PHYSIOLOGICAL AND ECOLOGICAL STUDIES OF SOUTHWESTERN PHASEOLINAE

by

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TABLE OF CONTENTS

TABLE OF CONTENTS -- Continued

LIST OF TABLES

LIST OF ILLUSTRATIONS

ABSTRACT

Fourteen taxa of the legume subtribe Phaseolinae native to the southwestern United States and Mexico were collected primarily in southern Arizona, between 1977 and 1980. Seeds were increased at the University of Arizona Campbell Avenue Farm in 1978 and 1979.

Significant differences in seed weight were found both within and between species. The between-species weights varied 56-fold. The amount of hard seed was found to vary from 7.7 to 98.7 percent. Seedling morphology and emergence type for many species is described. Germination using a thermogradient plate demonstrated a positive relationship between elevational and temporal distribution and germination temperature range of the species studied.

The flowering period of each species is described quantitatively and insect visitation of flowers is reported. Tolerance to temperature extremes, drought and waterlogging is discussed.

Significant differences in stomate densities and sizes were found, but no clear correlation appears to exist between adaptation and either stomate size or density. The more xeric species have greater leaf succulence than the mesic species.

Southwestern Phaseolinae are a group of herbaceous ephemerals, with both annual and root perennial types represented. Representatives exist in diverse habitats, from Sonoran desert to ponderosa pine forest.

The plants are colonizer species, growing best in disturbed, but ungrazed sites.

CHAPTER 1

INTRODUCTION

Pulse crops are important to human nutrition, providing substantial amounts of protein, B vitamins, and iron. The legume subtribe Phaseolinae (papilionate legumes with knotty (gland-covered) peduncles and with a bearded style, Piper, 1926) is outstanding among pulses, having yielded 14 cultivated species grown for edible seeds or pods. Some of the more important species are: *Phaseolus vulgaris*, common bean, *P. lunatus*, lima bean, *P. acutifolius*, tepary bean, *P. coccineus*, runner bean, *Vigna unguiculata*, cowpea and *V. radiata*, mung bean. Throughout this work, members of the Phaseolinae will be referred to as "beans." With such a large number of important food plants providing a substantial portion of human nutrition, it is important to collect and evaluate wild species for traits which may prove to be valuable for bean improvement.

Wild species, in general, are inadequately collected, and often relationships between them and other wild or domestic taxa are confused (Hawkes, 1977). The need to study and collect these species is becoming urgent, since many wild species are being reduced by overgrazing and habitat destruction, often existing only as relic populations. With this need in mind, the following study was undertaken.

Wild beans have been investigated to a very limited extent, but, in general, little or nothing is known about even the basic physiological characteristics of the individual taxa. Usually knowledge is limited to a taxonomic description and approximate range of the species, with an unknown peripheral area as large as 200 kilometers or more not uncommon. The true taxonomic status of several members of the group is still not clear.

This thesis is a collection of diverse studies of the natural history, physiology, distribution, morphology, and anatomy of southwestern beans. It is the result of 4 years of observation of wild populations and 3 years of field and laboratory studies.

The primary area of this study was Southern Arizona, generally within 250 kilometers of Tucson; however, materials were utilized which came from New Mexico, and Baja California Sur, Mexico. In addition, many species studied extend far beyond the domain of the main study area, some ranging as far as South America.

Taxa included are:

Macroptilium atropurpureum (DC) Urban, Symb. Antill, 9:457 (1928).

Macroptilium heterophyllum (Willd.) Marechal & Bull. Jard. Tot. Natl. Belg. 44:444 (1978).

Macroptilium heterophyllum var *rotundifolium* (A. Gray) Marechal, Mascherpa & Stainier, Taxon 27:199 (1978).

Phaseolus acutifolius A. Gray, Pl. Wright. 1:43 (1852).

Phaseolus acutifolius var *latifolius* Freeman, Bot. Gaz. 56:412 (1913).

Phaseolus acutifolius var *tenuifolius* (Woot. & Standley) A. Gray, Pl. Wright. 2:33 (1853).

Phaseolus angustissimus A. Gray, Pl. Wright. 2:33 (1853).

Phaseolus filiformis Bentham, Bot. Voy. Sulph. :13 (1844).

Phaseolus grayanus Woot. & Standley, Contr. U.S. Natl. Herb. 16:139 (1913).

Phaseolus metcalfei Woot. & Standley, Contr. U.S. Natl. Herb. 16:140 (1913).

Phaseolus parvulus Greene, Bot. Gaz. 6:217 (1881).

Phaseolus ritensis Jones, Contr. West. Bot. 12:14 (1908).

Phaseolus supinus Wiggins & Rollins, Contr. Dudley Herb. 3:270 (1943).

Phaseolus wrightii A. Gray, Pl. Wright. 1:43 (1852).

CHAPTER 2

LITERATURE REVIEW

Taxonomy

The status of the Phaseolastrae group, which includes the Phaseolinae members with the style bearded on the inner side (including all southwestern Phaseolinae), was reviewed and revised by Marechal, Mascherpa and Stainier, 1978. Their study, using numerical taxonomic methods, divided the local Phaseolinae into two natural genera, *Macroptilium* and *Phaseolus*. Previously, all southwestern beans were assigned to *Phaseolus* (Piper, 1926). The distinctive characters of each genus are presented in Table 1.

The study by Marechal et al., 1978, largely based on herbarium specimens, suffered from a paucity of live specimens, particularly from the study area of this thesis. The reclassification of *P. acutifolius* into varieties *acutifolius* and *latifolius*, representing the wild and cultivated tepary bean, respectively, was made without the availability of wild variety *tenuifolius*. Nabhan (1978) clarified the taxonomic status of this species and Marechal (1979a), having seen live variety *tenuifolius*, is in agreement. The lumping of *P. metcalfei* to *P. ritensis* by Le Marchand, Marechal and Baudet (1976), was made without living material from the type locality. The work of Nabhan, Berry and Weber (1980) suggests the maintenance of the earlier status

Table 1. Characters distinguishing between Phaseolus and Macroptilium.[1]

Phaseolus	Macroptilium
Uncinate hairs present	Uncinate hairs absent
Pedicels longer than the calyx	Pedicel length less than or equal to that of the calyx
Floral bracts persistent to anthesis	Floral bracts caducous
Knots of the rachis not swollen	Rachis of inflorescence somewhat knotty at the insertion of the pedicels
Style closely coiled 1.5 - 2 turns	Keel and style closely curved at the tip
Standard with a small marginal indentation and a diffuse central thickening	

1. Translated after Marechal et al. (1978).

based on fruit, seed and seedling characters, none of which were employed by Piper (1926). Conspecificity of *P. wrightii* and *P. filiformis* was suggested by both Kearney and Peebles (1960, p. 484) and Shreve and Wiggins (1964, pp. 729-730).

Phaseolus supinus was not discussed in Marechal et al. (1978), but Marechal (1979c) considered it to be a variant of *M. pedatum*. The relative status of these species is still not clear, primarily due to the rarity of *P. supinus*, which is known from only three localities: the type locality, between Mazatan and Colorado, Sonora, Mexico (Wiggins and Rollins, 1943), Los Ruiz, Nayarit, Mexico (Delgado, 1979), and the vicinity of Sycamore Canyon near the Atascosa Mountains, Santa Cruz County, Arizona.

Interspecific Relationships

The chemotaxonomic study of Kloz, Klozova and Turkova (1966) indicates the relationship of the four cultivated *Phaseolus* species. *P. vulgaris* and *P. coccineus* are closely related, *P. acutifolius* is somewhat less related, and *P. lunatus* is distant. This work agrees with interspecific hybridization studies. The cross *P. coccineus* x *P. vulgaris* and its reciprocal is fairly easily made (Ibrahim and Coyne, 1975). *P. vulgaris* x *P. acutifolius* is more difficult (Honma, 1956), but can be accomplished with aid of embryo culture (Honma, 1955). The hybrid *P. acutifolius* x *P. coccineus* was sterile (Coyne, 1964). Other purported hybrids between *P. lunatus* and *P. vulgaris* (Honma and Heeckt, 1959) and *P. coccineus* x *P. lunatus* (Honma and Heeckt, 1958) are doubted by Smartt (1970).

Few reported hybrids have been obtained between domesticated and wild species. Lorz (1952) obtained a cross between P. lunatus and P. polystachyus, the eastern thicket bean. The hybrid plants were sterile, cytological studies showing six bivalents and 10 univalents (Dhaliwal, Pollard and Lorz, 1962). Braak and Kooistra (1975) succeeded in making the cross P. vulgaris x P. ritensis with embryo culture, despite strong interspecific barriers. The cross P. lunatus x P. ritensis (Le Marchand et al., 1976) produced plants which were semi-fertile. The wild material utilized may actually have been P. metcalfei (Marechal, 1979b). Marechal and Baudoin (1978) obtained P. vulgaris x P. filiformis. The hybrid was vigorous, but sterile, with irregular meiosis.

Germination Habits

Germination habits are not well known, but examples of both epigeal and hypogeal emergence are known in both Phaseolus and Vigna (Verdcourt, 1970).

The emergence of P. acutifolius was reported by Freeman (1918) as epigeal with sessile primary leaves. The seedlings of P. ritensis and P. metcalfei are reported in Nabhan et al. (1980) to have sessile primary leaves and unifoliate leaves at node 3 and petiolate primary leaves and trifoliate leaves at node 3, respectively.

Distribution, Ecology, and Physiology

Plants included in this study range spatially from Arizona to as far south as Argentina and elevationally from sea level to about 8500'

(Kearney and Peebles, 1960; Shreve and Wiggins, 1964; Marechal et al., 1978). Distributions as discussed in the literature are summarized in Table 2.

Wild P. vulgaris survives as a disturbance indicator, or colonizer species (Gentry, 1969). A similar niche is filled by P. acutifolius (Nabhan, 1978), and it is not unreasonable to assume that the entire group studied functions similarly. Growth of P. vulgaris (Gentry, 1969) and P. acutifolius (Nabhan, 1978) are tied to the late summer monsoon season. These plants are opportunistic ephemerals (Nabhan, 1978). Generally, the survival strategy of this group appears to be ephemeralism, either by seed or by a combination of seed and root perennialism (see Table 2).

Pollination Ecology

Within the cultivated Phaseolus species, only P. coccineus outcrosses extensively (Smartt, 1976), other than wild P. acutifolius, which is self-pollinated (Nabhan, 1978). The pollination ecology of the wild species has not been reported in the literature.

Reported Pests and Diseases

As is generally the case with wild plants, the pests and diseases of the southwestern Phaseolinae are not well known. However, P. metcalfei, P. filiformis and P. acutifolius have been screened for disease resistance (Hubbeling, 1957; Coyne and Schuster, 1973). P. metcalfei and P. filiformis were resistant to a plethora of bean

Table 2. Range and growth habit of southwestern Phaseolinae.

Species	Range	Published Elevation	Growth Habit[1]	Source[2]
Macroptilium atropurpureum	Southern Arizona and Texas, south to Ecuador and Peru	4000-5000'	P	b,c,d
Macroptilium heterophyllum	New Mexico and Arizona, south to Argentina	4000-7500'	P	a,b,d
Phaseolus acutifolius	New Mexico and Arizona, south to Guatemala	3000-6000'	A	b,c,d,e,f
Phaseolus angustissimus	Texas, New Mexico, Arizona and Northern Mexico	3500-7000'	P	a,b,d,h
Phaseolus filiformis	Arizona, Sonora and Baja California	1000-3000'	A	a,b,c
Phaseolus grayanus	Arizona, New Mexico and Northern Mexico	5000-8500'	P	b,d
Phaseolus metcalfei	Arizona, New Mexico, West Texas and Chihuahua	6000'	P	a,b,g
Phaseolus parvulus	Northern Mexico, New Mexico and Arizona	6500-8000'	P	a,b,d
Phaseolus ritensis	Arizona, Chihuahua and Sonora	4500-7000'	P	a,b,g
Phaseolus supinus	Southern Arizona, Sonora and Nayarit		P	c,f,h
Phaseolus wrightii	West Texas, New Mexico, Arizona and Sonora	1000-4000'	A	b,h

1. P - Perennial with tuberous root; A - Annual

2. a - Piper, 1926
b - Kearney and Peebles, 1960
c - Shreve and Wiggins, 1964
d - Marechal et al., 1978
e - Nabhan and Felger, 1978
f - Delgado, 1979
g - Nabhan et al., 1980
h - Based on specimen in University of Arizona Herbarium

diseases. P. acutifolius is the standard against which other beans are tested for resistance to common bean blight (Coyne and Schuster, 1973). The resistance of P. acutifolius has been transferred into commercial varieties of P. vulgaris (Coyne and Schuster, 1974). Seed damage to P. metcalfei by bruchid beetles was reported by Nabhan et al. (1980).

Physiological Adaptation

Studies of the "fit" of physiology to habitat are uncommon, for wild plants, particularly beans. Klikoff (1965), studying three California timberline meadow dominants, found that temperature and drought-tolerance adaptation, as measured by photosynthesis, paralleled the habitat conditions where each species occurred. Patten and Dinger (1969) had a similar finding with three Arizona hedgehog cacti (Echinocereus spp.). Thompson (1970) reported that temperature responses for seed germination must be closely linked with the ecological requirements of a habitat in order for a given species to establish and survive.

Macroptilium atropururem has an efficient, two-stage stomatal control mechanism which results in a high degree of drought avoidance (Ludlow and Ibaraki, 1979). P. ritensis is more drought-tolerant than P. lunatus (Suy, 1978), and the interspecific hybrid was intermediately drought-resistant. Smartt (1978) reported that the ecological range of teparies (P. acutifolius) is narrow, with a small germplasm base. Yields of over 2000 kg/ha for 2 years at 45°N latitude in Minnesota (Alvarez, Davis and Ascher, 1980) and 4000 kg/ha for July-planted teparies in Missouri (Buhrow, 1980), in addition to a wild range which extends for 1800 miles (Nabhan and Felger, 1978), put serious doubt as to the validity of Smartt's statement. Forbes, in Freeman (1918), stated:

> Teparies, the native beans of the region, are among the most valuable of these (southwest Indian) crops. Germinating quickly, enduring severe drought, setting seed in the hottest and driest weather, maturing in less time than ordinary beans and capable of producing two crops annually on the same ground, they are peculiarly well fitted to the region in which they survive.

Thomas and Waines (1980) found that teparies rooted to twice the depth of common beans grown under similar conditions.

Reproduction

The Phaseolinae being tropical in origin, are commonly short day plants. Allard and Zaumeyer (1944) found short day lengths were either required for flowering or promoted flowering in varieties of *P. vulgaris*, *P. lunatus* and *P. acutifolius*. Flowering of *P. coccineus* was promoted by long days. Hartman (1969) found photoperiodism in only *P. lunatus* and *P. vulgaris*, both responding to short days. Temperature often interacts with day length to influence the period of flowering. Padda and Munger (1969) found that flowering in *P. vulgaris* under long days and under different temperature regimes varied with variety, some promoted by low and others by high temperatures. Coyne (1978) found that high night temperatures delayed flowering in his photoperiod sensitive *P. vulgaris* lines. The combination of high day temperature with low night temperature resulted in most rapid flowering in *Gossypium hirsutum* (Mauney, 1967). High night temperature reduces podset in *P. lunatus* (Fisher and Weaver, 1974).

Germination Physiology

Impermeable Seed Coats

Hard seed is widespread in the Leguminosae (Barton, 1965). Kaplan (1965) stated that the seeds of wild (bean) species (*M. heterophyllum* and others) are 100% impermeable and remain so for periods of more than a year. In *P. vulgaris*, the major water entry area is either the raphe or the micropyle, depending upon cultivar, and to a lesser extent, the hilum. The hilum acts as a one-way hygroscopic valve, which allows the seed to equilibrate to the driest environment it has experienced (Harper, 1977).

Temperature Relations

In a review of earlier works, Edwards (1932) described the typical germination response for plants as an initial rapid germination at a relatively high temperature, followed by a shift to lower temperature for maximum germination. Lang (1965) discussed the earlier work of Sachs (1860), who introduced the concept of the cardinal points of temperature for plant growth, namely the optimum, the lethal maximum, and the lethal minimum temperature. Actually, for germinating seeds, a better term would be the thermal dormant or simply dormant minimum, since seeds which are moved to higher temperatures will generally germinate immediately. The cardinal optimum for germination shifts to lower values with time for many species (Lang, 1965). The width of the temperature interval for germination often increases with seed age. This is a manifestation of postharvest dormancy, and is due primarily to the presence of inhibitors (Lang, 1965). The effect of diurnal temperature fluctuation generally promotes both the speed of germination and high total germination (Lang, 1965).

Variation in temperature response within a single species is documented for Tsuga canadensis (Stearns and Olsen, 1958). Seeds of northern provenance had a lower optimum germination temperature than seed from southern sources. Temperature responses of weeds and cultivated plants are not known to vary with variety or source. Wilson (1928) found that various wheat varieties had the same cardinal germination temperatures. Collections of the weed Agrostemma githago from various European localities did not vary in germination response (Lauer, 1953; Thompson, 1973). Thompson (1972) stated that although little difference exists between germination response within a given crop, low temperature selection for germination has been effective in corn, sugar beets and onions.

Stomate Density

Stomate density has been found to vary with light intensity and duration, temperature, soil water status, and nutritional status of the plant. Cole and Dobrenz (1970) found that stomate density increased with leaf position in alfalfa. Stomate density on adaxial surface increased to node 7, then decreased in two soybean cultivars (Lugg and Sinclair, 1979). Leaves adjacent to the inflorescence of blue panicgrass had a low stomate density, compared to that of lower leaves (Dobrenz et al., 1969). Low stomate density was also associated with seedling drought tolerance. Sunflowers exhibit a higher stomate density when grown in full sun than when grown in shade (Penfound, 1931). Dry conditions increased stomate density due to less leaf expansion. The shade leaves of _Impatiens parviflora_ have epidermal cells which are much more convoluted than the sun leaves (Hughes, 1959). Meristematic activities of sun and shade leaves were similar, differences being attributed to greater expansion of shade leaves. Zelitch (1963) reported that stomate density is increased by high light intensity and long day length. Temperature seemed to have no effect on density, but high temperatures reduced functionality of stomates produced. This effect is confirmed by McCree (1974) for sorghum.

Freeland (1948) found little direct correlation between stomatal distribution and photosynthesis for many species. Miskin, Rasmusson and Moss (1972) found that barley plants with low stomate density transpired less water, but photosynthesis was not affected.

CHAPTER 3

MATERIALS

Of the 11 species presented in the study area, only two were available in USDA repositories in 1978 (Hudson, 1978). The collection of the various species was imperative for the completion of this project. Some seeds were obtained from Gary P. Nabhan and Dr. Robert E. Dennis, both members of the University of Arizona Plant Sciences Department at the onset of this study. The remainder were collected by the author.

Collection Methods

Habitats favorable for beans are generally mountainous with few good roads. Areas too difficult for automobile travel were collected from a trail motorcycle or on foot. Generally, the "road hunter" technique was useful to locate populations. This technique consisted of driving slowly along the highway watching for flowers or plants. Usually the largest and healthiest plants grow in disturbed areas, such as roadcuts, making them easy to locate, once the eye becomes trained. After a population was located, seeds were gathered on foot.

Collections were generally taken in the following manner. A representative sample of seeds was gathered from the area. Herbarium specimens showing representative plants were pressed. Plants were dug using an Estwing rock bar and hand sledge. This combination was particularly effective in rocky slopes and where the plants actually grew from cracks in outcrops and cliffs. Digging generally revealed an abundance of nodules on the smaller roots. Soil samples were stored in plastic bags and all relevant data recorded. Samples collected in this manner and used as innoculant produced abundant nodulation on species of beans present in the collected area (Burton, 1979).

Materials Utilized

Seeds collected were increased under field conditions at the University of Arizona Campbell Avenue Farm (CAF). Seeds were planted in a greenhouse and transplanted to furrow-irrigated field plots. Water was supplied as needed, and weeds were controlled by hand and mechanical means. Pods, which ripened irregularly, were hand-harvested at maturity and hand-threshed. Collections utilized in this study are listed in the appendix. Examples of these species are illustrated in Fig 1.

Fig. 1. Photographs of living specimens of southwestern Phaseolinae.

a. *Phaseolus filiformis* at the CAF.

b. *Phaseolus wrightii* growing on a vertical cliff along the Apache Trail, AZ, 700 m (2300 ft.).

c. *Phaseolus acutifolius* var. *latifolius* growing on volcanic talus, Sycamore Canyon, Atascosa Mtns., AZ, 1160 m (3800 ft.).

d. *Phaseolus supinus* growing in encinal vegetation, Sycamore Canyon, Atascosa Mtns., AZ, 1160 m (3800 ft.).

e. *Phaseolus supinus* from Fig. 1.d, removed to show plant form, Sycamore Canyon, Atascosa Mtns., AZ, 1160 m (3800 ft.).

f. *Macroptilium atropurpureum* at the CAF.

g. *Phaseolus acutifolius* var. *tenuifolius* at the CAF.

h. *Phaseolus angustissimus* at the CAF.

i. *Macroptilium heterophyllum* at the CAF.

j. *Phaseolus ritensis* at the CAF.

k. *Phaseolus metcalfei* growing from a roadcut along the Tombstone-Pierce road, Dragoon Mtns., AZ, 1830 m (6000 ft.).

l. *Phaseolus grayanus* growing in a semi-open *Pinus ponderosa*, evergreen *Quercus spp*. forest, Oracle Ridge, Santa Catalina Mtns., AZ, 2410 m (7900 ft.).

m. *Phaseolus parvulus* in habitat, General Hitchcock Campground, Santa Catalina Mtns., AZ, 1810 m (5940 ft.).

Fig. 1a.

Fig. 1b.

Fig. 1c.

Fig. 1d.

Fig. 1e.

Fig. 1f.

Fig. 1g.

Fig. 1h.

Fig. 1i.

Fig. 1j.

Fig. 1k.

Fig. 11.

Fig. 1m.

CHAPTER 4

SEEDS, SEEDLINGS, AND GERMINATION PHYSIOLOGY

Seed size affects seedling vigor, and determines, to an extent, the number of propagules a given plant may produce. Given equal amounts of photosynthate available for reproduction, a large seed producing plant produces fewer seeds than a small seeded one. Large differences exist between the seeds of the various species studied with respect to size, shape and texture.

The seedling morphology of the southwestern Phaseolinae has generally been neglected, except for _P. acutifolius_ (Freeman, 1918), _P. metcalfei_, and _P. ritensis_ (Nabhan et al., 1980). The seedling characters that exist are often diagnostic and important, especially in closely related species with small vegetative differences.

Studies of germination temperature responses should give a reasonable approximation of the range of thermal adaptation for various species. This information should be of use to plant breeders to assist in selecting wild species, which possess the ability to germinate under either unusually hot or cold conditions, for use in interspecific hybridization programs with domesticated species.

Methods

Seed Weight

Ten seed samples of various bean collections growing under assorted conditions were weighed to the nearest two-hundredth of a gram. Ten samples of each collection were weighed. Overall statistical differences were determined using Duncan's multiple range test. Significance of differences between identical collections grown under different conditions was determined using the Students t test.

Seedling Morphology

Seeds were scarified and planted in potting soil in pots. Approximately 2 weeks after planting at about 23°C, seedlings were observed for various morphological characters shown in Fig. 2.

Germination Physiology

Impermeable Seed Coats. Seeds of various collections were placed in dessicators with 0% relative humidity, maintained by P_2O_5 slurry (Winston and Bates, 1960) for a period of 15 days at ambient temperature (23°C) to induce maximum impermeability. Seeds were immersed in water for 48 hours, after which the number of imbibed and hard seeds was recorded. Due to limited numbers of available seeds for many of the species tested, statistical analysis was not utilized.

Effect of Temperature. Scarified seeds were analyzed on a one-way thermogradient plate, as described by Larsen (1971), except that

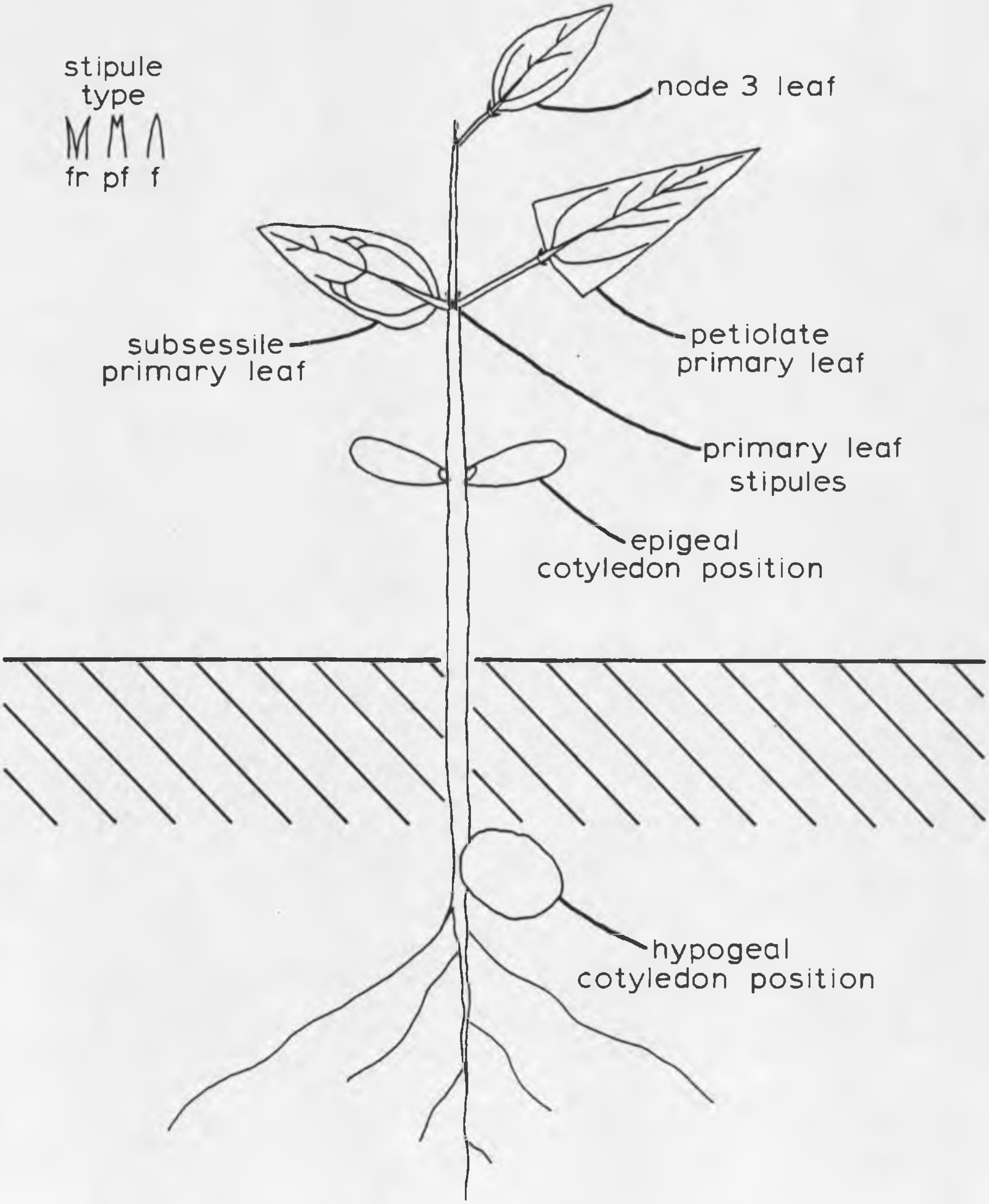

Fig. 2. Composite drawing of morphological characteristics of beans.

planting was in covered petri dishes (Falcon, 1012), placed on the thermogradient surface, with blotter paper cut to fit. This technique resulted in more even water distribution, particularly in the warmer regions of the plate, which have a tendency to dry out rapidly. Seeds were placed in equidistant rows (from 35 to 49 rows, depending upon seed size and quantity) perpendicular to the gradient. Gradient temperatures utilized ranged from 3.8 to 46 $\pm$ 1°C.

Germination was defined as radicle length greater than or equal to length of the major axis of the imbibed seed. Moisture levels were monitored twice and germination recorded once daily. Each sample was allowed 7 days for germination, which is adequate, since very little germination occurred after 5 days. Data were analyzed graphically, using the moving "average of 3" (Larsen and Skaggs, 1969). Germination was graphed only at initial response, 2 days, and 7 days to retain clarity.

Results and Discussion

Seed Weight

Seeds of the various species are illustrated in Fig. 3. The results of the overall study are presented in Table 3. It is interesting to note that there has been a 56-fold divergence of seed weight within the group studied. Seed size appears to be a relatively plastic trait within many species. Collections of *P. wrightii* and *P. filiformis* showed very highly significant increases in seed weight when grown under cultivation compared to the same populations in the wild. These

Fig. 3. Seeds of southwestern Phaseolinae.

a. Seeds of Phaseolus filiformis, collection BCFI. -- Small squares = 1 mm^2.

b. Seeds of Phaseolus wrightii, collection ATWRI. -- Small squares = 1 mm^2.

c. Seeds of Phaseolus acutifolius; columns from left to right, UNACCI, SYACL, SBACL, MBAC. -- Small squares = 1 mm^2.

d. Seeds of Phaseolus supinus, collection SYSU. -- Small squares = 1 mm^2.

e. Seeds of Macroptilium atropurpureum, collection UNAT. -- Small squares = 1 mm^2.

f. Seeds of Macroptilium heterophyllum var. rotundifolium, collection MHHTR. -- Small squares = 1 mm^2.

g. Seeds of Phaseolus angustissimus, top row, SAAN; bottom row, SCAN. -- Small squares = 1 mm^2.

h. Seeds of Phaseolus ritensis, rows from top to bottom; PMRI1, WHRI, SRRI. -- Small squares = 1 mm^2.

i. Seeds of Phaseolus metcalfei, top row, CMMT2; bottom row, PAMT. -- Small squares = 1 mm^2.

j. Seeds of Phaseolus grayanus, top row, CMGR1; bottom row, ORGR. -- Small squares = 1 mm^2.

k. Seeds of Phaseolus parvulus, collection ORPR. -- Small squares = 1 mm^2.

Fig. 3a.

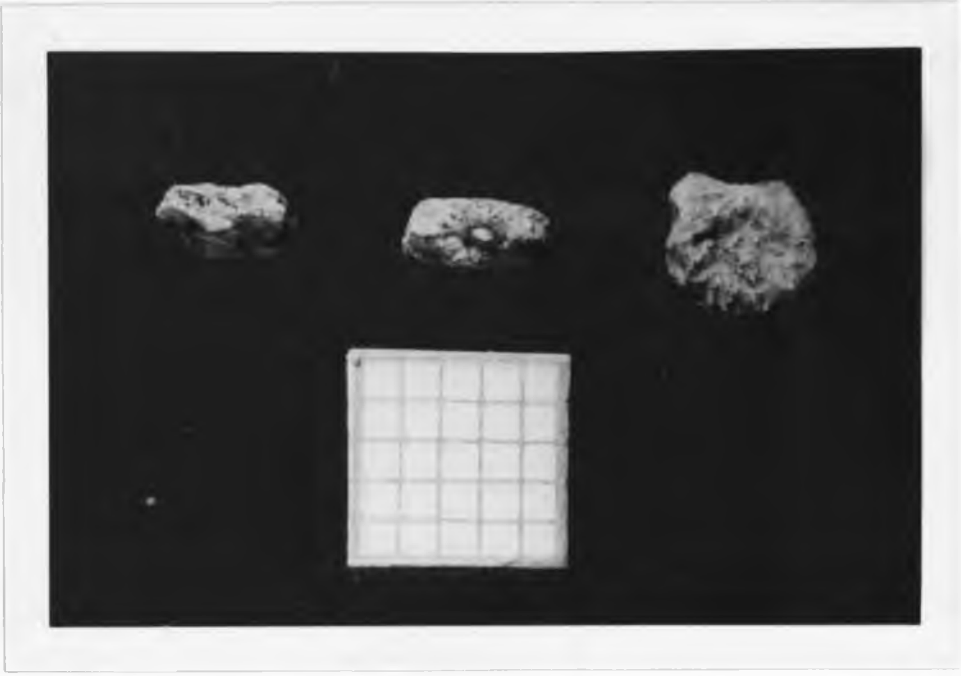

Fig. 3b.

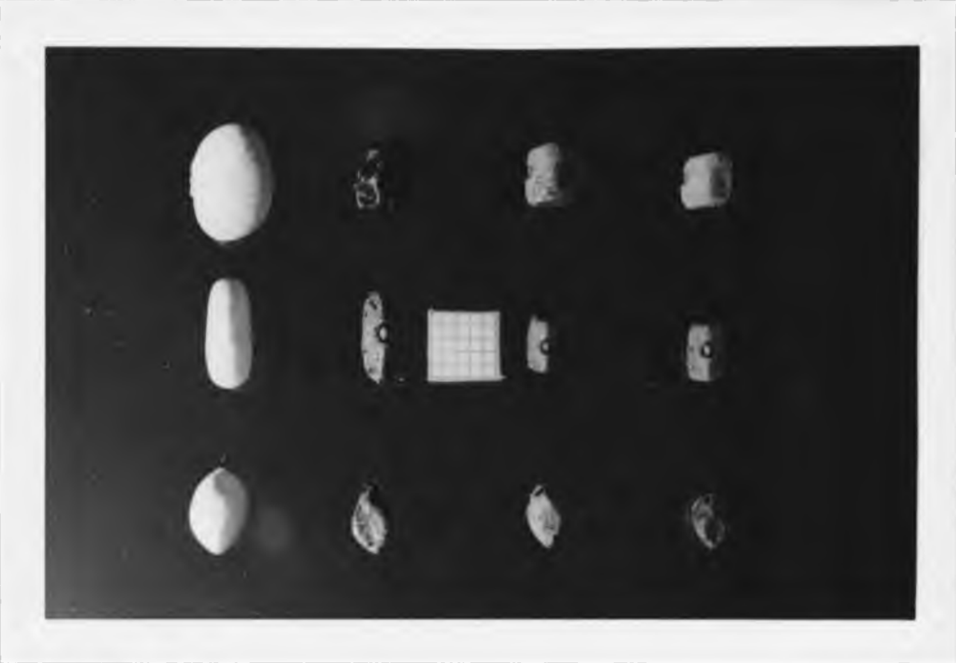

Fig. 3c.

Fig. 3d.

Fig. 3e.

Fig. 3f.

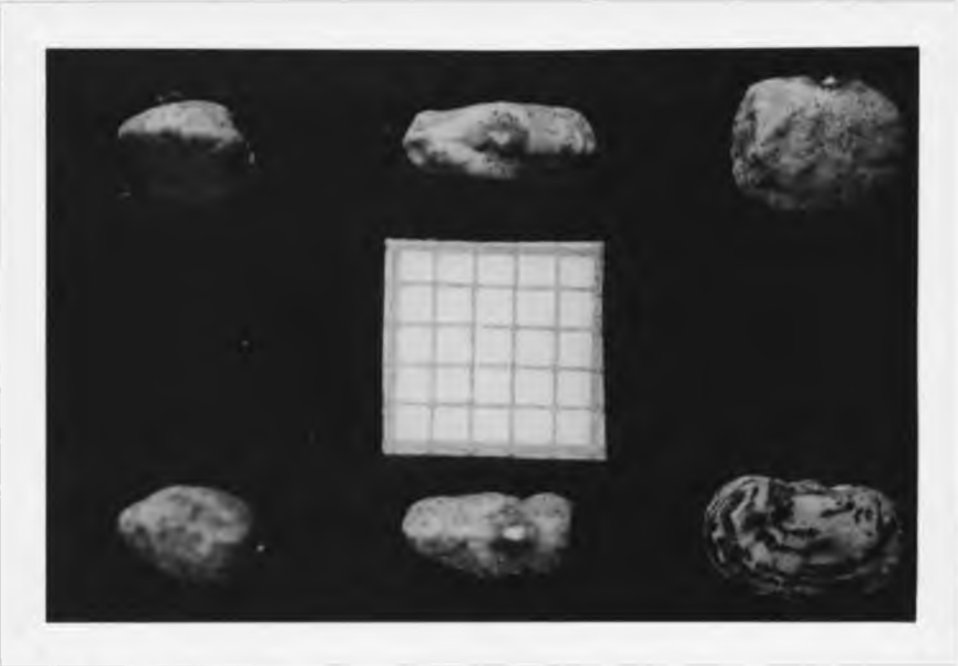

Fig. 3g.

Fig. 3h.

Fig. 3i.

Fig. 3j.

Fig. 3k.

Table 3. Bean seed weights based on population, locality, and growth conditions.

Species	Collection[1]	Year	Growth Conditions[2]	Mean Weight 10 Seeds (g)	Statistical Grouping[3]
Phaseolus parvulus	BPPR	1978	w	.051 ± .002	a
P. filiformis	BCFI	1978	w	.069 ± .007	a
Macroptilium heterophyllum var. *rotundifolium*	MHHTR	1979	f	.074 ± .008	a
P. wrightii	ATWR7	1978	f	.090 ± .010	ab
P. wrightii	ATWR1	1978	w	.091 ± .013	ab
P. filiformis	BCF1	1979	f	.099 ± .009	ab
P. wrightii	RTWR	1978	f	.118 ± .009	ab
M. atropurpureum	UNAT	1978	f	.118 ± .030	ab
P. supinus	SYSU	1980	g	.119 ± .005	ab
P. wrightii	ATWR1	1978	f	.125 ± .009	ab
P. angustissimus	SCAN	1979	f	.154 ± .013	b
P. acutifolius var. *tenuifolius*	MBAC	1978	f	.241 ± .010	c
P. acutifolius	MBAC12	1978	w	.269 ± .019	c
P. acutifolius var. *tenuifolius*	MBAC12	1978	f	.280 ± .011	c
P. acutifolius var. *latifolius*	SBACL	1979	g	.297 ± .018	c
P. ritensis	WHRI	1979	w	.441 ± .051	d
P. acutifolius var. *latifolius*	SYACL	1979	f	.527 ± .024	e
P. ritensis	SRRI	1978	f	.596 ± .074	f
P. grayanus	ORGR	1979	w	.664 ± .124	g
P. acutifolius domesticate	UNACC1	1978	f	1.308 ± .061	h
P. metcalfei	CMMT2	1979	f	2.181 ± .151	i
P. metcalfei	PAMT	1978	f	2.864 ± .262	j

1. Appendix.

2. w = wild; f = field-grown, Tucson, AZ; g = growth chamber.

3. Any means followed by the same letter are not significantly different at the .05 level, according to Duncan's multiple range test.

increases may be attributable to decreased competition and increased water availability under cultivation. This phenomenon was not observed, however, with the _P_. _acutifolius_ var. _tenuifolius_ collection. No significant differences were noted between wild and field-grown seed weights. This could be the result of heat stress counteracting the beneficial effects of reduced competition. Nabhan (1978) noted a decrease in seed weight of var. _latifolius_ under cultivation. The broad-leafed type SBACL differs significantly from other var. _latifolius_ collections, having no significant difference in seed weight from var. _tenuifolius_ collections. It should be noted that the SBACL seed utilized in this study was not grown under the same conditions as the var. _tenuifolius_ collections. Field-grown seeds of SBACL appear, however, to be very close in size to other var. _tenuifolius_ grown under identical conditions.

Population differences within the same species were observed in _P_. _metcalfei_ and _P_. _ritensis_, although the differences observed in _P_. _ritensis_ may actually reflect growth condition differences. Differences in seed size have also been observed between wild populations of _P_. _grayanus_, _P_. _acutifolius_, _P_. _ritensis_, and _P_. _metcalfei_ not included in this study.

Seedling Morphology

The results of this study are presented in Table 4. The most consistent characters were emergence type and primary leaf petiole length. The annual species all exhibited the epigeal cotyledon

Table 4. Bean seedling morphology, emergence type and growth habit.

Species	Primary Leaf Stipules[1]	Primary Leaf Petiole[2]	Primary Leaf Shape	Node 3 Leaflet Number	Emergence	Growth Habit[3]	Collections[4]
P. acutifolius tenuifolius	PF, F	S	Deltoid-lanceolate	3	E	AN	MBAC, SRAC
P. acutifolius latifolius	PF, F	S	Deltoid	3	E	AN	SBACL, UNACC1, SYACL
P. grayanus	F, PF	P	Sagittate, deltoid	3,rarely 1	H	PR	ORGR, CMGR1
P. wrightii	F	P	Cordate	3	E	AN	OPWR, ATWR7, RTWR
P. filiformis	F	P	Cordate	3	E	AN	BCF1
P. ritensis	F, PF	S	Ovate, lanceolate	1	H	PR	PMR1, SRR1, CHR1, WHR1
P. metcalfei	FR	P	Deltoid	3	H	PR	SMMT2, PAMT, DRMT
P. angustissimus	F	P	Ovate-lanceolate, base cordate	3	H	PR	SCAN, SAAN
P. parvulus	PF	S	Ovate-lanceolate	3	H	PR	BPPR, ORPR
P. supinus	PF, F	P	Ovate-lanceolate	3	H	PR	SYSU
M. heterophyllum	F	P	Ovate, cordate	3	H	PR	CMHT, SYHT
M. heterophyllum rotundifolium	F	P	Cordate	3	H	PR	MHHTR
M. atropurpureum	F	P	Cordate	3	Barely E	PR	UNAT

1. F, fused to tip; PF, partially fused; FR, free.
2. S, sub sessile; P, petiolate; E, epigeal; H, hypogeal.
3. AN, annual; PR, perennial.
4. Appendix.

character. The perennials were hypogeal, except for _M. atropurpureum_, which actually exhibits an intermediate type of emergence, though slightly epigeal. One would suspect that emergence type is important in establishing root perennialism, at least within the group studied. The placement of a node below the surface of the ground due to hypogeal germination could be the reason for this phenomenon.

The node 3 leaflet number functions well as a distinguishing factor in all _P. ritensis_ and _P. metcalfei_ populations so far observed, as is petiole length. _P. wrightii_ and _P. filiformis_ are indistinguishable as seedlings, adding support to possible conspecificity. The varieties of _P. acutifolius_ are easily distinguishable from each other by differences in primary leaf width. Varieties of _M. heterophyllum_ are indistinguishable as seedlings.

Germination Physiology

Impermeable Seed Coats. The results of this test are presented in Table 5. There appears to be a tendency for increased hard seed coats within the genus _Macroptilium_ relative to _Phaseolus_. A statistical test involving _P. supinus_ (actually a _Macroptilium_) and others such as _M. pedatum_ as well as the species studied here compared to a sampling of _Phaseolus spp_. from the same general region should prove to be enlightening. The hard seed percentage of 97.8 for _M. heterophyllum_ compares favorable with that of Kaplan (1965), but many of the other species do not. Considerable variation in hard seed coats exists within _P. vulgaris_ (Kyle and Randall, 1963), and it would not be surprising to

Table 5. Hard seed percentage in various bean collections.

Species	Collection[1]	Habitat[2]	Sample Size	% Impermeable
Phaseolus acutifolius domesticate	UNACCI		90	7.7
P. filiformis	BCFI	d	100	40.0
P. ritensis	SRRI	e, o	45	40.0
P. angustissimus	SCAN	e, o, p	45	62.0
P. acutifolius var. latifolius	SYACL	d, e	90	78.9
P. metcalfei	PAMT	o	27	81.0
P. acutifolius var. tenuifolius	MBAC	e, o	90	86.7
P. wrightii	ATWRI	d	90	90.0
P. grayanus	ORGR	o, p	45	93.3
Macroptilium heterophyllum var. rotundifolium	MHHTR	e	90	97.8
M. atropurpureum	UNAT	o	90	98.7

1. Appendix.

2. d = desert; e = oak savanna; o = oak woodland; p = pine forest.

find similar variability in the related *Phaseolus spp*. From the data, it is not obvious that any clear trend exists as to relationship of habitat to amount of hard seed in a given species.

Other Types of Dormancy. Observation of the southwestern Phaseolinae over 3 growing seasons resulted in the conclusion that other types of dormancy are relatively unimportant within this group. Planting immediately after harvest resulted in complete germination with *P. acutifolius*, *P. wrightii*, *P. filiformis* and *P. metcalfei*. Germination within ripe pods in contact with soil after rains or irrigation has occurred in the field with *P. wrightii*, *P. filiformis*, *P. acutifolius*, *P. metcalfei* and *P. ritensis*.

Effect of Temperature. Fig. 4 shows germinating seeds (UNAT) on the thermogradient. Germination responses are illustrated in Fig. 5. Species are listed relative to optimum elevation (see Chapter 8, Fig. 10), with high altitude species at the top and low elevation species at the bottom.

The curves from this study follow completely the pattern discussed by Edwards (1932) and Lang (1965). There was a rapid initial germination at relatively high temperatures, followed by a gradual shift to lower temperatures for maximum germination with time.

The most obvious differences in germination response between species are the decrease of early optimum temperature, and particularly, the decrease in the lethal maximum with increase in elevation. This is as would be expected, since the temperatures at high altitudes are

Fig. 4. Thermogradient plate shown with cover removed. -- (a) Seeds shown in the center column are Macroptilium atropurpureum; (b) Closeup of center of Fig. 4a.

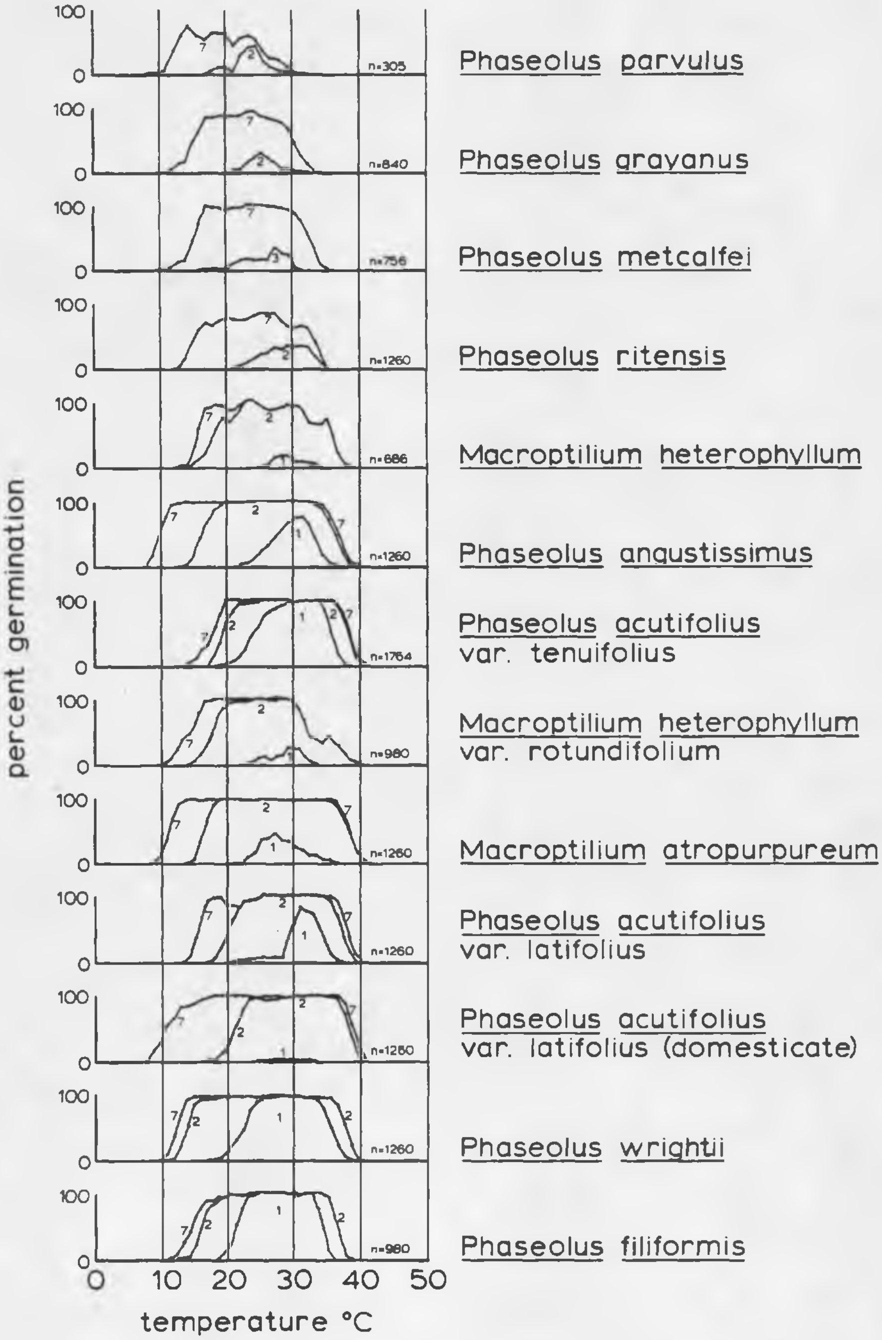

Fig. 5. Effect of temperature upon germination of southwestern Phaseolinae. -- Numbers near germination response lines indicate number of days.

considerably lower than those at lower elevations, and these plants generally grow during the same period, specifically the summer monsoon season.

Seeds of relatively arid environments (*P. filiformis*, *P. wrightii*, *P. acutifolius*, *P. angustissimus*, *M. heterophyllum* and *M. atropurpureum*) germinated much more rapidly than seeds of species adapted to more mesic environments (*P. ritensis*, *P. metcalfei*, *P. grayanus*, *P. parvulus*). The extreme examples of germination speed are seen in *P. wrightii* and *P. filiformis*, which at favorable temperatures will have essentially complete germination 18 hours after the seeds have been exposed to moisture. The very slow germination of *P. metcalfei* which was recorded resulted in part from a 1-day delay of seed inhibition, due to the large size and round shape of these seeds.

The width of the response curve is a measure of specificity of germination seasonality. The species with pronounced biseasonality (*P. wrightii*, *P. angustissimus*, and *P. filiformis*) all have a relatively wide germination temperature range (about 25 to 30°C). The spring germination of *P. acutifolius* wild forms appears to be prevented by a low temperature dormancy mechanism. This appears to have been selected against in domesticated *P. acutifolius*, which germinates at low temperatures comparable to high altitude and biseasonal species (*P. parvulus*, *P. angustissimus*). The high altitude species (*ritensis* and above on Fig. 10) have narrower germination temperature ranges (about 20°C) than other species from lower regions, excepting *P. acutifolius* var. tenuifolius. Apparently, there is a selective advantage to having a more restricted germination response to temperature in these areas, where growing season length is limited more by frost than water availability.

CHAPTER 5

REPRODUCTION

Reproduction of the southwestern Phaseolinae is controlled by a complex of environmental factors including day length, temperature and water availability. Generally, seed production follows the summer rainy season, with notable exceptions. Most of the species studied are attractive to insects, producing both pollen and nectar. In wild populations, insect visitation seems to be lower than in the same species under cultivation, possibly because of the more dispersed nature of wild stands, and also the increased competition from other plants, both for water and pollinators.

Herbarium Study

A study was conducted with dried specimens at the University of Arizona Herbarium (ARIZ) to determine the approximate times of flowering and fruiting of Phaseolinae found within and near Arizona. Specimens were rated for presence or absence of flowers, set fruit, immature fruit, mature fruit, and dehisced fruit. If a particular fruiting stage was especially abundant, this was noted. Specimen dates were grouped into 1-week periods and plotted to delineate peaks of flowering and fruiting. Probably due to the cryptic nature of the Phaseolinae when not in bloom, most specimens are collected from flowering, rather than fruiting specimens. This resulted in rather fragmentary data for fruiting except for the more common, well-collected species. The curves also include observations from the subsequent section.

Fig. 6 shows the results of this study. It is notable that members of the filiformis group, including _P. filiformis_, _P. wrightii_, and _P. angustissimus_ (Piper, 1926) are quite adaptable in their flowering responses. The spring peaks correspond to a period of increasing temperatures and continued water availability from winter and early spring precipitation. The summer peak corresponds to the summer rainy season, which all of the species studied can utilize. It is important to note that although no summer maximum is shown for _Phaseolus wrightii_, it is probable that such a peak of flowering occurs in years with adequate summer rainfall. Specimens from Texas and New Mexico, and Arizona material under cultivation in Tucson all have the ability to complete their life cycles during this period.

Live Material Study

Plants growing under growth chamber, field, and natural conditions were observed irregularly throughout the growth periods of the species studied. Notes were taken as to growth conditions, stage of growth, flowering, insect visitation, fruiting and senescence. The results of this study are summarized in Table 6.

The day length sensitivity data are valid to 14 hours 20 minutes, the maximum day length at Tucson, Arizona. For _P. acutifolius_, day length sensitivity varies with collection locality in the wild and with

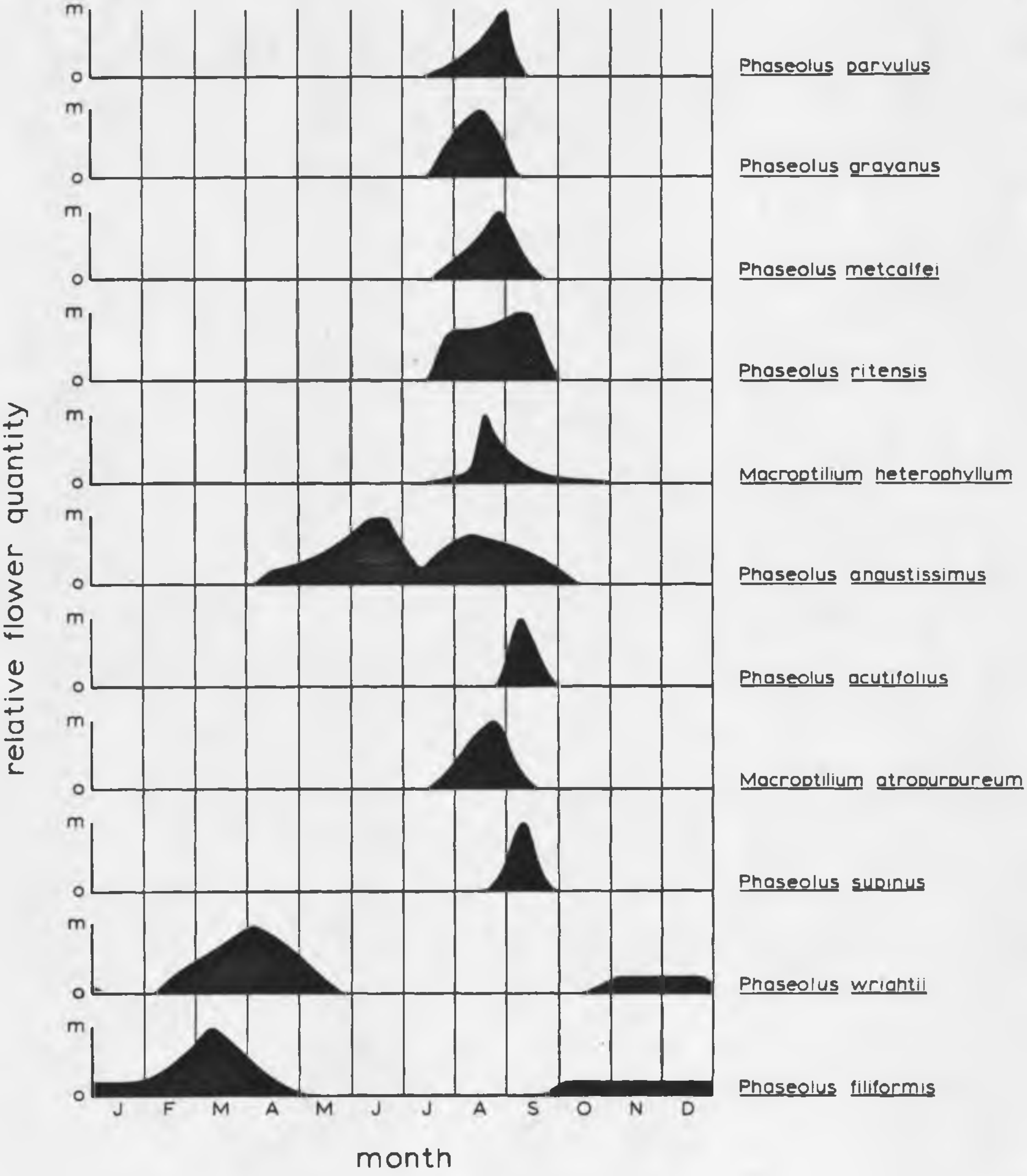

Fig. 6. Flowering of southwestern Phaseolinae. -- M = maximum; 0 = none.

Table 6. Daylength sensitivity, insect visitation and heat tolerance for fruitset of southwestern Phaseolinae.

Species	Day Length Sensitivity	Max. Day Length for Flowering If Known	Ability to Pollinate Shown by Insect-Free Environment	Attractiveness To Pollinators[1]	Flower Color[2]	Fruitset in Hottest Weather >100°F (100-110°) Daytime High
Phaseolus acutifolius var. *latifolius* - domesticates	+ -	Variable	+	L (under favorable cond. H)	W,LV	Reduced
Phaseolus acutifolius var. *latifolius* - wild	+	Variable AZ types-13 hr	+	L	LV	Reduced
Phaseolus acutifolius var. *tenuifolius*	+	Variable AZ types-13 hr	+	L	LV	Reduced
P. angustissimus	-			M	P	Reduced
P. filiformis	-		+	H	P	Normal
P. grayanus	?			M	P	None
P. metcalfei	+?			M	P	Low (see text)
P. parvulus	+	13.5 hr	+	?	P	None
P. ritensis	+?			M	P	Reduced
P. supinus	+	13 hr	+	?	O	Unknown
P. wrightii	-		+	H	P	Normal
Macroptilium atropurpureum	-			H	B	Normal
Macroptilium heterophyllum	-			H	O,Y (rare)	Normal

1. H - Highly attractive; M - moderately attractive; L - Low to unattractive.

2. B - Purplish black; LV - light lavender; O - orange; P - various shades of pink; W - white; Y - lemon yellow.

cultivar. Day-neutral types are found rarely in wild tepary populations. The reproduction of _P. metcalfei_ and _P. ritensis_ suggests an interaction between day length and temperature tolerance for seed set. In wild populations, fruitset begins in early August (day length 13 hr 40 min). However, in Tucson, under a higher temperature regime, pod retention does not begin until early September for _P. ritensis_ and about September 20 for _P. metcalfei_. Similar temperatures for both August and September in the 1979 study implies that high temperature tolerance for seed set increases as day length decreases.

Insect Visitation

Attractiveness to pollinating insects is shown in Table 6, and documented insects on flowers of bean species is shown in Table 7.

Species studied which are attractive to insects are also good producers of nectar, as evidenced by the high visitation by nectar-gathering honey bees. Further, the field was often filled with the sweet smell of _P. wrightii_ nectar on hot summer days. The visitation by pollinating insects, particularly Hymenoptera, indicates that a fairly high degree of outcrossing is possible in entomophilous species.

Single plant collections of seed from wild populations of _P. ritensis_, attractive to insects, and _P. acutifolius_, unattractive to insects, illustrate this phenomenon. _P. ritensis_ grown at Campbell Avenue Farm were found to be segregating for several seed coat characters and for leaflet shape and size. Wild _P. acutifolius_ was found to breed true for all observed characters over two growing seasons.

Table 7. Insect visitation of southwestern Phaseolinae flowers at Tucson, Arizona, 1980.

Order	Family	Species	Common Name	Documented Phaseolinae Visitation[1]
Hymenoptera		*Polistes exclamans arizonensis* Snelling.	Paper wasp	AT
	Halictidae	*Lasioglossum* (Chloralictus)		WR
		Nomia tetrazonata Ckll.		HT
	Megachilidae	species "C"		WR
		Megachile sp. "A"	Leaf cutter bee	AT, WR, HT
		Megachile sp. "B"	Leaf cutter bee	HT, WR
	Anthophoridae	*Xylocarpa californica arizonensis* Cresson.	Carpenter bee	AT, HT
		Centris sp.		WR
	Apidae	*Bombus sonorus* Say.	Sonoran bumble bee	HT, AT, MT, RI, WR, FI
		Bombus sp.	Bumble bee	GR
		Apis mellifera L.	Honey bee	HT, AT, MT, RI, AC, AN, FI
Coleoptera		*Collopsis* sp.		WR
Lepidoptera		*Pyrgus communis* Grote.		HT
		Lerodea eufala Edwards.		HT
		Colias eurytheme Boisduval.		HT
		Hemiargus ceranus gyas Edwards.		AT

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[1] AC - *P. acutifolius*; AN - *P. angustissimus*; AT - *M. atropurpureum*; FI - *P. filiformis*; GR - *P. grayanus*; HT - *M. heterophyllum*; MT - *P. metcalfei*; RI - *P. ritensis*; WR - *P. wrightii*.

Domesticated teparies are occasionally very attractive to honeybees, and segregation for seed color characters, flower color, and stem color have been observed (Fig 7).

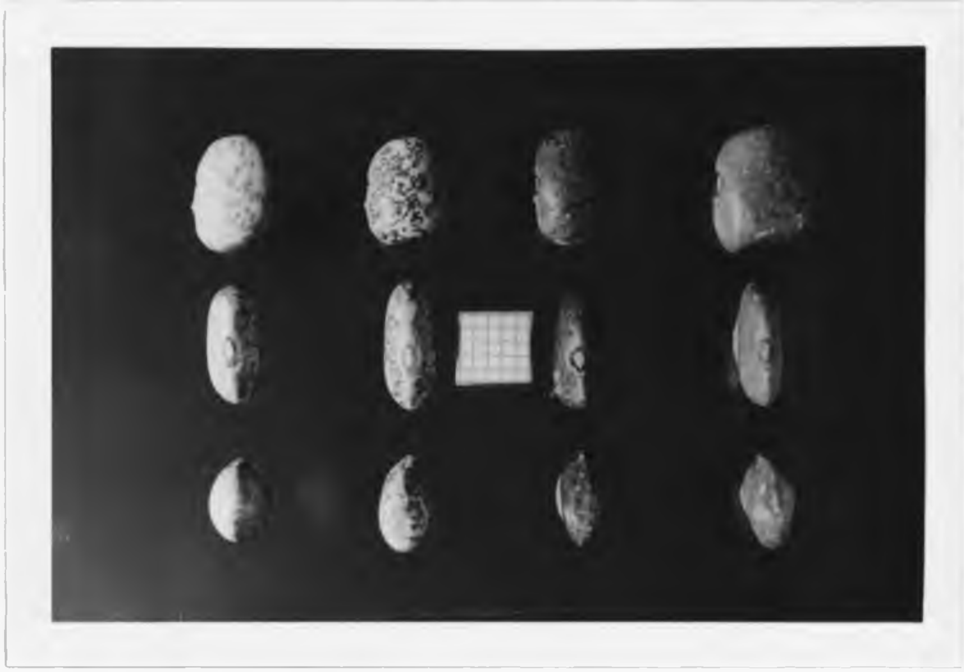

Fig. 7. Segregation of seedcoat color in domesticated Phaseolus acutifolius. -- The two left columns represent the variation of the parent line; the right two columns show seeds of offspring.

CHAPTER 6

LEAF ANATOMY

A study of leaf anatomy was conducted to determine the relationships between environmental adaptation and leaf structure of the southwestern Phaseolinae. Stomate densities and sizes were recorded, and other general observations were noted.

Methods

Samples of mature leaves were collected from seed increase plots at the University of Arizona Campbell Avenue Farm if available. The remaining samples were taken directly from the wild or from growth chamber grown specimens, as noted in Table 8. Specimens were fixed in Craf III or FAA, dehydrated and infiltrated through a TBA, toluene, Paraplast series (Berlyn and Miksche, 1976). Permanent slides were prepared and stained with aniline blue and safranin. Stomate densities were determined using a calibrated microscope field diameter for individual counts. The minimum total area was .16 mm^2, except for replication two of _M_. _atropurpureum_ which had an area of .087 mm^2. For most species and replications, the area measured was about .40 mm^2. The two fixative types were run as replications for this test. Stomate sizes (guard cell major axis) were measured with an eyepiece micrometer. Ten

Table 8. Leaf stomate densities of various bean collections grown under different conditions.

Species	Collection[1]	Growth Conditions[2]	Leaf Surface[3]	Stomates (mm^2)	Statistical Grouping[4]
Phaseolus parvulus	ORPR	g	upper	0	a
Macroptilium atropurpureum	UNAT	f	upper	0	a
P. grayanus	GH[5]	w	upper	16	a
P. filiformis	BCFI	f	upper	66	a
P. wrightii	OPWR	f	upper	144	b
P. metcalfei	PAMT	f	upper	166	b
P. grayanus	GH	w	lower	182	b,c
P. acutifolius var. *latifolius*	UNACC2	f	upper	197	b,c,d
P. wrightii	OPWR	f	lower	211	b,c,d,e
P. filiformis	BCFI	f	lower	212	b,c,d,e
P. metcalfei	PAMT	f	lower	215	b,c,d,e
P. ritensis	PMRI2	f	upper	215	b,c,d,e
P. acutifolius var. *tenuifolius*	MBAC7	f	upper	223	b,c,d,e,f
P. acutifolius var. *latifolius*	SYACL	f	upper	225	b,c,d,e,f
P. angustissimus	SCAN	f	upper	231	b,c,d,e,f
M. heterophyllum var. *rotundifolium*	MHHTR	f	upper	294	c,d,e,f,g
M. heterophyllum	SYHT	f	upper	304	d,e,f,g
M. atropurpureum	UNAT	f	lower	320	e,f,g,h
P. supinus	SYSU	g	upper	325	e,f,g,h
P. ritensis	PMRI2	f	lower	326	e,f,g,h
P. angustissimus	SCAN	f	lower	334	f,g,h
M. heterophyllum var. *rotundifolium*	MHHTR	f	lower	338	f,g,h
P. acutifolius var. *tenuifolius*	MBAC7	f	lower	366	g,h
P. acutifolius var. *latifolius*	SYACL	f	lower	376	g,h
P. acutifolius var. *latifolius*	UNACC2	f	lower	380	g,h
M. heterophyllum	SYHT	f	lower	406	g,h
P. parvulus	ORPR	g	lower	431	h
P. supinus	SYSU	g	lower	586	i

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1. Appendix.
2. g = growth chamber; f = field; w = wild, 50% filtered shade.
3. Upper = adaxial surface; lower = abaxial surface.
4. Any means followed by the same letter are not significantly different at the .05 level according to the Newman-Keuls (SNK) procedure.
5. General Hitchcock Campground, Santa Catalina Mtns., AZ.

measurements were taken of each epidermal surface possessing stomates. Data were analyzed using the Student Newman-Keuls' Procedure (Keuls, 1952).

Results and Discussion

Line drawings of the epidermal surfaces of the various species are illustrated in Fig. 8. The results of the stomate density study are summarized in Table 8. It should be noted that specimens from either wild or growth chamber conditions had been grown under conditions of reduced light, and lower stomate densities are probably recorded than would be expected from these same plants under full sunlight. Significantly more stomates appeared on the abaxial surface in about half the species studied within each species. The others maintained a consistent, though not significantly greater stomate density on the lower leaf epidermis. In no instance was the number of stomates greater on the adaxial than the abaxial surface within a given species.

The results of the stomate size study are presented in Table 9. Significant stomate size differences exist between some of the species. Differences are difficult to detect, due to the large variation in stomate size. For example, the lower epidermis of P. ritensis had extreme values of 17.6 and 27.4 µm stomate length. Only P. grayanus showed a significant difference in size between upper and lower epidermal stomates.

Although real differences appear to exist in both stomate size and density between species, there does not appear to be a correlation between habitat preferences and stomates. Rather than decreasing stomate

Table 9. Stomate sizes of upper and lower epidermal surfaces of various bean collections.

Species	Collection[1]	Growth Conditions[2]	Leaf Surface[3]	Stomate Size[4]	Statistical Grouping[5]
Phaseolus acutifolius var. *latifolius*	SYACL	f	lower	20.0	a
P. acutifolius var. *latifolius*	SYACL	f	upper	20.0	a
P. ritensis	PMRI2	f	upper	20.7	a,b
P. acutifolius var. *tenuifolius*	BMAC7	f	upper	20.7	a,b
P. supinus	SYSU	g	upper	21.0	a,b
P. acutifolius var. *latifolius*	UNACC2	f	lower	21.2	a,b,c
Macroptilium heterophyllum	SYHT	f	lower	21.3	a,b,c
P. supinus	SYSU	g	lower	21.4	a,b,d
M. atropurpureum	UNAT	f	lower	21.5	a,b,c
P. acutifolius var. *tenuifolius*	MBAC7	f	lower	21.9	a,b,c
P. ritensis	PMRI2	f	lower	21.9	a,b,c
P. acutifolius var. *latifolius*	UNACC2	f	upper	22.2	a,b,c
M. heterophyllum	SYHT	f	upper	22.2	a,b,c
P. angustissimus	SCAN	f	upper	23.0	a,b,c,d
M. heterophyllum var. *rotundifolium*	MHHTR	f	lower	23.1	a,b,c,d
M. heterophyllum var. *rotundifolium*	MHHTR	f	upper	23.1	a,b,c,d
P. angustissimus	SCAN	f	lower	23.1	a,b,c,d
P. filiformis	BCFI	f	lower	23.2	a,b,c,d
P. filiformis	BCFI	f	upper	23.3	a,b,c,d
P. parvulus	ORPR	f	lower	23.4	a,b,c,d
P. grayanus	GH	w	lower	24.0	b,c,d,e
P. wrightii	OPWR	f	lower	24.0	b,c,d,e
P. metcalfei	PAMT	f	lower	24.5	c,d,e
P. metcalfei	PAMT	f	upper	26.0	d,e
P. wrightii	OPWR	f	upper	26.6	e,f
P. grayanus	GH[6]	w	upper	28.5	f

1. Appendix.
2. g = growth chamber; f = field; w = wild, 5-% filtered shade.
3. Upper = adaxial surface; lower = abaxial surface.
4. Guard cell major axis in µm.
5. Any means followed by the same letter are not significantly different at the .05 level according to the Newman-Keuls (SNK) procedure.
6. General Hitchcock Campground, Santa Catalina Mtns., AZ.

Fig. 8. Epidermal appearance of southwestern Phaseolinae.

a. Epidermis of *Phaseolus filiformis*: left, adaxial surface; right, abaxial surface.

b. Epidermis of *Phaseolus wrightii*: left, adaxial surface; right, abaxial surface.

c. Epidermis of wild *Phaseolus acutifolius* var. *latifolius*: left, adaxial surface; right, abaxial surface.

d. Epidermis of *Phaseolus supinus*: left, adaxial surface; right; abaxial surface.

e. Epidermis of *Macroptilium atropurpureum*: left, adaxial surface; right, abaxial surface.

f. Epidermis of *Phaseolus acutifolius* var. *tenuifolius*: left, adaxial surface; right, abaxial surface.

g. Epidermis of *Phaseolus angustissimus*: left, adaxial surface; right, abaxial surface.

h. Epidermis of *Macroptilium heterophyllum*: left, adaxial surface; right, abaxial surface.

i. Epidermis of *Phaseolus ritensis*: left, adaxial surface; right, abaxial surface.

j. Epidermis of *Phaseolus metcalfei*: left, adaxial surface; right, abaxial surface.

k. Epidermis of *Phaseolus grayanus*: left, adaxial surface; right, abaxial surface.

l. Epidermis of *Phaseolus parvulus*: left, adaxial surface; right, abaxial surface.

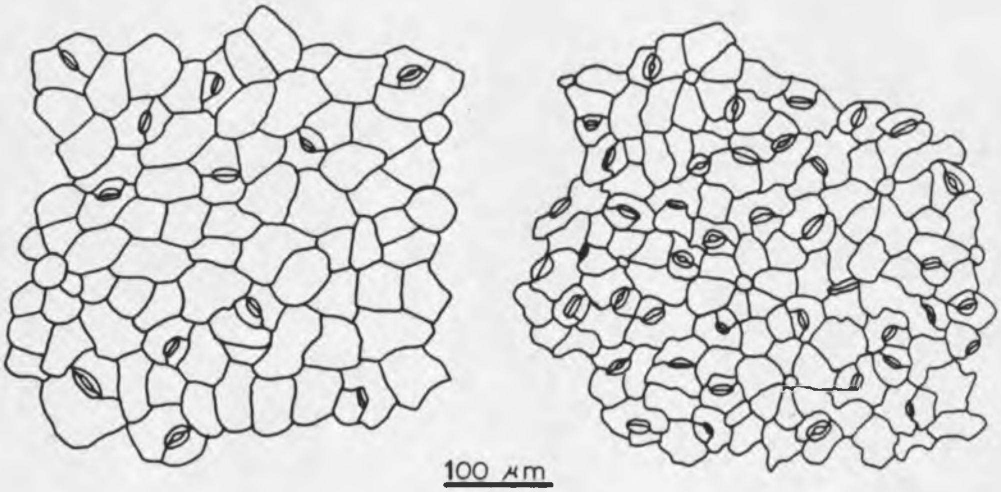


Fig. 8a.

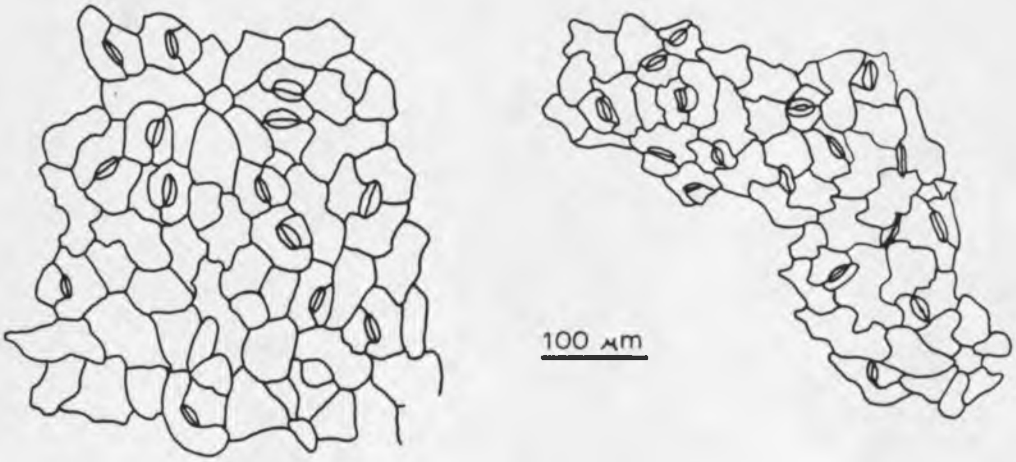
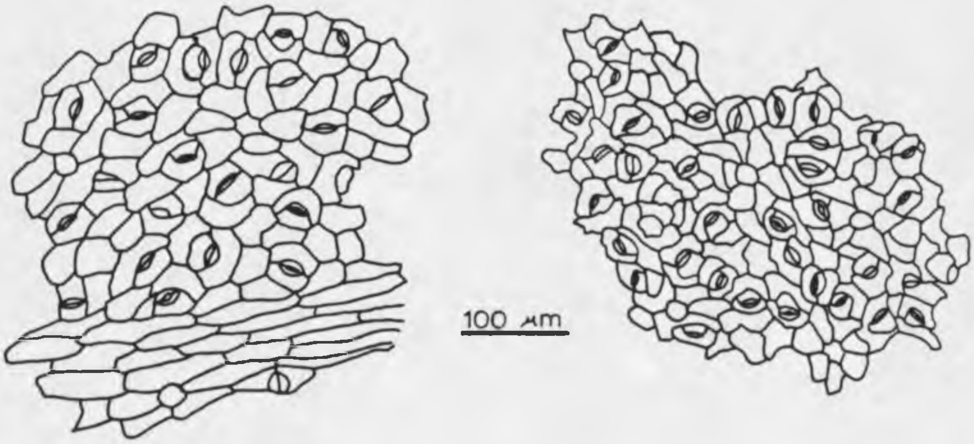


Fig. 8b.



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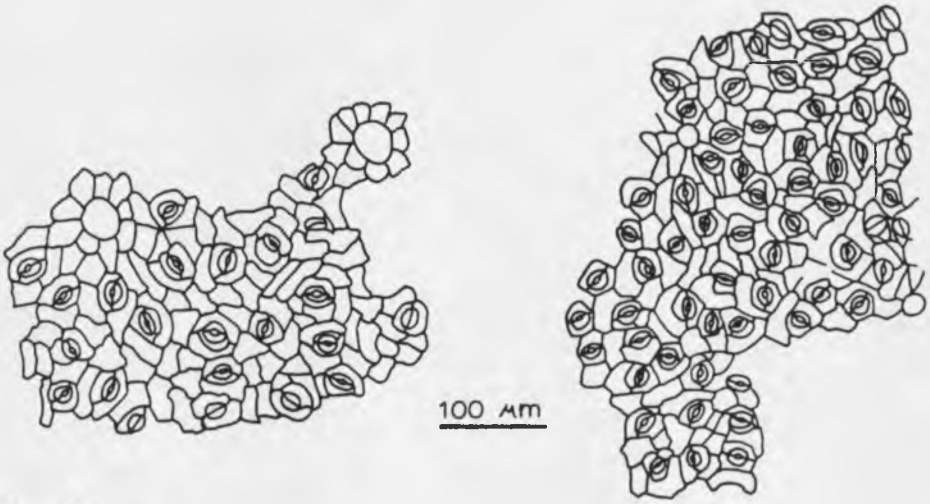

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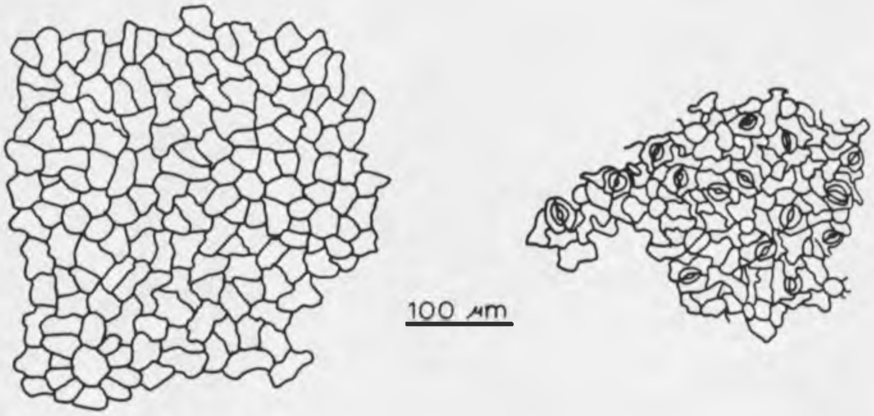

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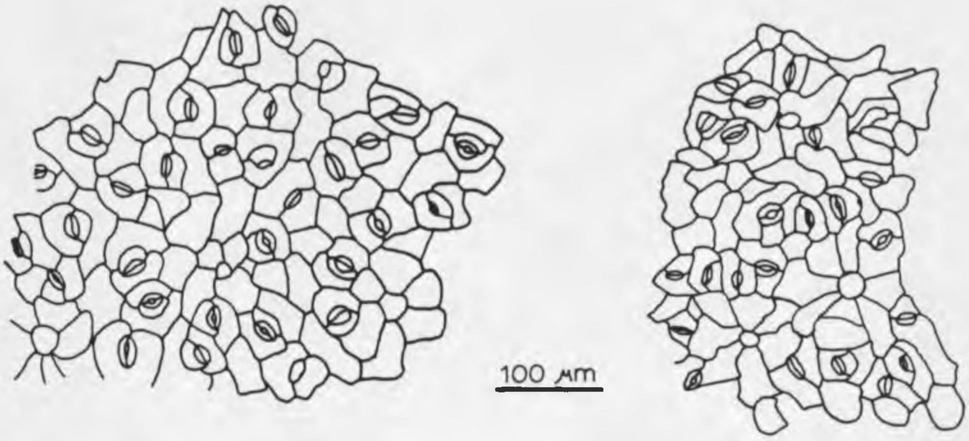

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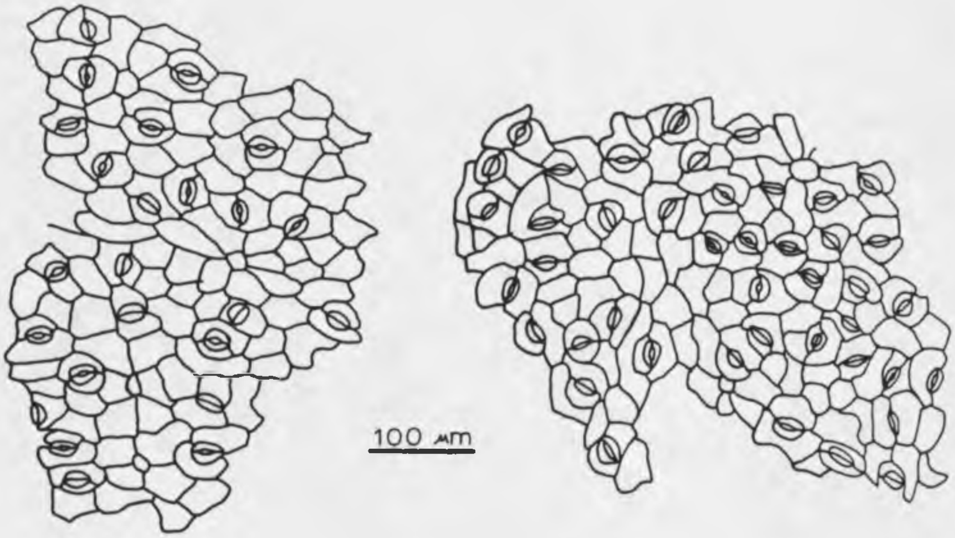

Fig. 8g.

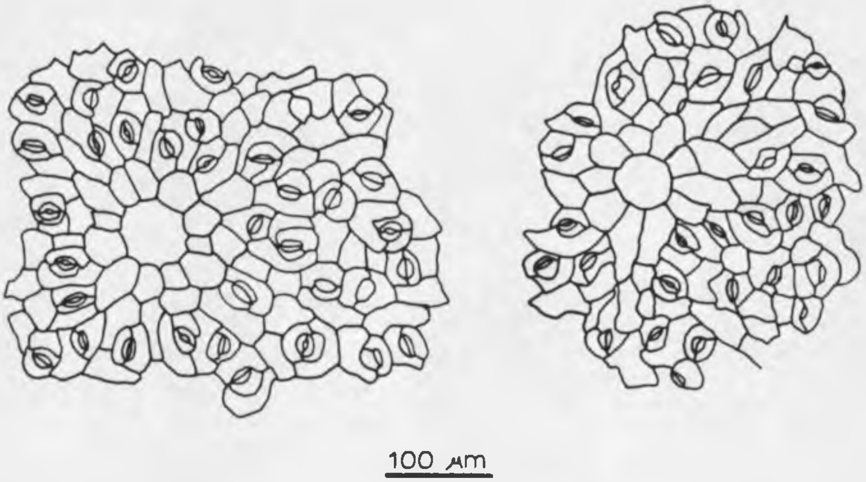

Fig. 8h.

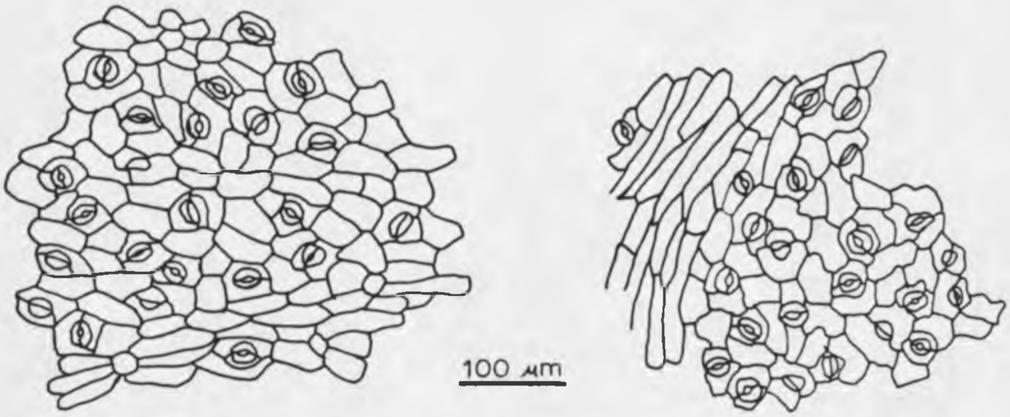

Fig. 8i.

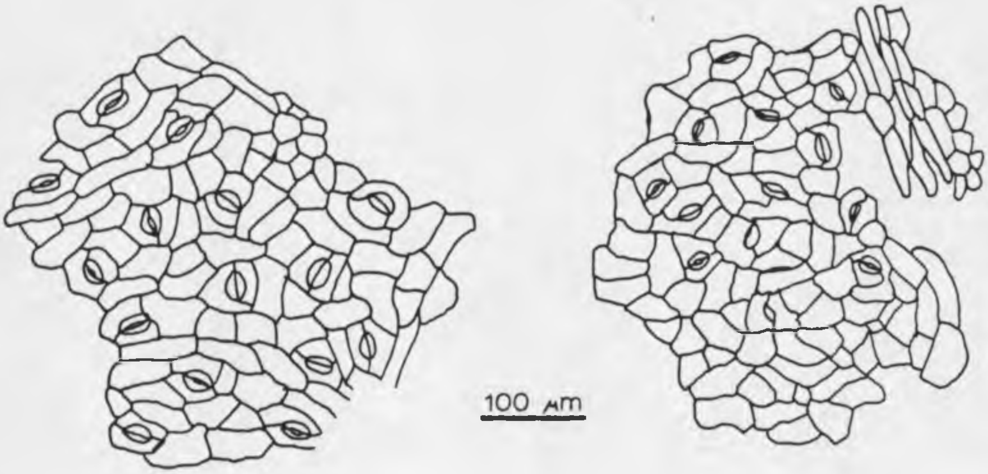

Fig. 8j.

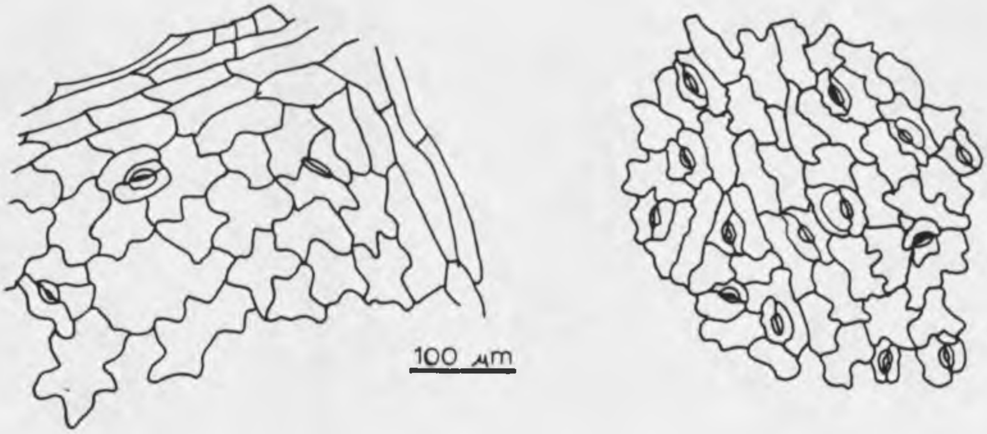

Fig. 8k.

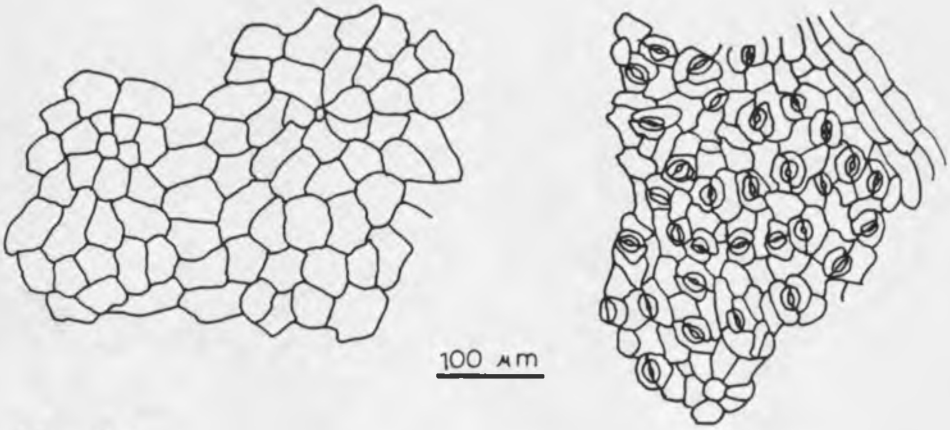

Fig. 8l.

density in more xeric environments, it appears that several species (*P. wrightii*, *P. filiformis*, *M. heterophyllum*, and *M. atropurpureum*) have responded with increased leaf succulence.

CHAPTER 7

STRESS TOLERANCE

Except for the tepary bean, cultivated *Phaseolus spp.* are poorly adapted to both temperature extremes and water stress. *Macroptilium atropurpureum* cv. "Siratro" is poorly adapted outside of the tropics. It is important to evaluate wild germplasm for stress tolerance in order to make this information available to plant breeders for possible utilization in interspecific hybridization programs. Such procedures could result in a significant extension of the areas suited to cultivation of domesticated *Phaseolus spp.*, especially into regions currently too hot, arid, or cold for bean culture. Cultivars developed and grown within current zones of adaptation would possess the ability to produce a crop in otherwise unfavorable years with droughts, cold springs, or unusually hot summers.

Water Stress Tolerance

Plants were observed for sensitivity to drought and water logging over three growing seasons from 1978 to 1980 under field conditions at the Campbell Avenue Farm. Drought reaction was observed particularly closely for a 24-day period during the hottest part of the growing season from 16 June to 10 July 1980, on which day the field was over-irrigated and remained with standing water in the furrows for 2 days. The mean high and low temperatures for this period were 41°C

(105.4°F) and 23°C (73.5°F), respectively, with extremes of 43.9°C (111°F) and 14.4°C (58°F). Plant reactions of the various species present were recorded and ranked. Results for drought tolerance and waterlogging tolerance are summarized in Tables 10 and 11, respectively.

Table 10. Drought tolerance of southwestern Phaseolinae.[1]

Very Tolerant	Tolerant	Intolerant
Phaseolus angustissimus	*Macroptilium heterophyllum*	*Phaseolus ritensis*
Phaseolus wrightii	*Phaseolus acutifolius*	*Phaseolus metcalfei*
Phaseolus filiformis	*Macroptilium atropurpureum*	

1. Order of listing within a category indicates relative tolerance within that group most resistant at top.

Very tolerant - Growth normal or slightly reduced.
Tolerant - Reduced growth but no wilting of leaves or senescence.
Intolerant - Wilting or senescent leaves.

Table 11. Waterlogging tolerance of southwestern Phaseolinae.[1]

Tolerant	Partially Tolerant	Intolerant	Completely Intolerant
Phaseolus metcalfei	*Phaseolus filiformis*	*Phaseolus ritensis*	*Phaseolus angustissimus*
Phaseolus acutifolius	*Phaseolus wrightii*		
Macroptilium atropurpureum	*Macroptilium heterophyllum*		

1. Tolerant - Growth nearly unaffected, little or no yellowing.
Partially tolerant - New growth yellowed, recovery within 3-5 days after soil conditions improved.
Intolerant - Growth severely affected; recovery within 1-2 weeks.
Completely intolerant - Plants died.

Tolerance to Temperature Extremes

Cold

A series of several radiation frosts in November and early December 1979 presented a unique opportunity to evaluate the frost tolerance of several species of beans growing at the Campbell Avenue Farm. The results of this study are summarized in Table 12. Frost tolerance was shown to be present in several species, but none could approach the resistance present within *P. wrightii*, Fig. 9, showing the typical reaction of a frost-resistant plant. Note the dead plants of the same species immediately adjacent to the still-flowering specimen. Eleven frost-tolerant *P. wrightii* plants were moved into a greenhouse and increased for further study.

Heat

The evaluation of heat tolerance under field conditions is considerably more difficult than cold tolerance, since plants are not killed outright, but deteriorate over an extended period of time. Efficiency of seedset is a good indication of heat tolerance, since reproduction is affected in a stressed plant (see Chapter 6, Table 6). As expected, the heat resistance of the various species appears to parallel, although at a higher temperature, the germination response curves of the same species (see Chapter 4, Fig. 5). Of 123 *P. grayanus* plants planted in 1979, none survived long enough to produce seeds. *P. parvulus* grown in a greenhouse with a maximum temperature of 34°C died after about a month with obvious signs of stress. Both *P. ritensis*

Fig. 9. Frost-tolerant Phaseolus wrightii (right of stake). -- Notice that this plant is still in bloom and the adjacent plants of the same species frozen by -6 to -7°C temperatures behind and to the left of the tolerant plant.

and *P. metcalfei* are near their limits of heat tolerance in Tucson, with very high seedling mortality.

Summary

Resistance to environmental stresses is present in several of the species studied. *P. wrightii* has the best overall stress adaptation of the species studied. *P. acutifolius* also has good general stress tolerance, but it is less cold-tolerant. Several other species possess special tolerances to stress conditions, and may find use for specific needs. *Macroptilium heterophyllum* has potential for increasing the useful range of Siratro into colder climates, since it has the ability to tolerate extreme cold in a dormant condition.

CHAPTER 8

NATURAL HISTORY

Figure 10, compiled from herbarium specimen data and field notes, is a semi-quantitative elevational distribution of southwestern beans within Arizona and northern Mexico. Elevations are listed in feet, since available topographic maps and most herbarium specimens use this system. Band width is roughly proportional to species abundance at a given elevation. Good correlations can be made between elevational distributions and germination temperature responses for most species (Fig. 5).

Species with overlapping elevational and regional ranges would be expected to be found growing sympatricly and this is often the case (Table 12). Two species which have not been documented sympatrically are _P. ritensis_ and _P. metcalfei_. Research into the distribution of these species is showing, at least in the northern parts of their respective ranges, that their distributions probably do not overlap, _P. ritensis_ being found in the somewhat drier areas south of the Gila River and west of the Dragoon Mountains in Arizona.

Two phases of the life cycle of these plants are often unsuccessful: seed production and seedling establishment. In dry years nearly complete mortality of seedlings of _P. acutifolius_, _M. heterophyllum_ and _P. supinus_ has been observed. Low temperatures usually restrict winter

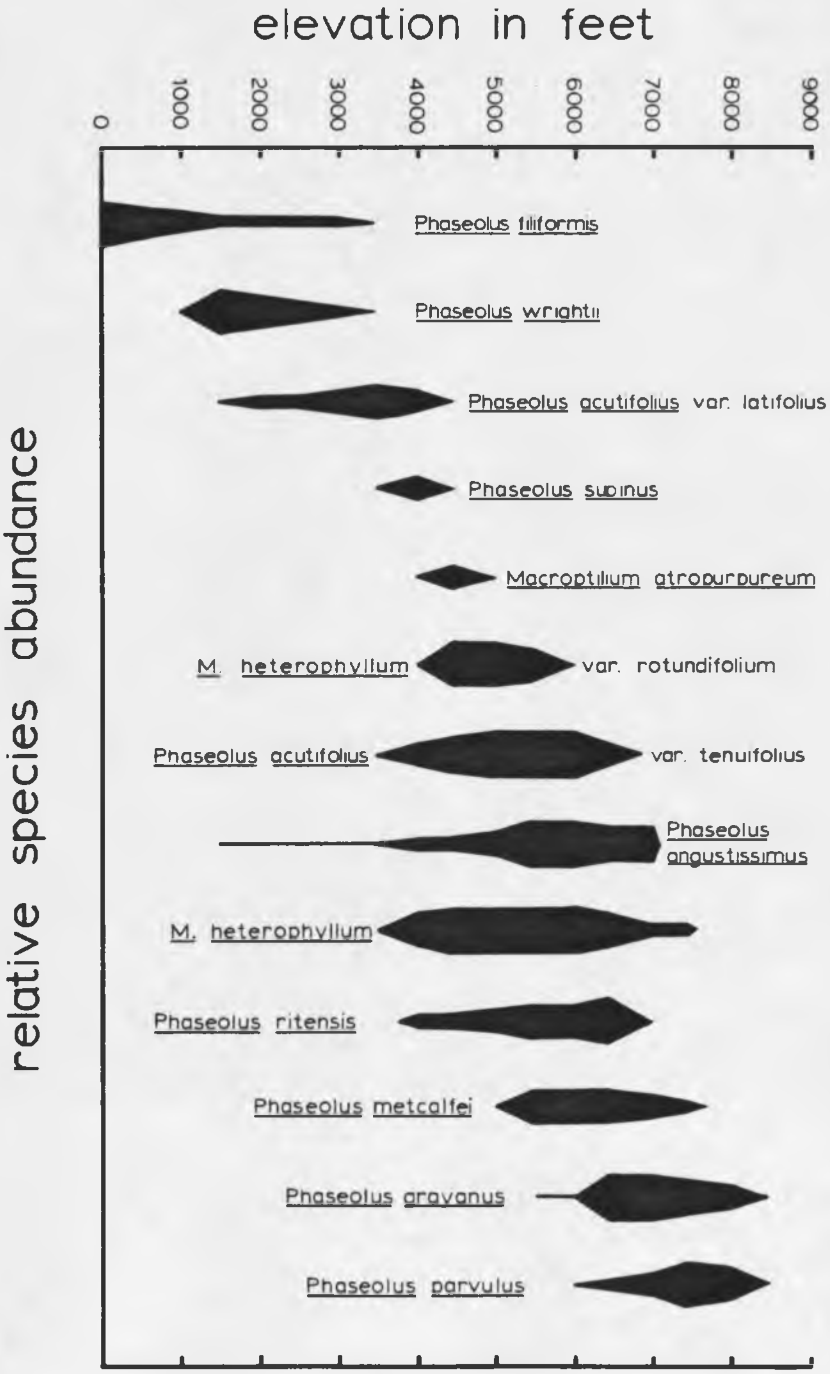

Fig. 10. Elevational distributions of southwestern Phaseolinae.

Table 12. Observed sympatric Phaseolinae, localities, and associated vegetation.

Locality	Species Present[1]	Vegetation
Sycamore Canyon Atascosa Mountains, AZ	ACT, ACL, HT, SU, RI	Riparian canyon surrounded by oak savanna
Barfoot Park Chiricahua Mountains, AZ	GR, PR	Ponderosa pine forest and clearings
Oracle Ridge Santa Catalina Mountains, AZ	GR, PR	Ponderosa pine, oak forest
San Augustine Pass near Organ, NM	AN, ACA	Oak savanna
Mount Hopkins Road Santa Rita Mountains, AZ	RI, HT, HTR, ACT	Oak savanna
Italian Ranch Trail Rincon Mountains, AZ	RI, ACT, HT	Oak savanna
Nogales-Duquesne Road Patagonia Mountains, AZ	RI, ACT	Oak woodland
Granite Peak, Whetstone Mountains, AZ	RI, ACT	Oak savanna
Road to Parker Canyon Lake Canelo Hills, AZ	RI, ACT	Apache pine-oak woodland
Cochise's Stronghold Dragoon Mountains, AZ	MT, GR	Oak woodland
Chiricahua National Monument Chiricahua Mountains, AZ	MT, GR	Oak woodland
Southern end of Franklin Mountains, El Paso, TX	AN, WR, ACA[2]	Chihuahuan desert scrub

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1. ACA = *P. acutifolius* var. *acutifolius*
ACL = *P. acutifolius* var. *latifolius*
ACT = *P. acutifolius* var *tenuifolius*
AN = *P. angustissimus*
GR = *P. grayanus*
HT = *M. heterophyllum*
HTR = *M. heterophyllum* var. *rotundifolium*
MT = *P. metcalfei*
PR = *P. parvulus*
RI = *P. ritensis*
SU = *P. supinus*

2. Found at similar elevations within a 3-mile radius, not known to be truly sympatric.

survival of P. wrightii to rocky south slopes of mountains. As an extreme example of low reproduction, a population of 50+ P. ritensis plants in the Oro Blanco, AZ vicinity has not produced seed for 3 years (1978-1980).

Seed predation within the seed increase plot by whitewing doves was very high on all species present except P. metcalfei, which probably escaped because of its large seed size. Under wild conditions, seed predation should be much lower, since the seeds match the substrates where the plants grow.

Seed dispersal is accomplished primarily by dehiscent legumes, secondarily by vine extension with reproduction upon the plants' peripheral parts, by moving water, and possibly by passing through the digestive tract of seed predator and grazing animals, although this last has not been shown. This information is summarized in Table 13.

Pests have been observed upon or within the fruits of several species. In addition to bruchid damage of P. metcalfei (Nabhan et al., 1980), weevils of the genus Apion have been observed within pods of P. grayanus and P. parvulus in the Chiricahua Mountains, Arizona. At least two unidentified Lepidopterous species infest pods of P. wrightii, P. filiformis, P. angustissimus and P. ritensis. The pests of wild beans is a subject in need of further research.

Conclusion

Southwestern beans, functioning as ephemerals in a harsh and unpredictable environment, are the products of eons of natural selection.

Table 13. Plant size, growth habit, seed crypticity, dehiscence, and dispersal of seed.

Species	Growth Habit[1]	Growth Form	Maximum Vine Length	Seeds Mimic	Dehiscence	Other Seed Dispersal
P. acutifolius	A	Mound, climbing vine	2-4 m	Angular pebbles	Strong, delayed	Eaten by whitewing doves. Moved along watercourses during storms.
P. angustissimus	P	Sprawling vine	1-2 m	Volcanic pebbles, Rough scree "	Strong, immediate	Eaten by whitewing doves. Probably dispersed to an extent by stream flooding.
P. filiformis	A	Mound, climbing vine	1 m	Rough scree "	do.	Eaten by whitewing doves.
P. grayanus	P	Sprawling vine[3]	1-2 m	Waterworn "	Intermediate, somewhat delayed	
P. metcalfei	P	Sprawling vine	5 m	Rabbit scat, Waterworn "	Weak, immediate	Eaten by rodents (Goodding, 1946); inflated seed floats on water.
P. parvulus	P	Spindly, climbing vine	40 cm	Pebbles	Intermediate, delayed	
P. ritensis	P	Sprawling vine	5 m	Waterworn "	Strong, immediate	Eaten by whitewing doves. Some stream dispersal.
P. wrightii	A	Mound, climbing vine	1 m	Rough scree "	Strong, immediate	Eaten by whitewing doves.
P. supinus	P	Creeping vine	1 m	Pebbles	Strong, immediate	Indehiscent and geocarpic pods placed up to 1 m from old root by parental vine growth, forming colonies.
M. atropurpureum	P	Sprawling vine[3]	6 m	Pebbles	Strong, immediate	Eaten by whitewing doves.
M. heterophyllum	P	Sprawling vine	1 m	Pebbles	Strong, immediate	Eaten by whitewing doves.

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1. A = annual; P = perennial.
2. Strong dehiscence: pod separates with an audible crack; intermediate dehiscence: inaudible, but with sufficient force to eject seeds; weak dehiscence: weak curling, seeds simply fall to the ground.
3. Some of these plants will climb in relatively shaded habitats.

The greatest test of survival for these plants has been the ability to grow and reproduce rapidly enough to beat the post-monsoon drought. However, since the advent of domesticated grazing animals, many populations have been reduced to relics of formerly large ranges. Damage can also be inflicted by wild herbivores. Bighorn sheep have reduced stands of P. wrightii in the Ragged Top, AZ area with the help of man-made water catchments, which allows them to remain in a given area for an extended period. Overgrazing in this area is so severe that browse shrubs are being killed by the sheep. We are presented with many species, some highly successful, some apparently nearing extinction. Many populations recorded in old herbarium specimens are no longer in existence. Hopefully, these materials, which may present a valuable, and certainly irreplaceable, genetic resource will be protected and preserved before it is too late.

APPENDIX

SOUTHWEST PHASEOLINAE UTILIZED

Southwest Phaseolinae utilized.

Species	Field Designation	Collection Number[1]	Locality[2]	Notes	Source
Phaseolus acutifolius var. latifolius	UNACC1		Originally from Sinaloa	White domesticate	W.D. Hood
	UNACC2		"	Brown "	"
	DHACC3	GN 610	"	Mottled "	"
	PI 310-801		Nicaragua	Mottled "	J.G. Waines
	PI 310-802		Nicaragua	White "	"
	SYACL		Sycamore Cyn., Atascosa Mts.		
	SBACL		San Bernardo, Sonora		
Phaseolus acutifolius	SRAC	9	Agua Caliente Canyon, Santa Rita Mts.		
	MBAC	8	Molino Basin, Santa Catalina Mts.		
	SYACT		Sycamore Cyn., Atascosa Mts.		
	CMACT1	2	Rd. to Portal, Chiricahua Mts.	6800'	
	CMACT2	4	"	6100'	
	PMACT	5	Nogales-Duquesne Road, Patagonia Mts.	Some plants w/peduncles w/ as many as 8 flowers	
	RMACTP	3	Italian Ranch Trail, Rincon Mts.	From drought refuge	
Phaseolus angustissimus	SCAN	12	Sunset Crater		R.E. Dennis
Macroptilium atropurpureum	UNAT	1	Unknown		G.P. Nabhan
Phaseolus filiformis	BCF1		Sierra Laguna, Baja CA Sur		
Phaseolus grayanus	ORGR		Oracle Ridge Trail, Santa Catalina Mts.		
	CMGR1		Ancient Lake Beds, Chiricahua Mts.		
	CMGR2		Natural Bridge Trailhead, Chiricahua Mts.		

Southwest Phaseolinae utilized. -- Continued

Species	Field Designation	Collection Number[1]	Locality[2]	Notes	Source
(continued)	CMGR3		Road to Portal, Chiricahua Mts.		
			Methodist Camp, Chiricahua Mts.		R.E. Briggs
Macroptilium heterophyllum	RNHT	17	Ruby-Nogales Road		
	CMHT		Chiricahua National Monument		
	SYHT		Sycamore Canyon, Atascosa Mts.		
var. *rotundifolium*	MHHTR	18	Mt. Hopkins Rd., Santa Rita Mts.		
	PMHTR		1 mile north of Duquesne, Patagonia Mts.		
Phaseolus metcalfei	PAMT	GN 734, 21	Pinos Altos, NM		G.P. Nabhan
	CMMTI	22	Near Ancient Lake Beds, Chiricahua National Monument		
	CMMT2	R.E. Briggs 1	East of Barfoot Park on Portal Rd., Chiricahua Mts.		R.E. Briggs
	DRMT	142	Dragoon Mts.		
Phaseolus parvulus	ORPR	19	Oracle Ridge Trail, Santa Catalina Mts.		
	BWPR		Bear Wallow, Santa Catalina Mts.		
	BPPR	20	Barfoot Park, Chiricahua Mts.		
Phaseolus ritensis	SRRL	23	Agua Caliente Canyon, Santa Rita Mts.		
	GVRI	24	Geology Vista, Santa Catalina Mts.		
	SYRI		Sycamore Canyon, Atascosa Mts.		
	MHRI	25	Mt. Hopkins Road, Santa Rita Mts.		
	PMRI 1, 2	26	Nogales-Duquesne Rd., Patagonia Mts.		
	WHRI	139	Granite Peak, Whetstone Mts.		
Phaseolus supinus	SYSU	144,147,155,156	Sycamore Canyon, Atascosa Mts.	New to U.S.	

Southwest Phaseolinae utilized. -- Continued

Species	Field Designation	Collection Number[1]	Locality[2]	Notes	Source
Phaseolus wrightii	RTWR	30	Ragged Top, Silverbell Mts.		
	ATWR 1-7	27,28,29	Various collections along the Apache Trail near Canyon Lake		
	OPWR		Near Dripping Spring, Puerto Blanco Mts.		

1. Or voucher specimen number.

2. Arizona localities unless otherwise noted.

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