

Scrophulariaceae—Figwort family

Penstemon **Schmidel**

penstemon, beardtongue

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Growth habit, occurrence, and use. The genus *Penstemon* comprises about 230 species of perennial herbs and subshrubs, most of which are found in western North America. Although most of the species are herbaceous, there are many more subshrubby species than are treated here. Several shrubby species from California that were formerly included in the genus *Penstemon* have been transferred to the closely related genus *Keckiella* Straw. In the previous edition of the Seed Manual, Hylton (1974) treated these species under the name *Penstemon*.

Subshrubby penstemon species occur in most vegetation types of the western United States, from warm desert shrublands to alpine fell-fields (table 1). They are most often found on well-drained, rocky or sandy, infertile soils with sunny exposure. Some species, such as Bridges penstemon, are widely distributed and of wide ecological amplitude, whereas others, such as crevice penstemon, are restricted

both geographically and ecologically. Many penstemons are pioneer plants that occupy natural disturbances such as rock-slides, making them useful for erosion control along roadsides and for mined land reclamation. They are used to some extent as browse by domestic and wild ungulates, and the seeds are used by rodents, birds, and ants. But perhaps the most important use for penstemons is in ornamental horticulture. Many of the penstemons are among our most outstandingly beautiful wildflowers, and the subshrubby species are no exception (Nold 1999). They are easily grown in cultivation, and many species have found their way into garden catalogues specializing in plants for low-maintenance landscapes. One named variety that is commercially available is shrubby penstemon 'Purple Haze'. Some of the warm-desert species are not hardy in cultivation in the North, although some of these, for example, crevice penstemon, can be successfully grown in containers.

Table 1—*Penstemon*, penstemon, beardtongue: habitat and geographic distribution

Scientific name(s)	Common name(s)	Habitat*	Geographic distribution
<i>P. ambiguus</i> Torr.	moth penstemon, bush penstemon, gilia beardtongue	Sandy soil; desert shrubland, pinyon–juniper	S Nevada to S Utah, Kansas, & Oklahoma
<i>P. fruticosus</i> (Pursh) Greene	shrubby penstemon, bush penstemon	Shallow soils; spruce–fir, lodgepole pine	N Rocky Mtns from British Columbia to Idaho
<i>P. leonardii</i> Rydb.	Leonard penstemon, Leonard's beardtongue	Sagebrush–grassland to aspen–conifer	SE Idaho to S Utah
<i>P. linarioides</i> Gray	toadflax penstemon	Sagebrush–grassland to ponderosa pine	Utah & Colorado to Arizona & New Mexico
<i>P. petiolatus</i> Brandeg.	crevice penstemon, petiole beardtongue	Limestone crevices; warm desert shrubland	E Mojave Desert
<i>P. platyphyllus</i> Rydb.	sidehill penstemon, broadleaf beardtongue	Mountain brush; aspen– conifer	Wasatch Mtns, N Utah
<i>P. rostriflorus</i> Kellogg <i>P. bridgesii</i> Gray	Bridges penstemon	Warm desert shrubland to alpine	Widespread in W US
<i>P. sepalulus</i> A. Nels.	littlecup penstemon, littlecup beardtongue	Sagebrush–grassland to aspen–conifer	Wasatch Mtns, N Utah

Source: Cronquist and others (1984).

* May include forest type.

Flowering and fruiting. Penstemon flowers are borne in elongate racemes that are often held above the leafy stems, though this habit is often less pronounced in the subshrubby species. The flowers consist of a 5-toothed cuplike calyx, a tubular or snapdragon-like corolla made of 5 fused petals, 5 stamens mounted on the interior of the corolla tube, and a superior 2-chambered ovary that contains many ovules. One of the 5 stamens is sterile, that is, it has no anther, and is often covered with long hairs and exerted from the corolla, hence the name “beardtongue.” The flowers are pollinated by a variety of insects and hummingbirds, and flower form, color, and arrangement in each species reflect specialization to attract particular pollinators. Most penstemons flower in the spring or early summer, though some—for example, Bridges penstemon—are midsummer-flowering. Flowering is indeterminate, with the youngest flowers at the tip of each flowering stalk. After fertilization, the ovaries develop into 2-valved capsules that split open at the tip and sometimes along the sides. The numerous gray to black, angular seeds are dispersed by the shaking action of the wind.

Seed collection, cleaning, and storage. Penstemon seeds are usually harvested by hand-stripping or clipping the flowering stalks into containers. Capsules generally begin to split open from 6 to 8 weeks after the plants are in full flower, with those at the base of each stalk ripening first. Stalks can be clipped before the capsules start to open, as long as the seeds can be seen darkening through the ovary wall. If the stalks are clipped after the capsules begin to open, care must be taken to avoid excessive spillage during harvest. For most species, the window of opportunity for harvest is quite wide, as capsules are held upright on the plant and seeds are dispersed only gradually. The harvested material should be dried carefully to avoid molding, espe-

cially if it is collected when somewhat green. The capsules will open after harvest, and for small lots, the seeds can be shaken free and collected by screening. For commercial seedlots, processing with a hammermill or barley de-bearder, followed by a fanning mill, is the usual procedure. Seedlots can readily be cleaned to high purity (>95%).

Penstemon seeds are generally quite small, though size varies considerably among species (table 2). Viability at harvest is usually high (table 2). Damage by seed beetles and other insects during ripening is common, but unfilled and damaged seeds are usually removed in cleaning, so that yield rather than seed quality of the cleaned lot is affected. Penstemon seeds are orthodox in storage behavior, as they keep well in warehouse storage if maintained at moisture contents of 8 to 11%. There is little loss of viability during 5 years, and seeds stored for 15 years may still show viability as high as 50% (Stevens and others 1981, 1996).

Seed germination and testing. The germination requirements of penstemon seeds vary widely, both among and within species (Kitchen and Meyer 1991; Meyer and others 1995). Some species have seeds that are germinable without pretreatment and unaffected by chilling, whereas other species have seeds that are nondormant and negatively affected by chilling, and still others have seeds with a positive requirement for chilling (table 3). In general, seeds of species of the desert Southwest and coastal and cis-montane California are the least likely to have a chilling requirement, whereas those from the Great Basin, Rocky Mountains, and Sierras are more likely to require chilling. Within a species (Bridges penstemon, for example), the length of the chilling requirement is positively correlated with the length of time seeds are likely to spend under snow cover in winter (Meyer 1992; Meyer and Kitchen 1994; Meyer and others 1995).

Table 2—*Penstemon*, penstemon, beardtongue: seed data

Species	Seeds/weight				Mean % viability	Samples
	Mean		Range			
	/g	/oz	/g	/oz		
<i>P. ambiguus</i>	1,000	28,000	820–1,270	23,000–36,000	90	6
<i>P. fruticosus</i>	3,500	98,000	3,230–3,850	90,000–108,000	68	4
<i>P. leonardii</i>	1,250	35,000	900–2,220	25,000–62,000	84	8
<i>P. linarioides</i>	810	23,000	720–900	20,000–25,000	84	4
<i>P. petiolatus</i>	2,700	77,000	2,640–2,800	74,000–78,000	98	2
<i>P. platyphyllus</i>	1,460	42,000	1,390–1,590	39,000–45,000	95	3
<i>P. rostriflorus</i>	2,260	64,000	1,560–2,940	44,000–82,000	87	14
<i>P. sepalulus</i>	1,700	48,000	1,350–2,000	38,000–56,000	85	6

Source: Meyer (2002).

Table 3—*Penstemon*, penstemon, beardtongue: germination data after 0 to 24 weeks of chilling*

Species	0 wk	4 wk	8 wk	12 wk	16 wk	24 wk	Samples
<i>P. ambiguus</i>	35	21	19	10	16	31	3
<i>P. fruticosus</i>	6	19	14	19	40	83	4
<i>P. leonardii</i>	0	1	22	82	80	80	2
<i>P. linarioides</i>	0	0	1	6	12	10	2
<i>P. petiolatus</i>	100	—	—	100	100	100	1
<i>P. platyphyllus</i>	1	55	66	99	97	100	7
<i>P. rostriflorus</i>	18	17	54	83	—	98	3
<i>P. sepalulus</i>	3	25	37	83	86	100	2

Sources: Kitchen and Meyer (1991), Meyer (2002), Meyer and others (1995).

* Germination percentage for seeds subjected to 0 to 24 weeks of chilling at 1 to 2 °C followed by 4 weeks of incubation at 10/20 °C.

The germination requirements of penstemon seeds generally change very little in dry storage; dormancy status is affected only by conditions during time spent in the imbibed state (Meyer and others 1995). For species and populations from middle elevations in the West, there is rarely a natural dormancy-breaking treatment that will remove dormancy in all seeds of a lot. For those that respond positively to chilling, this is manifest as a fraction that will not respond to chilling of any duration. These seeds form a persistent seed-bank under natural conditions, and it is not known how they eventually become germinable. Treatment with gibberellic acid can remove seed dormancy or shorten the chilling requirement for many (but not all) species of penstemon (Kitchen and Meyer 1991). This method may or may not be feasible in a production setting, depending on the degree to which gibberellic acid affects seedling quality. Penstemon seeds germinate best at cool temperatures, and germination at temperatures higher than 20 °C may be completely suppressed, a fact to keep in mind when attempting to produce plants from direct sowing in the greenhouse (Allen and Meyer 1990). Light usually has little effect (Meyer and others 1995).

The quality of penstemon seeds may be evaluated using tetrazolium (TZ) staining, a germination test with chilling or gibberellic acid, or a combination of these. A general seed-testing rule for the genus has been adopted by the Association of Official Seed Analysts (Kitchen and others 1999). This test calls for 2 separate procedures. In the first procedure, seeds are placed on blotters saturated with 500 ppm gibberellic acid, chilled at 2 to 5 °C for 60 days, and incubated at 15 or 10/20 °C for 14 days. Post-test viability of ungerminated seeds is then determined with TZ staining. This procedure is used to determine total viability for the seedlot, and TZ staining on non-incubated seeds may be substituted. In the second procedure, seeds are incubated at

15 or 10/20 °C in the light for 28 days. This second procedure is used to determine the size of the nondormant fraction.

Tetrazolium staining is carried out by allowing the seeds to imbibe water for 24 hours, piercing their seedcoats with a needle, immersing them in 1% TZ for 12 hours at room temperature, and then bisecting them longitudinally for evaluation. The embryo is a small, sausage-shaped body embedded in the copious endosperm. Non-viable embryos usually do not stain at all but remain a yellowish color. Even light pink staining indicates a viable embryo, as evidenced by comparisons with maximum germination percentages for numerous seedlots (Kitchen and Meyer 1991). A simple cut test can be used in place of TZ staining for recently harvested seeds, as the presence of a firm, white, viable embryo is quite evident.

Field planting and nursery practice. Most penstemon species can be established from direct seeding. Seeds should be broadcast on a firm seedbed and lightly covered, raked, or pressed in. Planting should take place in late fall or early winter for most species, except in the summer rainfall areas of the Southwest, where seeds of nondormant species should be sown just before summer rains. Nondormant species may be spring-seeded in the North but may require supplemental water to establish. Penstemons are susceptible to fusarium wilt diseases in cultivation and should not be fertilized or overwatered. They are more likely to survive in coarse, rapidly draining soils that have not previously been used for agriculture. The young seedlings cannot survive heavy competition from weeds or aggressive perennial grasses.

Penstemons may also be readily produced from seeds in container culture. They grow well in a coarse medium in elongated containers such as those used to produce conifer seedlings. Seeds of nondormant species may be direct-sown, whereas chilled seeds or germlings may be planted for those

species with seeds that require chilling. The seedlings will be ready for hardening-off and outplanting in 3 to 4 months, but they can be held much longer if necessary. Survival of outplanted stock is usually high, as long as plants are watered-in well at the time of transplanting and care is taken

to eliminate air pockets around the roots. Plants both from direct seeding and outplanting usually flower the second year, and individuals of the subshrubby species can live for 10 years or more. If seed stalks are not clipped, most plants will readily self-seed.

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