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PENSTEMON in your garden [Revised]

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PENSTEMON **in your garden**



University of Nebraska College of Agriculture
The Agricultural Experiment Station
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A new race of hardy perennials is appearing in American gardens. These are the penstemons, a genus of plants closely related to the familiar snapdragon, which may become important ornamentals as they become better known. This bulletin shows the possibility of the genus as an ornamental, suggests species and species hybrids of possible value to Great Plains gardeners, provides information about propagation and culture and encourages gardeners to engage in penstemon breeding as an avocation.

ON THE COVER: Selection 6857—A multispecies hybrid

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PENSTEMON

in your garden

R. D. Uhlinger & Glenn Viehmeyer¹

In 1946 a small group of gardeners formed the American Penstemon Society. The organization is dedicated to bringing this showy genus of wildflowers into cultivation and promoting its use as an ornamental.

Had the organizers known the difficulties inherent in bringing a genus of wildings into cultivation, the society might not have come into being. Most early attempts to hybridize species native to the plains and mountains were unsuccessful. As early as 1928, Viehmeyer attempted a series of crosses of native western species without success. The effort was abandoned as an "impossible" task. In that attempt, not a single seed resulted from several hundred pollinations involving several species mated in all possible combinations. A. C. Hildreth cites similar results at the Cheyenne Horticultural Field Station.

Fortunately, the members of the new society were not aware that breeding and domesticating penstemons was "impossible." They sent an expedition into the wilds to collect plants and seed, members became collectors and, even more important, a *seed exchange* was established that provided members with access to a wide range of materials. Species that do not meet in nature were placed in intimate contact in gardens and the stage was set for the occurrence of natural hybrids. Here curious amateurs began attempting crosses, not knowing the task was an "impossible" one.

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A controlled hybrid of *Penstemon grandiflorus* x *P. murrayanus*, the discovery of a chance hybrid in a population of *P. grandiflorus* seedlings, and the "Flathead Lake" hybrid were destined to play a leading role in domesticating the penstemon (2, 3, 8). Viehmeyer was the first to undertake a planned program of intercrossing species using the Flathead Lake hybrid to make the breakthrough (12). Many amateurs have added their efforts toward improving the penstemon with the result that thousands of complex hybrids are appearing and a few of the better of these are filtering into the Nursery trade.

THE GENUS PENSTEMON

Penstemon is truly an American plant. The genus is confined to North America, with the exception of a single species that has crossed the Bering Strait to the Asian mainland. Few American genera have wider geographical or ecological distribution.

Penstemon species are native from the Atlantic to the Pacific and from Alaska to Central America. They are found growing in alpine meadows, on talus slopes, rock ledges, sandhills, prairies, canyons, mountaintops, flood plains, deserts, in fact every sort of habitat except swamps.

Morphologically, penstemon species vary as greatly as do their ecological preferences. They range from tiny rock plants less than an inch tall to herbs taller than a man. Among the 300 species, subspecies and forms are herbaceous plants, woody evergreens and even a climber. Most wild penstemons are specialized plants (adapted to particular habitats) that fail in the garden unless their native habitat is simulated. Disease is the greatest threat and pure species tend to be short-lived. Most of them are best left to the specialist and breeder as building blocks for creating better hybrids.

For the average gardener, hybrids are the most satisfactory. They are less sensitive to environment, have greater vigor and often live longer. Hybrid penstemons that "breed true" for plant type are now available. These *do not breed true* for all characters but are uniform enough for garden use, even in advanced generation material. Colors are clear and there is little of the muddiness that appears in volunteer populations of such ornamentals as petunia, which "runs out," unless constant selection is practiced to keep the variety "pure."

Perhaps it would make the story clearer to be a little more specific and follow a cross through the first and second generations.

Penstemon barbatus Nutt. is a native of the plateaus and deserts of the southwestern United States, and ranges southward to Mexico. Through thousands of generations in this habitat, it has become adapted to drought and heat and produces its brilliant scarlet flowers season after season. To the north of the range of *P. barbatus*, the blue-flowered *P. strictus* Benth. grows in high mountain valleys and on mountainsides. The two species cross rather readily in the garden to produce hybrids better adapted to garden culture and more ornamental than either parent.

The first generation of *P. barbatus* x *P. strictus* is intermediate between the two parents and much more vigorous than either. The flowers are not red as those of *P. barbatus*, nor are they the blue of *P. strictus*; instead they are purple.

If these purple flowered hybrids are grown in isolation and allowed to produce seed, plants grown from this seed will have red, purple and blue flowers in the ratio of 1 red:2 purple:1 blue (This is Mendelian segregation for the single factor pair, red and blue).

Less obvious is the segregation of characters that determine adaptiveness, which also follow the rules of Mendelian segregation, though in a far more complicated manner. Going back to the *P. barbatus* and *P. strictus* parents we find that *P. barbatus* has evolved in a desert where it has accumulated a genetic complex that fits it to live through intense drought and heat, while *P. strictus* evolved on high plateaus and mountainsides, where there are both more moisture and lower temperatures than occur in the habitat of *P. barbatus*.

When the two species cross, the first generation germ plasm is a combination of parental germ plasms, one of which is adapted to heat and drought and the other to cold with moisture. The first generation hybrids combine characters for tolerance to heat, cold, drought and moisture. They are intermediate in their environmental requirements. When seed of these first generation hybrids is planted, segregation for adaptation occurs, but it is a far more complicated process than the simple segregation for color. Tolerance for heat, cold, drought and moisture is controlled by many factors (genes) that interact to produce the end results. (Geneticists call such segregation multifactorial.) In the second and subsequent

generations, multifactorially controlled characters recombine to form a multitude of variant individuals.

Actually, in a species cross such as the one being discussed, there are potentially millions of possible gene combinations. Each of these may react to the environment in a different manner. At the one extreme of the hybrid population (if it is large enough) one might expect to find a few individuals that are more tolerant of heat and drought than the desert species *P. barbatus* and at the other extreme, individuals that are more cold-moisture tolerant than the montane *P. strictus*.

To the breeder this means that he will encounter (in large advanced generation populations) segregates reasonably well adapted to any environment physically intermediate between the desert and the mountaintop. By choosing the individuals best adapted to his garden and interbreeding them, he may expect to approach the highest level of adaptation (to conditions prevailing in his garden) inherent in the combined germ plasms of the parental species. For practical purposes, the following broad principles may be stated:

1. If two species, which occupy different environments in nature, are crossed, the first hybrid generation will require an intermediate environment for optimum performance.

2. Advanced generations, if large enough, will contain individuals that exceed the tolerance of the parental species to limiting factors of the new environment.

3. The breeder, working with a segregating population in any intermediate habitat, may expect to select (if the population is large enough) lines fairly well adapted to the particular habitat in which he is growing his advanced generation population.

4. The "raw hybrids" that are the result of interspecific hybridization offer the amateur breeder excellent material for penstemon improvement. By selecting and interbreeding those segregates best adapted to his garden he can isolate strains that perform well and consistently. To do this he needs only the most rudimentary instruction in plant breeding. The process is almost automatic if he chooses his breeding material from that part of the segregating population best adapted to his breeding plots.

The amateur or professional breeder should be aware that the breeding behavior of the interspecific hybrid is considerably different than that of intraspecific hybrids in that characters are inherited in

entire chromosomes or blocks of chromosomal material (1). As a result, genes are linked in inheritance and do not assort independently. Such linkage may persist for generations.

Examples of this are found in the Fate hybrid of *P. grandiflorus* x *P. murrayanus*. In the Fate hybrid the narrow corolla, perfoliate bract and elongate inflorescence of *P. murrayanus* has persisted through 15 or more generations as have the inflated corolla, non-perfoliate but clasping bracts and more compact inflorescence of *P. grandiflorus*. The two forms are interfertile but the three characters retain the original association without recombining (4).

In the case of the Flathead Lake complex, the "shark head" corolla shape of *P. barbatus* and *P. labrosus* dominate flower shape to the exclusion of the spreading lobes of all blue flowered parental species. Only by repeated backcrosses to a species having spreading lobes are the erect upper and reflexed lower lobes replaced by the character of spreading lobes.

Female fertility in F₁ species crosses is often much reduced. This reduction ranges from about 60 to 100%. However, female fertility is rapidly recovered in advanced generations. Data on male sterility have not been studied.

These high levels of sterility may account for the failure of whole classes of phenotypes to appear in the F₂ and subsequent generations. One may suspect that embryos bearing certain combinations of germ plasm are not viable.

There appears to be a cumulative effect in certain segregates which makes the individual hybrid less affected by conditions that might hamper or destroy the species parent(s). Uhlinger and Viehmeyer, working separately at North Platte, Nebraska, are selecting segregates with better garden survival and greater disease resistance.

Meyers (10), hybridizing within the subgenus *Dasanthera*, states: "*Penstemon barrettiae* hybrids (with other *Dasanthera* species) do so much better in my garden than the Columbia River plants do that I would bet that they would do better in the more difficult areas." *P. barrettiae* is endemic in the Columbia River gorge (7).

The F₂ and advanced generations of a two-species cross may be depauperate in phenotypes as reported for the Fate hybrid above. Double crosses involving germ plasms of several species (multispecies hybrids) can be expected to yield greater numbers of

morphologically distinct segregates as well as segregates with wider adaptation and greater disease resistance.

PENSTEMON BREEDING

Since the discovery of the role of intermediary parents in penstemon breeding (Viehmeyer, 2), the genus is no longer a difficult one with which to work. The materials represented by the hybrids now available are sufficient to engender a whole race of new ornamentals. Yet these hybrids represent only a fraction of the species of the genus *Penstemon*. Other sections and other species may offer even greater possibilities to the hybridist.

By following the suggestions given below, the amateur or professional breeder may venture into unexplored areas and, perhaps, bring entirely new ornamentals into being.

Plant breeding is no longer only the vocation of the expert trained in the science of genetics. It has also become an avocation for hundreds of amateurs. These amateurs may well become the greatest single force for the improvement of ornamentals. Their activity is even now overshadowing the effort of the few professionals, simply because of their numbers.

Dr. Frank E. Palmer (11), onetime director of the Ontario Horticultural Experiment Station, a man who has made plant breeding his hobby and his lifetime profession, has this advice for the amateur: "There is no particular need to worry about genetics, although such knowledge can be useful. Generally leave genetics to the geneticists. Their knowledge is their livelihood. You're a hobbyist out to enjoy yourself—part of the attraction of plant breeding is that it is an art rather than a science."

To Palmer's comment we might add "Plant breeding is creative work within the reach of anyone who is willing to spend a few hours studying a text on breeding methods or visiting with a plant breeder." You need not be a highly trained scientist to be an effective plant breeder. Remember that genetics is only one of the tools you will learn to use as you work. If you are interested you will soon pick up the things you need to know. The following paragraphs give the techniques of penstemon breeding.

Emasculation

The flower of the penstemon is a “perfect flower” in the sense that it has both male and female parts. The male parts, the anthers, are attached to the corolla or petals. The female parts consist of stigma, style and ovary. The latter organ develops into the capsule. Penstemon flowers are borne in a multiflowered spike or panicle and to facilitate the work of breeding, it is desirable that the number of individual flowers in the cluster be reduced. This is shown in Fig. 1 where A and B show a cluster of penstemon buds before and after thinning.

The next step in penstemon breeding is to emasculate the flowers of the plant chosen as the female parent. This must be done before the pistil is mature. A bud in the proper stage is shown in Fig. 1 C. Actually, the operator has considerable latitude and the bud may be emasculated as much as three or four days before the flower would normally open.

Emasculation is performed by grasping the lower side of the bud and pulling outward as indicated in Fig. 1 D. The way in which the corolla is pulled away is important. By grasping the lower side of the bud, injury to the developing pistil is avoided. With a little practice anyone can emasculate a flower each second.

Danger of pulling the entire flower bud off the plant is practically eliminated if the operator supports the bud by holding the calyx (green sepals) between the thumb and forefinger of one hand and removes the corolla and its attached stamens with the other hand. After the corolla has been removed there is no need to cover the flower to avoid contamination. None of the insects that normally pollinate penstemon will visit a flower so mutilated and the probability of accidental pollination by midges or flies is too remote for consideration.

Pollen Collection

Anthers of the selected male parent are collected just as the flower is opening or just after it has opened. The former is preferable since it eliminates the possibility of visiting insects contaminating the anthers with foreign pollen.

After anthers are collected, they should be spread on a pane of glass and dried in a warm room out of the wind and sun. As they dry,

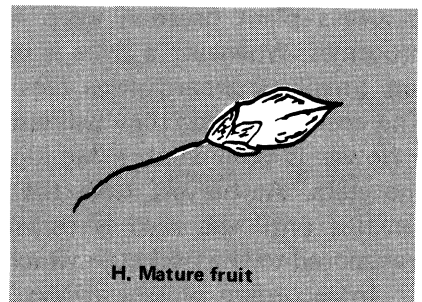
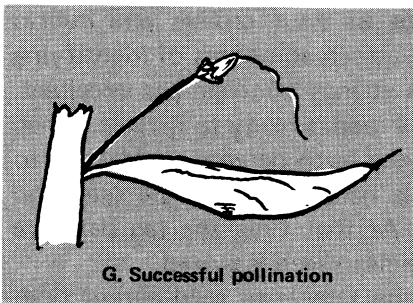
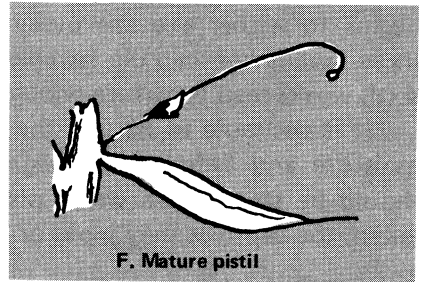
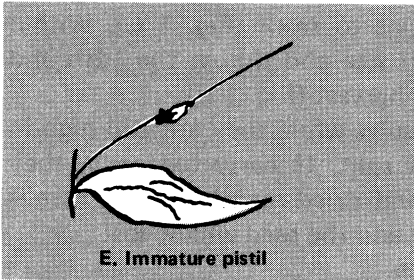
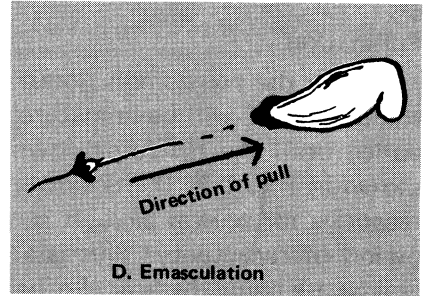
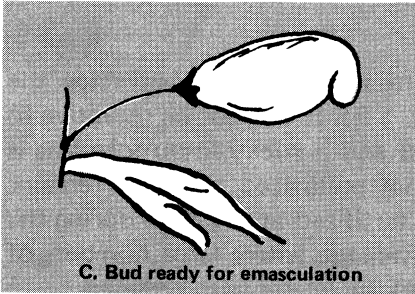
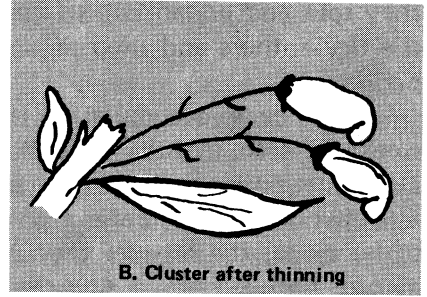
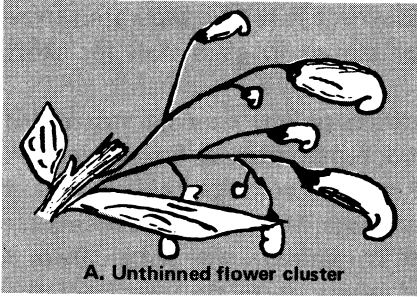


Fig. 1. Techniques of penstemon breeding (see text).

they split and pollen falls to the glass where it can be separated from the dry anthers and used at once or stored in glass vials for short periods.

Evidence is accumulating that dried pollen may be stored for weeks or even months if held at low temperatures. Some workers claim that pollen can be frozen and kept for prolonged periods. More information is needed about pollen storage. If only a few crosses are to be made, the breeder may prefer to squeeze the pollen from a mature anther onto a fingertip and apply it to the pistils of the chosen female parent.

Pollination

When the penstemon flower is emasculated in the bud stage, the enclosed pistil will be immature (Fig. 1 E). It will not be receptive to pollen until the tip turns downward and a sticky knob forms as is shown in Fig. 1 F. If the flower is not pollinated, the pistil remains receptive for several days. It can be fertilized at any time during the period of receptivity. This is an advantage where large numbers of crosses are being made or if other work interferes with crossing.

As soon as a flower has been successfully pollinated, the style begins to wither and the ovary begins to swell (Fig. 1 G). Within three weeks the capsule reaches full size and during the fifth and sixth weeks seed is mature enough to harvest (Fig. 1 H).

It is desirable to harvest the capsules while they are still high in moisture and before they begin to split. If harvested early, they should be stored in a warm place and dried rapidly. Unless care is taken, the capsules may mold or heat and the seed will be lost.

Keeping Records

As a plant breeder, keep records of your crosses and hybrid progenies. Whenever a cross is made, attach some sort of identifying tag. Small cardboard price tags with strings attached are excellent. The cost is low and they will last until seed is ready to harvest. When a flower is pollinated, a tag identifying both parents is attached to the stem. At harvest time the tag is harvested with the seed and remains until the seed is threshed. At that time the tag data are transposed to the packet in which the clean seed is stored.

In recording crosses always list the female or seed parent first. This is the standard method of writing pedigrees in plant breeding, exactly the reverse of animal pedigrees.

SELECTION OF PARENTAL MATERIALS

The penstemon breeder has many choices of parental material. He may choose to work with existing hybrids where by selection pressure alone he should make rapid progress if he has specific objectives. Most of the available hybrids have several species in their immediate background. These are, for the most part, "raw" hybrids in which little if any selection has been done. The Flathead Lake complex today involves germ plasms of over 25 species which represent at least five Sections of the genus.

Table 1. Species of penstemon which may be crossed with the Flathead Lake Complex.

Section <i>Anularius</i> ^a	<i>P. labrosus</i> ^b
<i>P. acuminatus</i>	<i>P. lanceolatus</i>
<i>P. angustifolius</i> ^b	<i>P. runyonii</i>
<i>P. arenicola</i>	<i>P. cardinalis</i> ^b
<i>P. buckleyi</i> ^b	
<i>P. cyathophorus</i>	Section <i>Habroanthus</i>
<i>P. fendleri</i>	<i>P. alpinus</i> ^b
<i>P. grandiflorus</i> ^b	<i>P. brandegei</i> ^b
<i>P. hadeni</i> ^b	<i>P. caryi</i>
<i>P. lentus</i>	<i>P. comarrhenus</i> ^b
<i>P. osterhoutii</i>	<i>P. cyananthus</i>
<i>P. pachyphyllus</i>	<i>P. cyaneus</i>
<i>P. secundiflorus</i> ^b	<i>P. cyanocaulis</i>
<i>P. versicolor</i>	<i>P. fremonti</i>
	<i>P. garretti</i> ^b
Section <i>Aurator</i> ^a	<i>P. glaber</i> ^b
<i>P. albidus</i> ^b	<i>P. halli</i>
<i>P. auriberbis</i>	<i>P. kecki</i>
<i>P. calcareus</i>	<i>P. laevis</i>
<i>P. cleburnei</i>	<i>P. leiophyllus</i> ^b
<i>P. cobaea</i> ^b	<i>P. mensarum</i> ^b
<i>P. concinnus</i>	<i>P. neomexicanus</i> ^b
<i>P. dolius</i>	<i>P. nudiflorus</i>
<i>P. eriantherus</i> ^b	<i>P. parvus</i>
<i>P. gormani</i>	<i>P. payettensis</i> ^b
<i>P. grahami</i>	<i>P. pennellianus</i>
<i>P. guadalupensis</i>	<i>P. perpulcher</i>
<i>P. jamesi</i>	<i>P. saxorum</i>
<i>P. miser</i>	<i>P. scariosus</i>
<i>P. moffatti</i>	<i>P. speciosus</i> ^b
<i>P. monoensis</i>	<i>P. strictus</i> ^b
<i>P. nanus</i>	<i>P. subglaber</i>
<i>P. parvislorus</i>	<i>P. tidestromi</i>
<i>P. pumilus</i>	<i>P. uintahensis</i> ^b
<i>P. triflorus</i> ^b	<i>P. unilateralis</i> ^b
<i>P. whitedi</i>	<i>P. virgatus</i>
	<i>P. wardi</i>
Section <i>Elmigera</i>	Section <i>Facicularis</i>
<i>P. barbatus</i> ^b	<i>P. Kunthi</i> ^b
<i>P. eatoni</i> ^b	

^a Species belonging to sections *Anularius* and *Aurator* may be used in crosses with considerable difficulty. This is due in part to flower morphology and in part to what appears to be genetic isolating factors.

^b Species marked thus have been successfully used in crosses.

The breeder may choose to attempt to bring additional species into the breeding complexes. This is more difficult but by using the proper hybrid as a female parent he may hope to bring most of the species listed in Table 1 into the breeding complex.

The breeder may choose to attempt new interspecific crosses and will find many species pairs in complete reproductive isolation. Interspecific crosses are, in the authors' opinion, to be resorted to only when methods one or two cannot be used or in genetic studies. An exception to this exists in the subgenus *Dasanthera* where all members of the group are apparently interfertile and produce hybrid swarms where they make contact.

The *Peltanthera* of the southwest produce intrasectional hybrids in nature as reported in "The California Penstemons" by Everett (7). These hybrids and others are listed in Table 2. (2-9) A population of *P. angustifolius* and *P. secundiflorus* make contact in the Wildcat Hills area and show evidence of gene exchange. However, the possibility of interspecific and intersectional hybridization in other

Table 2. Natural, garden and controlled species hybrids in the genus Penstemon.

Abbreviations used in Table: A—*Anularius*; AU—*Aurator*; D—*Dasanthera*; E—*Elmigeria*; Hesp—*Hesperothamnus*; G—*Graciles*; H—*Habroanthus*; No.—*Nothochelone*; P—*Peltanthera*; Cont.—controlled cross; Gar.—Chance cross in a garden; Nat.—natural cross in the wild.

Hybrid species parents	Sectional affiliation ^a	Origin	Reported by—
Flathead Lake <i>P. barbatus</i> x ?	E x H	Nat.	Johnson, Anna
<i>P. barbatus</i> x <i>P. comarrhenus</i>	E x H	Nat.	Gould & Phillips
<i>P. clutei</i> x <i>P. palmeri</i>	P	Gar.	Saltzer, Mrs. J.
<i>P. canescens</i> x <i>P. hirsutus</i>	G	Gar.	Bennett, R. W.
<i>P. fruticosus</i> x <i>P. lyalli</i>	D x No.	Nat.	Davidson, L. Herbert, M.
<i>P. glaber</i> x <i>P. cobaea</i>	H x AU	Gar.	Viehmeyer, G.
<i>P. spectabilis</i> x <i>P. cordifolia</i>	P x Hesp.	Gar.	Saltzer, Mrs. J.
<i>P. grandiflorus</i> x <i>P. murrayanus</i>	A x P	Cont.	Fate, Fred
<i>P. unilateralis</i> x <i>P. labrosus</i>	H x E	Cont.	Viehmeyer, G.
<i>P. antirrhinoides</i> x <i>P. cordifolius</i>	Hesp.	Nat.	Keck, D. D.
<i>P. centranthifolius</i> x <i>P. grinnelli</i> = x <i>P. dubius</i>	P	Nat.	Davidson, A.
<i>P. centranthifolius</i> x <i>P. spectabilis</i> = x <i>P. parishii</i>	P	Nat.	Keck, D. D.
<i>P. grinnelli</i> x <i>P. speciosus</i> = x <i>P. peirsoni</i>	P x H	Nat.	Munz & Johnson
<i>P. palmeri</i> x <i>P. spectabilis</i> = x <i>P. bryantae</i>	P	Nat.	Keck, D. D.
<i>P. pseudospectabilis connatifolius</i> x <i>P. eatoni undosus</i> = x <i>P. crideri</i>	P x E D	Nat.	Nelson, A.
Shrubby penstemon, subgenus <i>Dasanthera</i>		Nat. Cont.	Many reports of hybrid swarms

^a *Dasanthera*, *Nothochelone* and *Hesperothamnus* are subgenera, not section.

than the Flathead Lake hybrid complex is a largely unexplored but potentially promising field for the hybridist.

The listing in Table 2 is by no means complete but it does indicate possibilities for new combinations of germ plasm.

The frequency of natural crossing between species and the Flathead Lake complex has increased to a degree that has caused the American Penstemon Society to list species seed grown in gardens separately from that collected from natural stands.

SPECIES CROSSES

The hybridization of pure species is a challenge to breeders. The difficulties are many but rewards may be great. Species exist as entities because they are isolated from each other and do not hybridize. They are prevented from crossing by distance (allopatric species), or gene exchange is prevented by reproductive isolating mechanisms, though they share a common habitat (sympatric species).

The breeder who attempts to cross species must expect failure far oftener than success. Yet it is he who, with his rare successes, will provide the building blocks basic to future progress. As each successful interspecific hybrid is produced, a link in the chain of reproductive isolating mechanisms breaks. With each such break, new areas are opened for exploration.

It is probable that most of the species belonging to the sections of the genus listed in Table 1 can be hybridized with the Flathead Lake Complex. These represent only about one-third of more than 300 species, subspecies and races native to North America. Extensive as the present exploration of the genus has become, there are many important areas untouched.

Examples of the possibilities and the needs for further exploration are:

1. In the Rocky and Cascade Mountains, on the high plateaus and mesas of the Great Basin and across the southwestern deserts are found the subgenera *Dasanthera*, *Hesperothamnus* and *Saccanthera*; and the section *Ericopsis*. These groups have among their species some of the most ornamental forms of penstemon. All of them include shrubs and subshrubs and it seems likely that interhybridization might well yield shrubby plants of wide adaptation and high ornamental value.

2. The great section *Spermunculus*, numbering about 60 species, inhabits a vast range of habitats. While not as showy as some of the western species, they still include many excellent ornamental forms. Even more important, some of the eastern members of the section have characters for disease and insect resistance lacking in the natives of the plains and mountains. These qualities make it important that these species be brought into the breeding program.

3. The southern species of section *Fasciculus*, e.g., *P. campanulatus*, *P. gentianoides*, *P. gentryi*, *P. hartwegi*, *P. isophyllus*, *P. kunthii*, *P. perfoliatus* and *P. pulchellus*, also have high disease resistance and large, brilliant flowers. These should certainly be included in breeding programs that will combine their disease resistance and flower quality with the hardiness of northern penstemons.

Before these can be utilized it will be necessary to discover intermediary forms that can be used to inactivate the isolating mechanisms that separate them. Presently, most attempts to hybridize within and between these important groups of species have not been successful. A few hybrids are known and most of these are intrasectional. Intersectional crosses should be attempted to discover or produce intermediaries that would bridge gaps presently "unbridged."

The hybridizer adventurous enough to attempt to bring strongly isolated species into a breeding complex must be prepared to make hundreds and possibly thousands of crosses in the hope of producing the single fertile individual that might be used as an intermediary in gene exchange. In so doing, he will be adventuring beyond the frontiers of present knowledge and be strictly "on his own." Table 2 gives a list of known hybrids for his guidance.

The hybrid material listed in Table 2 probably represents only a fraction of the hybrids that have occurred in nature and in the garden. Under natural breeding conditions the chance hybrid usually fails to persist because it cannot compete with the parental species or because of backcrossing with a parental form.

In the first case, the hybrid simply disappears from the breeding population.

In the second case, the hybrid merges with the parental species to which its germ plasm adds some increased variability.

Another phenomenon encountered in nature is the occurrence of "hybrid swarms," which occur where the ranges of interfertile

species overlap. The hybrid swarm, consisting of individuals in which characters normally restricted to the isolated species are combined, arises at the point of contact. The swarm may persist for long periods of time without spreading far beyond this point (the authors would suggest the hybrid swarm and immediately adjacent individuals of the parental species may have particular value as a source of breeding material, because of their inherent variability).

Hybrid swarms do not "swamp" the parental species, though it is conceivable they might do so if an environmental change unfavorable to the parental forms should occur.

In the garden, where many species are brought into intimate contact, an entirely different situation prevails. The hybrid has a greater chance of survival. It is likely to be noticed because of its greater vigor and different appearance, and its seed collected and planted. The grower may not recognize it as a hybrid but the fact that it is different may assure its perpetuation.

Observations of seedling populations produced from garden-grown seed indicate that gene exchange between species grown together in the garden is occurring at an ever increasing rate. Such gene exchange is significant since it indicates the reproductive isolation which effectively separates species in nature may fail when those species meet in the artificial habitat of a garden. Careful observation of garden material should discover forms valuable for breeding purposes. Though the area of species hybridization is a difficult and often a frustrating one, it is fascinating. The plant breeder with the inquiring type of mind will find it a challenge worthy of his attention.

BREEDING BEHAVIOR

In many ways the inheritance of color in penstemon crosses follows the patterns of color inheritance in Snapdragon (*Antirrhinum majus*) with various modifying genes involved. Most of the blue x red crosses give a purple F₁ but red in the F₂ generation is often diluted to corals and pinks.

Plant size is controlled by many genes (multifactorial) and F₁ seedlings are nearer to the larger parent in size. This may be an expression of hybrid vigor (heterosis).

Perhaps the most important result of hybridization is the effect upon garden fitness of the resulting hybrids. Whereas the species is

adapted to a particular habitat, the hybrid usually has wider range of adaptation in the F₁. In the F₂ the population segregates for a still greater range of adaptation.

It also seems evident that disease tolerance increases in hybrid populations and that characters for disease resistance may be cumulative in certain interspecific combinations. This, if true, may go far toward making the penstemon a better garden subject. Uhlinger at the University of Nebraska North Platte Station and Viehmeyer in his nursery have selected segregates that are superior in leaf-spot tolerance. These are being intercrossed in hope of further increasing disease tolerance.

SOURCES OF BREEDING MATERIAL

The would-be penstemon breeder is faced with the problem of obtaining breeding material. There are few commercial sources of penstemon seed or plants at present but this situation seems likely to change rapidly. The breeder has two possible sources of breeding stock. He may collect species from the wild—a slow and costly process if he desires a wide range of material—or he may obtain material from others.

Fortunately, the American Penstemon Society, a non-profit organization, maintains a seed exchange for its members and anyone can become a member by paying a small membership fee. (Secretary of the Society is Mrs. Merle Emerson, P.O. Box 64, Somersworth, New Hampshire 03878; Seed Exchange Director, Mrs. Robert McQueen, Wedekind Rd., Sparks, Nevada 89431.) This exchange lists over a hundred species as well as most of the hybrid forms that are appearing. Seed is collected from both wild stands and garden-grown populations. New species and new hybrids appear in the list annually.

PENSTEMON PROPAGATION

Propagation by Seed

Penstemons are easily grown from seed if the grower simulates the conditions existing in the native environment of each species. These are plants either directly or recently from the wild, where for thousands of years they have adapted to specific environmental

conditions. They are often adapted to a narrow range of habitat and do not thrive under ordinary garden culture.

In nature, seed falls to the ground where it germinates with minimum soil coverage. In the garden, care should be taken not to cover the seed too deeply. Large-seeded kinds will tolerate seed covered to 1/4 inch but the fine-seeded kinds should not be covered with more than 1/16 inch of soil or may be surface-sown and only pressed into the soil.

Seed should be sown in well prepared, very firm seedbeds any time between mid-October and early March. Most species are native to cold climates and their seed germinates better if exposed to low temperatures between planting and germination. Germination of seed exposed to low temperature is generally higher than that of seed sown in the spring. Indeed, if planting is delayed until soil temperatures become warm, seed may not germinate until the following year. Removing the seedcoats by hard rubbing or by rubbing on a sheet of sandpaper makes the seed easier to plant. The sandpaper treatment seems to have a beneficial scarifying effect in some cases.

A surer method of starting penstemon from seed is to plant the seed in pots or flats in midwinter and expose these to cold for several weeks. After receiving the cold treatment, the flats may be taken inside, where germination should occur in about ten days. If the flats are taken inside in February, and forceful culture given, considerable bloom may be expected during late summer and fall. Early first-season bloom is important to the breeder, for it permits him to grow a generation a year.

If seed is from controlled crosses or is limited in quantity, the surest method of obtaining plants is to plant in a sterile growing medium and feed with a nutrient solution. This method is recommended for all rare seed and is almost mandatory for the fine-seeded species of *Dasanthera*, *Saccanthera* and *Spermunculus*.

Here are three formulas for growing medium the authors have used.

Formula 1. One part each, by volume, washed river sand and concrete aggregate grade vermiculite. The sand must be washed completely free of silt before being mixed with the vermiculite.

Formula 2. Two parts by volume of sharp sand, two parts horticultural perlite and one part peat moss.

Formula 3. Two parts garden soil (sterilized), two parts horticultural perlite and one part peat moss. Fill the flat 2/3 full and cover with an inch of milled sphagnum. Sow the seed in the sphagnum.

Flats are filled with either mixture, and sides and corners are packed firmly. Seed then is planted as it is in soil, though planting depth may be slightly greater because of the very porous nature of the medium. After exposure to cold the flats are brought inside and watered with a nutrient solution. Any of the completely soluble fertilizers used for hydroponic culture are satisfactory. At North Platte, Rapid-Gro, Hyponex and Plant-Marvel have given good results.

Perhaps the greatest advantage of soilless culture is the almost total elimination of seedling diseases. Disease control is the most important feature of seedling culture and is particularly critical in starting many species. Another advantage of soilless culture is the control which the grower may exercise on rate of growth. Plants may be forced into rapid growth by regular weekly feeding, or growth may be stopped by withholding fertilizer and plants may be held in good growing condition.

When seedlings in the seed flat reach the four to six leaf stage, they may be transplanted to other flats, spaced 2½ x 2½ inches apart, or to individual pots for growing to sizes suitable for field planting. Handled thus, and transplanted to the field in late May or early June, many plants bloom soon enough to ripen seed the following fall. This is a decided advantage to the breeding program.

In the field, plants should be spaced a foot apart in the row. Rows should be spaced widely enough to permit cultivation. In the breeding blocks at the North Platte Experiment Station, plants are spaced a foot apart in the row and rows are spaced 40 inches apart to allow tractor cultivation. In the border, plants should be spaced one foot x one foot for all but the smaller kinds. For very strong-growing kinds a wider spacing may be desirable.

Propagation by Division and Layering

Many penstemon species and species hybrids are readily increased by division. Two-year clumps may yield as many as 10 or more divisions. Both the number and the quality of divisions may be increased by filling soil or sand into the base of the clump a year prior to division to cover the base of side shoots. Divisions are so

easily handled they may be established in the open even though taken when the plant is in full bloom. It is advisable, however, to cut divisions back and keep them well watered during establishment. Spring or early fall division is best.

Layering is particularly effective with species of *Dasanthera* and *Ericopsis*, and with the little red-flowered *P. pinifolius*. This group layers naturally and the rate of increase can be accelerated by mounding the many stemmed clumps.

Propagation by Cuttings

Most species of penstemon may be increased by cuttings, although some are difficult and slow to increase in this manner (e.g., the Fate-Seeba hybrids, *P. grandiflorus*, *P. murrayanus*, etc.). Cuttings require closer attention and a longer rooting time than do cuttings of such ornamentals as chrysanthemum and geranium. During the first few days after cuttings are set, frames covered with glass or plastic to maintain high humidity must be kept close to reduce transpiration and the tops should be syringed frequently on hot, dry days.

If cuttings are to be rooted in large numbers an intermittent mist system is a necessity. Such systems consist of a water supply under pressure and a time clock to activate and stop the mist.

Cuttings may be taken at any time during the growing season or from forced plants in winter. Cuttings may be softwood tip cuttings or may be cuttings from firmwood stems.

Tip Cuttings—These are taken from the terminal ends of growing shoots and are usually one or two inches long. Generally these are from basal shoots but in some species axillary shoots develop at the bases of flowering shoots. These stem and basal shoots often have root primordia and root quickly.

Cuttings should be taken with a very sharp knife. The cut should be made just below a node. If the cutting is very leafy the lower leaves should be removed and the rest of the foliage reduced in area to reduce transpiration (see Fig. 2).

Single Node and Single Eye Cuttings—Where rapid increase is desired, the propagator may resort to single node and single eye cuttings. These are taken from flowering stems or from elongated shoots. Single node cuttings are simply short pieces of stem with two

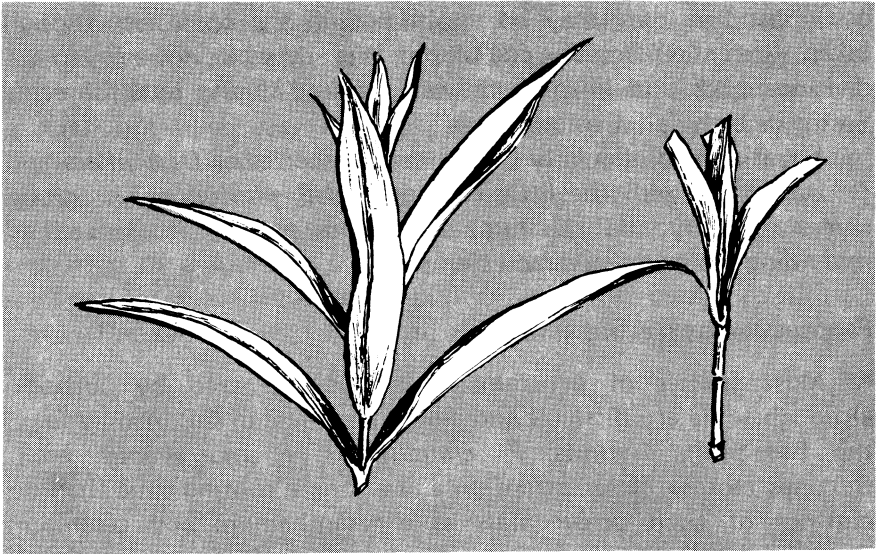


Fig. 2: Tip cutting. Cutting at left as taken from the plant. At right, ready for setting.

leaves attached. Single eye cuttings are the two halves of a single node cutting split down the middle (see Fig. 3).

Striking the Cuttings—Two methods have been satisfactory in striking penstemon cuttings. A close frame with bottom heat, and constant or intermittent mist, have given good results.

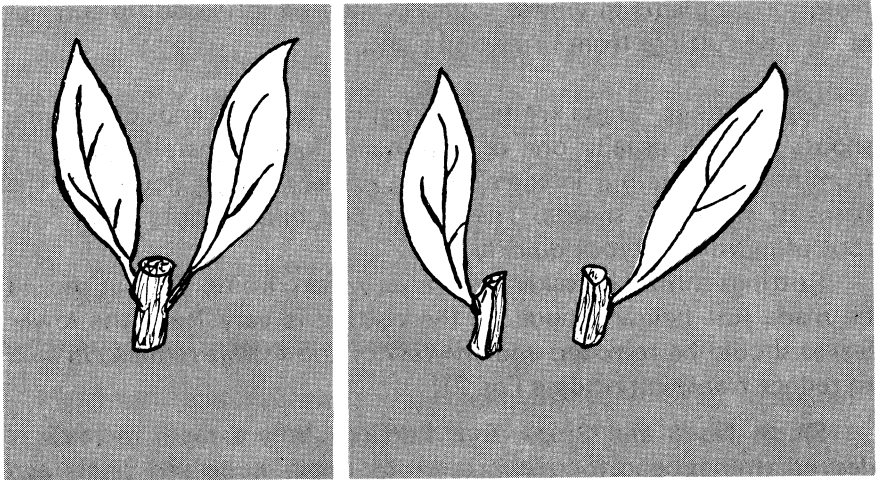


Fig. 3: Single node cutting at left. In drawing at right, the single node cutting has been split down the center to make two single eye cuttings.

If the close frame is used, it should be protected from full sun to avoid danger of scalding the cuttings. The close frame may be covered with glass but polyethylene film is less costly and entirely satisfactory. It is important that humidity be kept high during the first 10 days after the cuttings are set. After the cuttings are callused, less attention is necessary. If many cuttings are to be struck, a permanent frame is desirable. If only a few cuttings are to be rooted, they may be inserted in a flower pot of rooting medium and the pot enclosed in a polyethylene bag.

Constant or intermittent mist systems are best for rooting cuttings, because they eliminate much of the risk, increase the percentage of cuttings struck and require less attention from the grower. Mist is delivered through special nozzles and keeps the cutting foliage wet during the rooting season. Good misting nozzles will deliver as little as one gallon per hour. The water should be turned off in the evening and on in the morning, either by hand or with a time clock and solenoid valve.

Beds for misting should be located in full sun but must be protected from air currents that will drift the mist away from the cuttings. This means they must be enclosed in some manner that will control air currents but that will not exclude light. Where either constant or intermittent mist is employed, provision must be made to dispose of excess water.

Rooting Mediums

Perhaps the best of all rooting mediums is the expanded lava rock known as perlite. This material has high water-holding capacity and perfect drainage characteristics.

At the North Platte Experiment Station a mixture of equal parts of sand and perlite has given satisfactory results. Vermiculite may be substituted for perlite in the mixture but vermiculite used alone tends to become waterlogged.

The close cutting bed should be filled with the chosen rooting medium to a depth of 3 to 5 inches and should have at least 6 inches of air space above the surface of the medium. It should have a transparent cover to admit light. Bottom heat is best provided by soil heating cable laid beneath the rooting medium. Temperature should be controlled by a soil thermostat buried in the medium.

At the North Platte Station, cuttings are set in metal flats that are kept in the close frame until rooting starts and then moved to the greenhouse bench. This method is desirable where a variety of plants are being propagated because it permits removal of flats that can safely be placed on the open greenhouse bench and allows a continuous succession of flats of cuttings to be rooted in a single cutting frame.

Setting the Cuttings

After cuttings like those shown in Figs. 2 and 3 have been taken, they should be set immediately. Cuttings should never be pushed into the rooting system. This may injure the cutting and increase the danger of rot organisms attacking it. A slot should be opened in the rooting medium with a thin tool of some sort (a wooden pot label is good) and the cuttings should be placed in this slot. The rooting medium is then firmed about the cutting to insure intimate contact between cutting and medium. Before being placed in the slot, the base of the cutting should be dipped in a rooting hormone.

Penstemon cuttings root rather slowly, usually taking three or four weeks before they are ready for potting. Another three or four weeks must pass before the new plants are established and hardened for transplanting to the field. If ready for field transplanting by June 1, most kinds will bloom by fall. Summer struck cuttings may be field-planted by September 1 and be well established before freezing weather. If planting is delayed until after September 1, the propagator would be wise to transplant the cuttings to frames, where they can be mulched with coarse litter over the winter months.

PENSTEMON DISEASES²

The use of penstemons as garden plants is so new that our information about the diseases and insects that attack them is far from complete. It is certain that both will be important and that control methods will need to be determined. Our present knowledge is so sketchy that we can offer only suggestions in many areas. This is

²The authors express appreciation to Dr. John Weihing, Professor Plant Pathology (Agricultural Extension) and Superintendent, University of Nebraska Scotts Bluff Station for his advice and assistance in preparing the section on penstemon diseases.

particularly the case in disease control where the whole area must be explored. Pathogens must be identified and the best means of prevention discovered.

In the authors' opinion, disease is likely to decide the place of penstemons in horticulture. Bringing these wild species into the garden, growing them in habitats to which they are poorly adapted and exposing them to pathogens they seldom encounter in nature, sets the stage for trouble.

It appears that some of the "difficult" species are difficult because of diseases that either destroy or so damage them that they lose their ornamental qualities. Disease is a major reason why species from the arid and semi-arid plant growth regions fail in eastern and far western gardens. This has been true at North Platte and there is every reason to believe the problem would be critical in more humid climates.

Many of the pathogens that cause penstemon diseases are unidentified. Growers speak of root rot or leaf spot that damages or destroys plants but do not know the pathogens responsible, their life histories or control methods. Further, in most gardens no attempt is made to prevent disease. If a species or hybrid escapes disease it is a "good" penstemon; if it is attacked it is a "poor" one.

Leaf Diseases

Leaf spots. Several fungi attack the foliage of penstemon, causing a leaf spot symptom. The most common and severe noted at the North Platte Experiment Station is *Cercospora penstemonis*. It causes dark gray spots that vary in diameter from 1/8 to 1/2 inch. When these spots are numerous they coalesce to form large irregularly shaped dead areas or completely kill the leaf.

Other fungi that have caused leaf spots on penstemon are *Cercospora nivosa*, *Phyllosticta antirrhini*, *Septoria penstemonis*, *Ascochyta penstemonis* and *Sphaceloma penstemonis*. All of these organisms can live over the winter in old, dead, infected foliage. They form spores in the spring that are caught up by air currents and are carried to the new spring foliage. In the presence of moisture such as dew, rain or sprinkler irrigation the spores germinate and cause infection. Within the spot that results from infection, thousands more spores are produced which will contaminate more foliage and cause further infection.

The leaf spot diseases can be controlled by protecting the foliage from infection through (1) removing the old dead foliage before growth starts in the spring and (2) spraying with a protective fungicide.

Fungicides that should control most of these leaf spots include Zineb, Captan, Maneb, Phaltan and the copper-containing compounds. Consult with your state Extension plant pathologist for disease identification and recommended control if you fail to control a leaf spot disease. Thorough coverage of the foliage with the fungicide is necessary for satisfactory control among the susceptible sorts. Such coverage can be attained by adding a wetting agent to the spray solution. It will be necessary to spray the susceptible types every 7 to 14 days to keep a protective fungicide film over the entire plant surface.

Powdery mildew. Powdery mildew (*Erysiphe cichoracearum*) has been noted on penstemon in the state of Washington. This disease appears as a whitish mildew growth on the surface of the leaves, causing them to become crinkled and distorted. This same organism attacks many other ornamentals: achillea, anchusa, artemisia, aster, begonia, boltonia, calendula, companula, chrysanthemum, clematis, coreopsis, cosmos, dahlia, delphinium, eupatorium, gaillardia, golden-glow, goldenrod, helenium, hollyhock, inula, mallow, mertensia, phlox, salvia and zinnia to name a small selection of the 280 or more plants that powdery mildew will attack.

The powdery mildew fungus lives over the winter on old infected foliage. It can easily be controlled by dusting with sulfur or by spraying with wettable sulfur or one of the new specially developed mildewcides containing one of the Dinitro-phenyl crotonate compounds.

Rusts. Several rust species have been reported on penstemon throughout the United States. *Puccinia andropogonis* var. *penstemon* is common in Nebraska and throughout the eastern United States. This rust has an alternate host, *Andropogon*. In the western states, *Puccinia penstemonis*, *P. confragae* and *P. palmeria* have been reported as attacking penstemon but no alternate host has been indicated.

Rust appears as spots which are filled with an orange to reddish dust-like material. This material is actually a mass of microscopic spores. The rusts can be readily controlled by dusting well with sulfur or spraying with wettable sulfur or Zineb.

Soil Borne Diseases

Stem and crown rot. Stem and crown rot caused by *Sclerotium rolfsii* has been noted in the eastern and southern United States where this organism is commonly destructive on numerous ornamental plants. It requires moderately warm (70^o-100^o F.) and humid weather for development.

The first sign of this disease is the development of white wefts of fungus growth at the base of the stem, spreading up in somewhat fan-shaped fashion and occasionally growing out over the soil in wet weather. Plant tissues rot where the fungus has grown. The fungus produces small, round, tan bodies (sclerotia) the size, shape and color of mustard seed on the surface of the affected crowns and stem.

Control of *S. rolfsii* is difficult. The sclerotia are asexual propagation bodies that are extremely hardy to weather adversities and to chemicals. The home gardener in the region where this disease organism is present should watch for it and remove blighted plants with surrounding soil. Pouring a 1 to 1000 solution of mercuric chloride over the hole and crown of surrounding plants will prevent spread of the disease but will not kill the sclerotia that may have accidentally fallen to the soil. Soil that has become heavily infested with this organism should be sterilized with good sterilant such as chloropicrin, formaldehyde, Vapam or Mylone.

Root knot. The common root knot nematode, *Heterodera marioni*, which attacks over 1400 species of plants (most field, garden, ornamental and fruit crops except grains and grasses) has been reported as affecting the roots of penstemon. It causes the plants to wilt, turn yellow and die. The chief diagnostic symptom is the presence of small or large swellings or galls on the roots. They may be round or elongate or irregular in shape.

The female larvae of the root knot nematode enter the roots where they develop to maturity. As larvae, they are microscopic eel-shaped, wormlike organisms. The mature female becomes pear-shaped, white and glistening and may be seen as a white dot with the unaided eye. She extrudes a sac filled with 500 to 2000 eggs within the course of two or three months. The larvae move from the decaying knot and attack a root, causing another gall. The length of cycle from egg to egg varies with temperature. At about 80^o F. a cycle may be completed in only 25 days while at 67^o F. an average of 87 days is required per cycle. The root knot nematode is common throughout the U.S.

Nematode-infested plants cannot be rid of this pest. It is necessary to treat the soil and then plant clean plants. A number of excellent nematocide chemicals are available, including methyl bromide, ethylene dibromide and dichloropropane-dichloropropene. These are sold under various trade names. Follow the manufacturer's recommendations for application.

Virus Diseases

Cucumber mosaic. This disease appeared among the penstemon plantings at the North Platte Experiment Station where it caused stunting and leaf distortion. The causal virus is probably spread by some aphid species since peach, potato, cotton and lily aphids are proven vectors of this virus among its numerous other garden plant and weed hosts. Aphid control will not give absolute control of cucumber mosaic but may help to keep the incidence at a low level. Thus far, symptoms of cucumber mosaic have appeared only on species belonging to sections *Anularius* and *Peltanthera*.

No other virus diseases are reported in penstemon.

INSECTS THAT AFFECT PENSTEMON³

Aphids

These are the soft-bodied "plant lice" of the garden which may do considerable damage to plants if they are not controlled. Malathion is a good control for many kinds of aphids.

Cutworms

Cutworms may destroy young plants but are seldom serious in established plantings. They can be controlled with dieldrin or heptachlor.

False Plant Bug (*Nysius raphanus* Howard)

This small, greyish, almost silvery plant bug is about one-eighth inch long. At North Platte it has been a serious pest on radishes and

³The authors express appreciation to Dr. Kenneth Pruess, Associate Professor of Entomology at the University of Nebraska, for his assistance and advice in preparing the section on insects that attack penstemon.

lettuce and in 1959 it destroyed the bloom of a large penstemon planting at the Experiment Station by feeding on the young, growing shoots. The insect is inconspicuous and may be overlooked until serious damage has occurred. This pest may be represented in other parts of the country by other species. It is easily controlled with malathion or dieldrin.

Flea Beetle (*Dibolia* sp.)

The larva of this flea beetle is a leaf miner and is one of the most serious penstemon pests at the North Platte Station. The adult is a one-eighth inch long, shiny green beetle with an orange head and thorax. It is an active insect that jumps to the ground when the plant is disturbed. Eggs are laid in notches cut in the leaf and the flattened orange larva feeds within the leaf, protected from insecticides and predators by the leaf epidermis. The pest produces several broods during the growing season. Late season populations may be numerous enough to defoliate plants.

Mature larvae leave the leaf, drop to the ground, dig in and form a pupa chamber within the top inch of soil. After a brief rest, the adult emerges to repeat the cycle. Adults overwinter under debris, becoming active and feeding on warm days.

This leaf mining flea beetle seems to prefer penstemons of the Flathead Lake Complex and species belonging in sections *Aurator*, *Habroanthus* and *Elmiger* but appears to avoid species belonging to sections *Anularius*, *Saccanthera*, *Ericopsis* and *Fasciculus*.

At the North Platte Station, the flea beetle has been controlled with chlordane and malathion. Soil treatments with aldrin, dieldrin or heptachlor to destroy pupating insects may merit trial.

Grasshoppers

If numerous, grasshoppers may defoliate penstemon. These pests can be controlled with chlordane, aldrin, dieldrin and heptachlor.

Leafhoppers (many kinds)

These are small, swiftly moving insects, roughly wedge shaped, that either fly or jump at the least disturbance. The nymphs are small and inconspicuous and generally are found on the underside of leaves. They are more active than aphids. Leafhoppers are readily controlled with malathion.

Slugs

In Nebraska gardens, particularly in those where vegetation is lush and humidity high, the common garden slug may destroy small seedlings and transplants. This pest is difficult to control but will take poison baits containing metaldehyde.

Red Spider Mites

These tiny mites attack most penstemon species and hybrids during periods of hot, dry weather. They are generally found on the underside of leaves where they increase rapidly when climatic conditions are favorable. Badly affected leaves often show a greyish cast and the plant has an overall unhealthy look. Examination of the underside of such foliage will reveal the presence of tiny, almost microscopic mites under a very fine web that is attached to the leaf.

Sulfur and malathion have been effective in controlling spider mites at North Platte.

Tarnished Plant Bug or Lygus Bug

These are small, mottled brown bugs about three-sixteenths inch long. Fast moving and inconspicuous, they are likely to be overlooked. The nymphs look much like green aphids but are much more active. They damage plants by sucking juices and may cause deformed flowers or kill young growing tips. They may be controlled by malathion or most of the chlorinated hydrocarbons.

Verbena Bud Moth (*Endothenia hebesana* Walker)

The larva of this half-inch long moth is a serious penstemon pest and difficult to control because of the habit of tying leaves and buds together with a fine silky web. If flowering is over the insect may eat its way into a capsule and feed on the developing seed. Because of its habit of feeding within the capsule or leaf or bud cluster, contact insecticides are ineffective once the pest is established in such shelter.

The best control is prevention in the form of an insecticide with a long residual life. Growing plant parts should be sprayed at intervals of a week or ten days. This gives fairly good control but, since the insect rears several broods during a growing season, the treatment must be repeated at regular intervals. Chlordane has been

effective at North Platte. If only a few plants are involved, hand picking is effective. This insect has a wide range of host plants and has been observed on chrysanthemums, lilies, roses, strawberries and several other plants.

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