, or seeds shed at different times will differ in their germination behavior. This diversity may arise within a seed pod or between fruits produced at different times of the year.

Diversity in the degree of dormancy among hard seeds within multiseeded indehiscent pods was found by McComb and Andrews (1974) in five different annual species of *Medicago*. Seeds at the calyx end of pods were larger and softened more easily than smaller more distally positioned seeds. Bigger seeds were also softer in *Trifolium subterraneum* (Grant Lipp and Ballard 1964), *Indi-*

gofera glandulosa (Bhat 1973), and *Lotus uliginosus* (Chappuzeau 1930). This might be general among legumes, though there are unexplained exceptions (Black 1959; Gáspár et al. 1981). Although, for any one *Medicago* species in McComb and Andrew's experiments, small seeds showed greater dormancy than large ones, this relationship between seed size and dormancy did not hold between species. The species with the largest seeds was among those with the strongest dormancy. The fact that a consistent relationship between size and dormancy within species does not hold between species demonstrates very neatly that dormancy characteristics are not determined by a relationship with absolute seed size but by relative rates of seed and seed coat maturation.

Seasonal variation in the production of hard and soft seed has been found in the annual clovers *Trifolium incarnatum* and *T. hirtum* (Williams and Elliott 1960) and in *Astragalus cinicus* (Yasue and Ota 1958), and has been studied in some detail in the desert annual *Ononis sicula*. This plant disperses three kinds of seed whose colors, in increasing order of size are brown, green, and yellow. The three kinds of seed represent a developmental series. Brown ones frequently have immature embryos or are inviable but, if viable, will germinate immediately. Green seeds are generally nondormant but viable, and yellow seeds are generally viable and dormant. The proportions of green and yellow seeds produced in a clutch depend on the day length under which they are raised on the mother plant. In greenhouse conditions under short (8 h) days, green and yellow seeds are produced in about equal proportions, but under long (20 h) days the clutch consists almost entirely of yellow seeds. The production of brown seeds is usually small and not affected by day length (Evenari et al. 1966).

The switch from production of green to yellow seeds is determined by the relative rates of development of the dehiscent seed pod and the seeds inside it. Under long days, the development of the seeds overtakes that of the pod so that they are fully mature and dormant when shed. Under short days, seed maturation is slower and some seeds are shed in a nondormant, green condition.

Generalizations

Five principal generalizations about the development basis of somatic polymorphisms in seeds emerge from the literature on seed impermeability in legumes. (1) Differences in germination behavior are frequently associated with, and are the result of, differences in the timing of the initiation of seed development, the pace at which it proceeds, and the point at which it is terminated or interrupted by seed dispersal or harvest. (2) Polymorphism in seed size is frequently correlated with polymorphism in germination behavior. (3) Polymorphism within a clutch may occur between seeds within a fruit and/or between seeds in different fruits. (4) The type or ratio of types of seed produced may vary with time and season. As a result, the ratio of dormant:nondormant seed produced in a total clutch may vary depending on when seed production begins and ceases. (5) The degree of somatic polymorphism present in a clutch may be heritable.

A GENERAL MODEL OF GERMINATION POLYMORPHISM WITHIN CLUTCHES

The ontogenic process which generates differences in seed behavior through changes in developmental rates is analogous to the phylogenetic process called

heterochrony in which new forms evolve as a consequence of "changes in the relative time of appearance and rate of development of characters already present in ancestors" (Gould 1977, p. 2). Since the ontogenic process of diversification in seeds produces somatic polymorphism while the phylogenetic process of heterochrony produces changes between ancestor and descendant, I propose by analogy to call the former process *somatic heterochrony*.

Gould's (1977) clock model of heterochrony can be used very conveniently as a model of the somatic heterochrony which produces polymorphism within seed clutches. The clock model is illustrated in figure 1 where it is applied to the example of *Ononis sicula*. The face of the clock has three scales which represent the progress of developmental processes in three concentric parts of the seed: the pericarp or fruit, the testa, and the embryo. The extent of development in each of these tissues at any given time is indicated by the hands of the clock. A separate hand marks the pace of development on each scale and the hands move at independent rates which represent the independent ripening of each part of the seed. Relative differences in these rates of development in brown, green, and yellow seeds mean that when pericarp ripening is complete the seeds are shed with different germination characteristics. In *Ononis sicula* these differences are permanent but in other species development may continue after seed dispersal or harvest ("after ripening") and the within-clutch differences in germination disappear.

Plants within the same family tend to share the same basic seed structure (Corner 1976). The structural types of seed characteristic of different families differ most from each other in the relative development or reduction of tissues such as pericarp, testa, endosperm, and embryo which are present in almost all seeds rather than in the development of unique tissues (Bewley and Black 1978). The imposition of dormancy on seeds is a frequent feature of their ontogeny which is closely associated with the pace of development in the various tissues of seed and fruit (Amen 1968). The limited variety found in these tissues is reflected in a limited variety of basic seed dormancy types. Hence, for instance, the ubiquity of hard seeds among legumes.

Although the variety of means used by experimenters to break dormancy is huge and the environmental stimuli to which seeds respond are numerous (Angevine and Chabot 1979), it is still possible to classify the main kinds of dormancy into a limited number of types according to seed structure. Atwater (1980) distinguished eight groups in a sample of more than 370 herbaceous dicot species spread across 46 families. Though the details of the mechanism vary between taxa, seed dormancy in all these plants arises only (1) as the result of an immature embryo, and/or (2) because it is imposed on the embryo by the endosperm or seed coats in which it is invested. The latter kind of dormancy may result from chemical inhibition or impermeability to water or oxygen, but in either case it can be broken by excising the embryo or by rupturing or removing the seed coat. Grasses may be added to Atwater's list of families which fall into the second group (Appendix).

As we saw in the legumes, the appearance and intensity of dormancy in seeds in which this state is imposed by the seed coat is dependent upon the relative timing
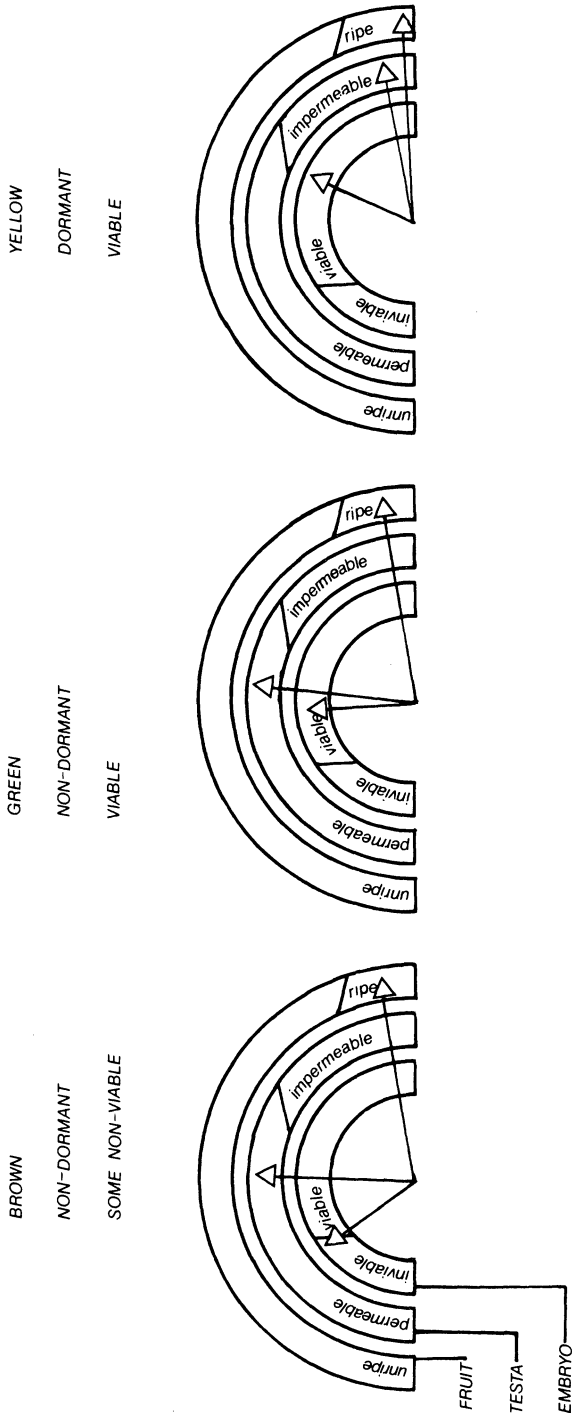
FIG. 1.—Clock model of somatic heterochrony illustrated by the development of 3 types of seed in *Ononis sicula*. The clocks are shown set in the 3 states reached at the moment of seed dispersal. See text for further explanation.

of embryo development, seed coat development, and dispersal. Similarly any dormancy mechanism which depends on the rate of development of an immature embryo or the rate of development of the tissue which surrounds the embryo is capable of producing somatic polymorphism through somatic heterochrony. Therefore it seems that one or other of the two basic types of dormancy mechanism may give rise to somatic polymorphism through somatic heterochrony in at least 47 families of plants.

Somatic heterochrony actually appears to be the cause of somatic polymorphism within clutches for a very wide variety of species. For example, Wellington (1956) found differences in the germination behavior of wheat grains (*Triticum vulgare*) which were related to their position in the spike and their state of maturity at harvest. Grain development involves three parallel ripening processes which proceed at independent rates (fig. 2). These occur in the pericarp, the testa, and embryo and all must be complete before a seed loses dormancy. Anthesis and seed development proceed basipetally in the two cultivars which Wellington studied. All grains of both varieties were dormant if harvested before the pericarp dried out. Apical grains of CV Holdfast germinated if they were prematurely dried showing that testa and embryo were already ripe, but apical grains of CV Atle and basal grains of both varieties required an extra period of "after-ripening" before dormancy was lost. These additional barriers to germination were caused by an impermeable inner layer of the pericarp in CV Atle and possibly caused by immaturity of the embryo in basal grains of both CVs (Wellington and Durham 1961; Wellington 1956).

Variation in the time taken to breach the various seed coats and the state of embryo maturity at harvest appear to account for both varietal and positional differences in germination behavior between wheat grains (fig. 2). Similar results with other cultivars of wheat have been obtained by Chaussat and Bouinot (1975) and Hardesty and Elliott (1956). Somatic heterochrony is the most likely cause of somatic polymorphism in seed germination wherever this polymorphism is related to position on the plant or inflorescence. On this basis it is implied in a very wide variety of species, some examples of which are listed in table 1.

DISCUSSION

Consequences of Somatic Heterochrony

The seeds of many of the crop species which have a germination polymorphism associated with a position effect exhibit only a transitory diversity in their germination characteristics. Embryos mature and seed coats are eroded or penetrated during storage so that developmental processes are completed in seeds which were immature and all the seeds in a clutch end up with the same characteristics. In other species such as *Ononis sicula* the diversity produced within clutches is fixed at the time of seed dispersal. Seeds of one morph may die or germinate faster than another, thus altering the ratio of morphs surviving in the seed pool, but in these species within-clutch diversity is a permanent, and presumably evolved feature of the life history. The existence of transitory, perhaps incidental, clutch
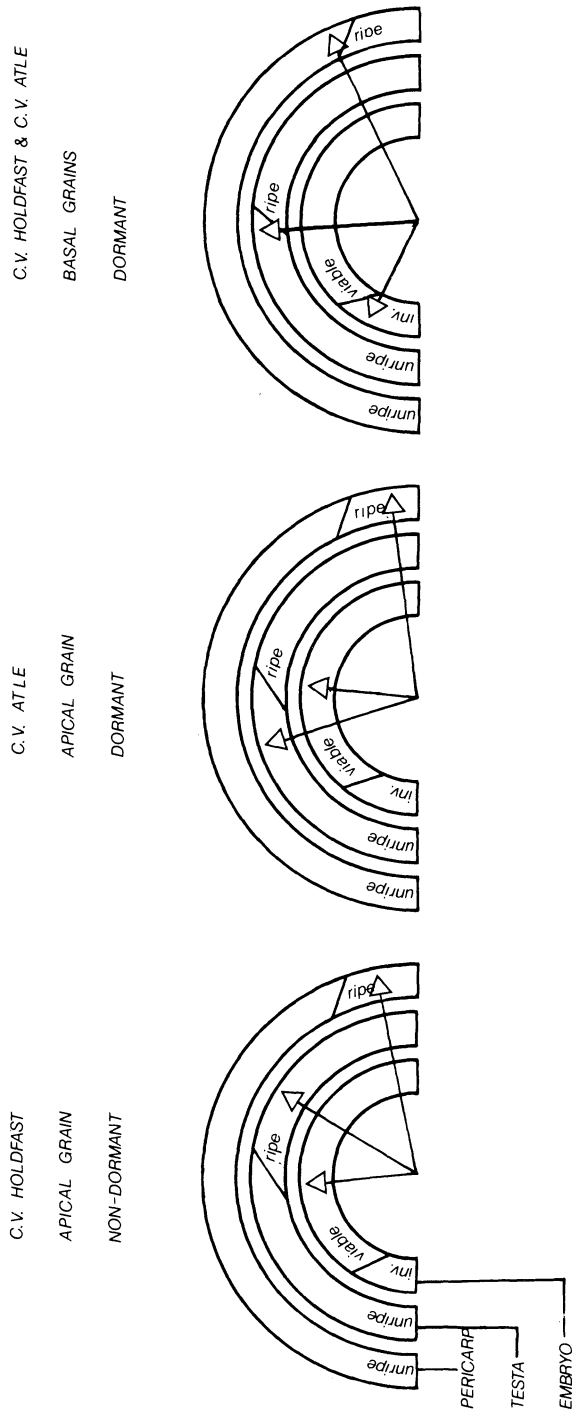
FIG. 2.—Variation in seed germination behavior within and between *Triticum vulgare* C.V.s. Holdfast and Atle represented by the clock model of somatic heterochrony. The clocks are shown set in the condition reached at harvest 5–8 wk after anthesis.

TABLE 1

SOME EXAMPLES OF SPECIES WITH GERMINATION POLYMORPHISM RELATED TO POSITION,
PROBABLY PRODUCED BY SOMATIC HETEROCHRONY

Species	Family	Source
Aellenia autrani	Chenopodiaceae	Negbi and Tamari 1963
Daucus carota	Umbelliferae	Gray 1979
Gossypium sp.	Malvaceae	Enileev and Solov'ev 1960
Medicago lupulina	Leguminosae	Sidhu and Cavers 1977
Mesembryanthemum nodiflorum	Aizoaceae	Gutterman 1980a
Phleum arenarium	Gramineae	Ernst 1981
Plantago coronopus	Plantaginaceae	Dowling 1933
Pteranthus dichotomus	Carophyllaceae	Evenari et al. 1971
Rumex crispus	Polygonaceae	Maun and Cavers 1971a, 1971b

diversity caused by developmental and positional effects in species like wheat and
so many other plants suggests that the evolutionary step from a uniform clutch to
a polymorphic clutch through somatic heterochrony should be a very easy one to
make.

Two annual desert species in the Chenopodiaceae described by Negbi and
Tamari (1963) provide examples of somatic polymorphism in seeds which have
evolved by somatic heterochrony. In *Aellenia autrani* and *Salsola volkensii* all
seeds commence development with a green embryo. During the course of later
development embryos lose their chlorophyll, seeds become yellow, and acquire
dormancy. However, the loss of chlorophyll is arrested in some seeds which are
produced at the end of the season and these dry on the mother plant while still
containing a green embryo. These seeds are nondormant. Dormancy in yellow
seeds of *S. volkensii* is partially broken by light and can be broken in both species
by removal of the seed coat. Yellow seeds of both species gradually lose their
dormancy with time and maintain viability longer than green seeds. As in the
Leguminosae, nondormancy and viable lifespan are inversely related in the two
seed morphs.

Werker and Many (1974) who studied the development of the two kinds of seed
in *A. autrani* have suggested that there are some additional morphological differ-
ences between the seed types which are not simply the result of arrested develop-
ment. It seems likely that such differences could have evolved as a means of fixing
a polymorphism which first evolved through simple arrested development and
somatic heterochrony. Two related species, *Kochia indica* and *Salsola inermis,*
produce only the green type of seed and may have derived this condition from
polymorphic ancestors. If an ancestral seed morph is eliminated from a poly-
morphic clutch to produce a change in the ratio of morphs in the clutches of
descendants, somatic heterochrony can give rise to phylogenetic heterochrony.
Thus the two phenomena can be closely linked. Evenari (1965) has suggested that
a mechanism of arrested development, like that found in *Allenia* could account for
germination polymorphism in many other species where the morphs are not so
easily distinguished by differences such as color.

Mother plants control the germination behavior of their offspring by encasing
them in seed coats which regulate embryo development or germination. This

regulation is itself a function of the pace of seed coat development and this is subject to the influence of the tissues which surround the seed coat. Thus the fruit and perianth may influence developmental processes in the seed coat and in turn influence germination of the seed. Shropshire (1973) showed that dormancy in seeds of *Arabidopsis thaliana* was influenced by the spectral quality of the light environment during development. Floral primordia irradiated with a light pipe transmitting light with a red/far red ratio of 0.6 produced seeds which were more than 90% dormant when tested in the dark. Floral primordia irradiated with light depleted in far red (R/FR = 7.0) germinated to over 90% in the dark. These results were not affected by the spectral composition of the light given to the rest of the plant. Kendrick (1976) pointed out that pigments in the fruit or seed coat could alter the spectral composition of the light reaching a seed during development and thereby determine subsequent germination behavior.

An extremely elegant series of experiments by Cresswell and Grime (1981) have shown how the phenomenon observed by Shropshire may explain differences in germination behavior between species and also differences within clutches. The latter differences originate by somatic heterochrony and in some cases the differences between species may have evolved by heterochrony.

Green leaves and tissues containing chlorophyll transmit much more far red than red light. Cresswell and Grime (1981) determined the rate of chlorophyll loss from seed-investing structure in 21 species of grasses and dicot herbs. In this diverse sample of species they found that the chlorophyll content of investing structures remained high during the development of species which exhibited a germination light requirement, but was low during the development of seeds without such a requirement. The expression of seed dormancy after dispersal in these species appears to be simply a function of the relative rate of chlorophyll loss in investing structures and the rate of seed maturation or drying (fig. 3). Cresswell and Grime (1981, p. 585) suggest that "differential rates of chlorophyll loss and/or seed drying within the same inflorescence may explain the germination 'polymorphism' with respect to light requirement reported for certain species."

Somatic Heterochrony, Within-Clutch Diversity, and Natural Selection

In temporally fluctuating environments natural selection tends to favor individuals possessing dormancy, perenniality, dispersal, or iteroparity. These are four major ways in which organisms may successfully inhabit an unpredictable environment. Dormancy and, in some situations, perenniality are means of avoiding unfavorable periods by escape in time, but the reappearance of favorable conditions must be detectable or predictable to the dormant organism. Dispersal is a means of avoiding unfavorable periods by escape in space and can be considered an alternative to dormancy.

Organisms in general, and perhaps plants in particular, do not always opt for just one of the three strategies that secure survival in a fluctuating environment (Lloyd, in press). Combinations of degrees of dispersal and dormancy are frequently found within a clutch. Maternal genotypes which allow all their seed progeny to germinate simultaneously are more vulnerable to extinction in a variable environment than genotypes which hedge bets by imposing dormancy on

LIGHT REQUIRING

WHEN SHED

NOT LIGHT REQUIRING

WHEN SHED

low
low
high
high

low
low
high
high

Chlorophyll content of
maternal investing
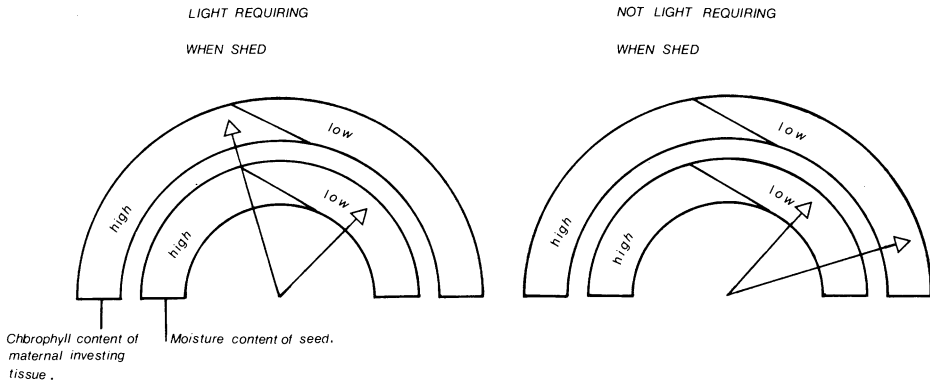tissue.

Moisture content of seed.

FIG. 3.—Relative rates of chlorophyll loss from investing tissues and seed ripening (measured as loss of water content) in light-requiring and non-light-requiring seeds.

some seeds and stagger germination within a clutch (Cohen 1966, 1967; MacArthur 1972; Venable and Lawlor 1980; Westoby 1981). Somatic heterochrony clearly provides an easy route for the evolution of bet-hedging.

There is a general suggestion in the literature concerning hard seededness in legumes, that plant populations which produce some dormant seed are less prone to extinction by natural hazards than those which produce only nondormant seed. A proper test of the optimality of bet-hedging should compare the survival of progeny from individual plants producing a diverse clutch and a uniform clutch. There are inherent overtones of group selection in the agronomist's interest in population survival which should not be carried over into an evolutionary study. Bearing in mind this reservation, there is some evidence that annual clovers growing in arid pastures which possess polymorphism for dormancy are more successful than those without it (Williams and Elliott 1960; Quinlivan 1971*a*). There is also evidence that dormancy polymorphism in alfalfa reduces the risk of crop failures caused by late frosts which kill off entire cohorts of seedlings (Dexter 1955).

Seeds with hard coats may remain viable in the soil for many years but the breakdown of this dormancy is accelerated by fluctuating temperatures. Temperature fluctuations are greater in the soil beneath gaps than beneath vegetation and this enables some predictiveness in the breaking of dormancy in *Trifolium subterraneum* (Quinlivan and Millington 1962; Quinlivan 1965) and probably other legume species. Impermeable seeds generally have longer viability than permeable ones when samples stored in the laboratory are compared (Evenari et al. 1966). It therefore seems unlikely that permeable seeds held in enforced dormancy by burial could fill the same role as impermeable ones as a hedge against environmental hazards. Long life and rapid breakdown of dormancy appear to be incompatible. A bet-hedging strategy in the legumes therefore demands at least two kinds of seed.

Somatic heterochrony is such a ubiquitous and easily induced process in seed development that the mere presence of germination polymorphism cannot be interpreted as having adaptive significance for a plant. Clearly there are situations in which the diversity in seed behavior produced by somatic heterochrony must

increase the fitness of a mother plant. The heritability of hard seededness and the seed polymorphism in *Ononis sicula* both indicate that natural selection can operate on somatic heterochrony to fix polymorphic behavior in a clutch. It should not be supposed that it always does so (Gould and Lewontin 1979).

Between-Clutch Diversity

The within-clutch diversity generated by somatic heterochrony arises from differential rates of development among seeds on the same plant. These developmental rates are often maternally and/or environmentally influenced (e.g., Juntilla 1971; Heide et al. 1976; Kigel et al. 1977, 1979; see Gutterman [1981b] for review) and may therefore also be responsible for differences in germination behavior observed between clutches and between populations exposed to different environmental conditions. For example differences in seed germination arising in this way have been observed between different altitudinal populations of *Chenopodium bonum-henricus* (Dorne 1981) and between annual crops of seed from *Rosa* spp. (Von Abrams and Hand 1956). In both cases differences between clutches are observed only in intact seeds and disappear when seed coats are removed. The discussion in this paper is confined mainly to within-clutch diversity but it is clear that this diversity and the differences in germination behavior between populations can arise from the same sources.

Limitations of the Model

The examples of within-clutch seed polymorphism discussed above exclude a class of plants which produce very different seeds on the same plant. Most extreme among these classical cases of heterocarpy are the (amphicarpic) species which produce separate subterranean and aerial fruit (see Ellner and Shmida 1981). Strong seed dimorphism is well known in *Atriplex* spp. (e.g., Beadle 1952) and *Salicornia* spp. (e.g., Grouzis et al. 1976; Ungar 1979) which produce seeds of different type from different aerial flowers. The ontogeny of these and similar differences in other species does not seem to have been studied and cannot be specifically included or excluded from the present model.

The Compositae contain a large number of species which express somatic polymorphism for seed size, shape, and behavior within individual capitula (e.g., Becker 1913). The germination differences between seeds from the same capitulum often disappear with the removal of the seed coat. Differences in seed behavior and morphology correlate with seed position in the capitulum and with the relative timing of anthesis across the capitulum (Burtt 1977), suggesting that in principle these differences may also be produced by somatic heterochrony.

SUMMARY

Germination polymorphism is commonly found among seeds in bulked samples. When the source of this variation in behavior has been investigated it often has been found to derive from differences between seeds produced within the same clutch (i.e., from the same mother). The ontogeny of these somatic polymor-

phisms is discussed with particular reference to the Leguminosae. Five generalizations emerge. (1) Differences in germination behavior are frequently associated with differences in the rate of seed development. (2) Polymorphism in seed size is frequently correlated with polymorphic behavior. (3) Polymorphism within a clutch may occur between or within fruit. (4) The type or ratio of types of seed produced may vary with time and season. (5) The degree of somatic polymorphism present in a clutch may be heritable.

A general model of seed development is described which can account for these five features of within-clutch diversity in germination behavior. The term *somatic heterochrony* is suggested for the process which involves differential independent rates of "ripening" in the tissues of seeds. Somatic heterochrony may be the cause of germination polymorphism in all species in which seed dormancy is the product of an immature embryo and/or a developing influence of the seed coats on germination. A large number of angiosperm families fall into these categories.

Somatic heterochrony may produce within-clutch diversity under the influence of natural selection. The same sources of variation may influence within-clutch and between-clutch (or interpopulation) differences in germination behavior. Given how easily seed development may be perturbed and produce changes in germination response, there is a danger in assuming that the diversity in seed behavior produced by somatic heterochrony is automatically adaptive. Finally, some limitations of the model are mentioned.

APPENDIX

ATWATER'S CLASSIFICATION OF SEED STRUCTURE TYPES AND THEIR
ASSOCIATED DORMANCY CHARACTERISTICS (after Atwater [1980])

Type of Seed Structure	Dormancy Type (in order of importance for each group)	Families Included in the Group
I. Seeds with dominant endosperm and immature dependent embryos		
A. Basal rudimentary embryos		
	IMM	Ranunculaceae
	CIE	Papaveraceae
		Fumariaceae
		Araliaceae
B. Axilliary linear embryo		
	IMM	Umbelliferae
	SCI(W)	Ericaceae
		Primulaceae
		Gentianaceae
		Solanaceae

APPENDIX (*Continued*)

Type of Seed Structure	Dormancy Type (in order of importance for each group)	Families Included in the Group
C. Axilliary miniature embryo		
	SCI(W)	Grassulaceae
		Begoniaceae
		Solanaceae
		Scrophulariaceae
		Lobeliaceae
D. Peripheral linear embryo		
	SCI(W)	Polygonaceae
		Chenopodiaceae
		Amaranthaceae
		Nyctaginaceae
		Aizoaceae
		Portulaceae
		Carophyllaceae
		Capuraceae
		Cactaceae
II. Seeds with residual or no endosperm and mature independent embryos		
A. Hard seed coat, limiting water entry		
	SCI(W)	Leguminosae
		Geraniaceae
		Anacardiaceae
		Sapindaceae
		Rhamnaceae
		Malvaceae
		Convolvulaceae
B. Thin seed coat with mucilaginous layer		
	SCI(O)	Cruciferae
		Linaceae
		Violaceae
		Labiatae
C. Woody seed coats with inner semipermeable layer		
	CIS	Rosaceae
		Zygophyllaceae
		Bahaminaceae
		Cistaceae
		Onagraceae
		Plumbaginaceae
		Apocynaceae
		Polemoniaceae
		Hydrophyllaceae
		Boraginaceae
		Verbenaceae
		Labiatae
		Dipsaceae
D. Fibrous seed coats with separate semipermeable membranous layer		
	SCI(W&O)	Compositae

Key to dormancy types: IMM, immature embryo; CIE, chemical inhibition by endosperm; SCI, seed coat impermeability to water (W) or oxygen (O); CIS, chemical inhibition by the seed coat.

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