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## Abstract

Survival, reproductive output, and transplant success were studied for an Iowa population of *Penstemon tubiflorus* (tube penstemon), a species that is rare to uncommon through much of its range. The population was discovered in 2003 and is one of only 6 populations that have been documented in Iowa. I began monitoring the new population when 2 cohorts were permanently marked, the first in 2005 and the second in 2007. I estimated survival, flowering, and reproductive output. Then, I introduced greenhouse-grown transplants to 2 new sites and the original site. Survival data showed that *P. tubiflorus* is a short-lived perennial (approximately 50% survival after 3 years) with substantial variation in the percentage of individuals that flower in a given year. Recruitment over the 5 years of monitoring varied from zero to 26 individuals per year. Transplant survival was site-specific. However, high survival and robust reproduction output of transplants at one site indicated that there are additional suitable sites near the parent population and suggested that these sites remain unoccupied due to limited seed dispersal. While it is unlikely that pollinator limitation is the cause of low reproduction, further study is needed on the pollination syndrome of the Iowa populations of this and other *Penstemon* species. Future studies should investigate the possibility that the species is limited by site-specific factors that inhibit germination and the survival of small seedlings.

## Keywords

Penstemon, rarity, prairies, recruitment, survival, transplant success

## Disciplines

Horticulture | Natural Resources Management and Policy | Plant Sciences

## Comments

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## SURVIVAL, REPRODUCTIVE OUTPUT, AND TRANSPLANT POTENTIAL OF *PENSTEMON TUBIFLORUS* (TUBE PENSTEMON)

Cathy Mabry<sup>1</sup>

**ABSTRACT.**—Survival, reproductive output, and transplant success were studied for an Iowa population of *Penstemon tubiflorus* (tube penstemon), a species that is rare to uncommon through much of its range. The population was discovered in 2003 and is one of only 6 populations that have been documented in Iowa. I began monitoring the new population when 2 cohorts were permanently marked, the first in 2005 and the second in 2007. I estimated survival, flowering, and reproductive output. Then, I introduced greenhouse-grown transplants to 2 new sites and the original site. Survival data showed that *P. tubiflorus* is a short-lived perennial (approximately 50% survival after 3 years) with substantial variation in the percentage of individuals that flower in a given year. Recruitment over the 5 years of monitoring varied from zero to 26 individuals per year. Transplant survival was site-specific. However, high survival and robust reproduction output of transplants at one site indicated that there are additional suitable sites near the parent population and suggested that these sites remain unoccupied due to limited seed dispersal. While it is unlikely that pollinator limitation is the cause of low reproduction, further study is needed on the pollination syndrome of the Iowa populations of this and other *Penstemon* species. Future studies should investigate the possibility that the species is limited by site-specific factors that inhibit germination and the survival of small seedlings.

**RESUMEN.**—Estudiamos la supervivencia, el rendimiento reproductor y el éxito de transplante en una población de *Penstemon tubiflorus* (tube penstemon) en Iowa, una especie rara o poco común en gran parte de su rango. Esta población fue descubierta en 2003 y es una de sólo seis poblaciones documentadas en el estado. El monitoreo de la nueva población comenzó cuando se marcaron permanentemente dos cohortes, una en 2005 y la segunda en 2007. Se estimó la supervivencia en la floración y el rendimiento reproductor. Transplantes crecidos en invernadero se introdujeron en dos nuevos sitios y en el sitio original. Los datos de supervivencia indicaron que esta especie es una planta perenne efímera (con una supervivencia de aproximadamente 50% después de tres años), con variación considerable en el porcentaje de individuos que florecen en un año determinado. El reclutamiento de la población nativa durante los cinco años fue monitoreado y varió de cero a 26 individuos entre años. La supervivencia de los transplantes fue específica de cada sitio. No obstante, una alta supervivencia y vigorosa rendimiento reproductor de los transplantes en un sitio indicaron que existen sitios adecuados adicionales cerca de la población parental, y sugiere que estos sitios permanecen desocupados debido a la limitada dispersión de semillas. Aunque es improbable que la causa de la baja reproducción se deba a una escasez de polinizadores, se requiere más investigación sobre el síndrome de polinización de las poblaciones de Iowa de esta y otras especies de *Penstemon*. Se debe investigar la posibilidad de que la especie se vea limitada por factores específicos al sitio que inhiben la germinación y la supervivencia de las plántulas.

*Penstemon tubiflorus* Nutt. (tube penstemon, white wand beardtongue) is one of 22 species of *Penstemon* that occur in the Great Plains region of North America (Great Plains Flora Association 1986), with 2 additional species recognized from the upper Mississippi Valley (Clinebell and Bernhardt 1998). Its range is centered in southwestern Missouri, northeastern Arkansas and Louisiana, and eastern Oklahoma and Kansas (USDA, NRCS 2009). It is typically found only in disjunct populations in the adjoining states of Texas, Mississippi, Tennessee, Illinois, Iowa, and Nebraska. Tube penstemon has also been found in widely scattered locations in Wisconsin, Kentucky, Ohio, Pennsylvania, New York,

Connecticut, Rhode Island, Massachusetts, Vermont, New Hampshire, Maine, and Canada; however, the plants found in New England and adjoining areas are considered adventive and naturalized (Great Plains Flora Association 1986).

Although tube penstemon appears to be extending its range westward in disturbed habitats (e.g., roadsides and old fields), it is currently listed as extirpated in Indiana, presumed extirpated in Ohio, and a state-listed species of special concern in Iowa and Tennessee (USDA, NRCS 2009). In a typology of rarity, tube penstemon appears to range widely and occur in several types of habitat, but it is constantly sparse; that is, it occurs in small, nondominant

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populations (Rabinowitz 1981). Despite the sparse populations in many parts of the species' range, a search of the literature revealed no information on basic demographic (e.g., longevity, recruitment) and reproductive features of the species that would explain its rarity and provide an underpinning for conservation and management. This information is especially important because the general consensus is that fragmentation is harmful to many native plants (Kwak et al. 1998, Hendrix and Kyhl 2000). Tube penstemon and other midwestern *Penstemon* species are native to tallgrass prairies, which have been reduced to <0.01% of their original area and persist as small fragments in the region (Smith 1997).

Most life history studies of *Penstemon* species have focused on aspects of reproductive and pollination biology (Clinebell and Bernhardt 1998, Clements et al. 1999, Mitchell and Ankeny 2001, Lewinsohn and Tepedino 2007). Only one of these studies included tube penstemon. In this study, a population in Missouri had a more restricted flowering period compared to 4 other *Penstemon* species and was also the only species pollinated extensively by the spicebush swallowtail (*Papilio troilus*) (Clinebell and Bernhardt 1998). Tube penstemon was not included in the pollinator-exclusion portion of the study, and information on the species' dependence on pollinators for fruit set versus its capacity for self-compatibility remains unknown. This information is important because it would indicate whether self-incompatibility combined with pollinator limitation restricts seed output and contributes to the sparseness of many populations. Studies of other rare *Penstemon* species have shown that seed set is not limited by lack of pollinator visits (Flessner and Stubbendieck 1992, Lewinsohn and Tepedino 2007), although this may not be the case for disjunct populations (Tepedino et al. 2007).

Much remains to be discovered about aspects of reproduction, colonization, and establishment for *Penstemon* species. To fully account for possible causes of rarity, full demographic studies are needed to identify potential bottlenecks in the plant life cycle (Münzbergova 2005). In particular, rare populations can be subject to demographic stochasticity or chance events in survival and reproduction that are unrelated to the environment (Menges 1986). Another possible explanation for bottlenecks is that even though less common species produce sufficient seed and are demographically stable, they are

limited by habitat specificity (Rabinowitz 1981), particularly by small and unusual habitats (Harper 1979), or are more vulnerable to environmental variation acting on demographic properties (Menges 1986). For example, *Penstemon haydenii* (blowout penstemon), a rare species in the Nebraska Sandhills, requires sand that has been exposed by active wind erosion, and *P. scarious* var. *albifluvis* (White River penstemon) in the Uintah Basin of Utah and Colorado requires shallow, calcareous soils stemming from oil shales of the Green River Formation (Lewinsohn and Tepedino 2007, Stubbendieck et al. 2007).

The purpose of this study was to establish baseline data on the survival, recruitment, reproductive output, and degree of self-pollination of *P. tubiflorus*, and to conduct a transplant study to gain insight into whether the species is limited by dispersal of seeds or by stringent site requirements. The overall goal of this work is to provide insight into the reasons for the species' sparse population size in Iowa and to provide a basis for a more detailed study of its reproductive and pollination biology.

#### METHODS

I discovered a new population of tube penstemon in 2003 at Camp Dodge, an Iowa Army National Guard base just north of Des Moines, Iowa. This population is one of only 6 total occurrences documented in Iowa and only the second documented since 1999. The other 4 populations date from 1934, 1940, 1950, and 1951 (John Pearson, Iowa Department of Natural Resources, personal communication). The population at Camp Dodge was first discovered during extensive surveys of 2 areas of about 2 ha each that had been maintained as mowed turf for decades but had developed components of native tallgrass prairie after mowing ceased. The population is located in an approximately 2-ha area with scattered trees and a mixture of native and nonnative grasses and forbs in the understory. The area was mowed multiple times during each growing season until 2002 and had a final mowing in fall 2003. Since then, there has been no management. The surrounding vegetation is a mosaic of mowed fields, fencerows, hayfields, sedge meadows, native prairie remnants, and wetlands. The area has been extensively surveyed, and no other populations of tube penstemon have been located. Soil type of the study site is Dickinson fine sandy loam. The plant composition of the study site is a diverse

mixture of native grasses, sedges, and forbs, with 132 native and 26 exotic species recorded at the site. Dominant grass and forb species include *Bromus inermis* (smooth brome), *Carex brevior* (plains oval sedge), *Carex molesta* (field oval sedge), *Anemone canadensis* (Canadian anemone), *Euphorbia corollata* (flowering spurge), *Heliopsis helianthoides* (ox-eye sunflower), *Monarda fistulosa* (wild bergamot), *Phlox pilosa* (prairie phlox), *Schizachyrium scoparium* (little blue-stem), and *Zizia aurea* (golden zizia). Scattered trees are dominated by *Quercus palustris* (pin oak) and *Juglans nigra* (black walnut).

Monitoring of the original population began in 2005 and has continued for 6 years. Plants were monitored at the time of flowering (June) and fruit maturation (August) each year, except for 2008, when they were monitored in June, and 2009, when they were monitored in early September. In 2005, twelve individual plants, which comprised all the individuals in the population that could be located, were permanently marked. For each plant, I counted flower and capsule numbers and measured stem height. For multi-stemmed plants, height was taken from the tallest stem. In addition, I collected a sample of 4 capsules per plant, which were dried and stored in individual packets. To estimate reproductive (seed) output, I counted seeds in each capsule and calculated a mean number of seeds per capsule. The estimate of total seed output was then obtained by multiplying the mean number of seeds per capsule by the number of capsules per plant. Percent survival and percent flowering for 11 of the 12 individuals of this cohort were recorded from 2006 to 2010. Due to troop training and foot traffic in the area, I could not relocate one individual after 2005, leaving a sample size of 11 for calculating percent survival.

In 2006–2010, I marked new recruits to this population and recorded survival of all previously marked individuals. In 2007, I collected reproductive data for a cohort of 26 recruited individuals. I counted flower and capsule numbers and measured stem height. In addition, I collected a sample of 3 capsules per plant from 12 randomly selected plants and estimated reproductive output by counting the number of seeds per capsule, calculating the mean per capsule, and multiplying this by the number of capsules per plant. Due to training and foot traffic that prevented relocation of all marked individuals, sample size was 23 in 2008 and 20 in 2009 and 2010. To determine whether there

was temporal variation in plant attributes, data for this cohort were compared with those from the original 2005 cohort.

I conducted a transplant study in order to assess whether dispersal or suitable habitat limited the establishment of new individuals. If dispersal is limiting, new populations should establish in suitable habitat once propagules are introduced. In contrast, if suitable habitat is limiting, introducing propagules will still fail to result in new populations because site conditions are unfavorable (Brudvig et al. 2011). In August 2005, I collected seeds from the 10 individuals that produced capsules. These were combined and stored dry until March 2006. Seeds were then cold-stratified from 23 March 2006 until 8 May 2006, when they were sown into flats at the Iowa State University Bessey Hall greenhouse. Two distinct sizes of rosettes developed in the flats: one large and one small. On 2 June 2006, the larger plants were moved to larger pots, while the smaller plants were maintained in flats. Growth continued until pots were moved to cold storage for the winter. Plants were moved outside in April 2007 until planting in May. To estimate plant size at the time of planting, I measured length and width of the 3 largest leaves on each plant before placing it in the ground. Large plant leaves had a mean length of 12.2 cm and width of 4.4 cm. Small plants were about half the size, with a mean length of 6.5 cm and width of 1.9 cm.

I selected 3 sites at Camp Dodge for transplanting. Tube penstemon typically occurs in dry upland prairies, in prairie remnants along railroads, on rocky limestone soils, and in open woods (Steyermark 1963). Tube penstemon may be outcompeted by tall dense vegetation (Ohio Department of Natural Resources 2010). Iowa populations have been found in prairie remnants and open fields (John Pearson, Iowa Department of Natural Resources, personal communication). Based on these descriptions, I chose 2 transplant sites that appeared to have a suitable combination of soil and vegetation structure. These sites were located approximately 0.5–1 km from the original population site. I also selected the site of the original population as a transplant site.

Both of the new transplant sites had relatively dry sandy soils and sparse vegetation cover. One transplant site was on a sandy flat area upslope from an old borrow site that is now a wetland. Both the borrow site and the uplands have

TABLE 1. Total population size and number of individuals recruited, 2005–2010, for *Penstemon tubiflorus* at Camp Dodge, Iowa Army National Guard, Johnston, Iowa.

Year	Population size	Number recruited
2005	12	—
2006	13	3
2007	37	26
2008	26	0
2009	25	6
2010	27	7

undergone extensive revegetation through both planting and natural recolonization, with wetland flora in the basin and a mixture of planted grasses and naturally colonizing forbs on the upslope area. This slope vegetation is predominantly *Bouteloua curtipendula* (sideoats grama), *Schizachyrium scoparium* (little bluestem), *Chamaecrista fasciculata* (partridge pea), *Crotalaria sagittalis* (arrowhead rattlebox), and *Strophostyles helvola* (wild bean). The second transplant site was an old field on sandy soils with a relatively sparse vegetation cover of cool-season grasses and native forbs dominated by *Bromus inermis* (smooth brome), *Lespedeza capitata* (roundhead lespedeza), and a small population of *Gentiana alba* (plain gentian). The third transplant site and the location of the native population had vegetation as previously described.

On 3 May 2007, I established 2 plots of 5 individuals of both large and small plants at each site, for a total of 10 large and 10 small plants. Plants were planted in 2 rows: one of 3 plants alternating with one of 2. Plants were placed approximately 0.5 m apart. In order to evaluate establishment under natural conditions, no management (e.g., supplemental watering or weeding) was carried out after planting. In June 2007, I recorded flower number per plant, and in August 2007, I recorded plant height and capsule number.

In order to estimate reproductive output, I randomly chose 4 plants per site and 3 capsules per plant for seed counts. I compared these data with the seed output per plant from the 2007 cohort of the natural population. Survival of transplants was recorded from 2007 to 2009; however, only transplants at the site of the original population could be monitored in the second season (2008). The former borrow site that received transplants was flooded by heavy rainfall in June, and the old-field site was disrupted by construction equipment. However, monitoring at all 3 sites was possible in 2009.

Finally, to evaluate whether tube penstemon is able to self-pollinate, I conducted a pollinator-exclusion study in 2010. A total of 15 plants flowered in 2010, 13 at the site of the original population, and 2 at the old-field transplant site. I selected 6 inflorescences to be excluded from pollination and bagged them with  $8 \times 10$ -inch bags made of mosquito netting. Three bagged inflorescences were compared with unbagged inflorescences on the same plant and 3 were compared with unbagged inflorescences on plants that were no more than 3 m away.

Inflorescences were bagged between 3 June and 7 June when the flowers were visible beyond the sepals but had not yet opened. They were removed on 9 July when flowering was complete and capsules had started to form. I counted the number of flowers and mature capsules per inflorescence to determine percent fruit set. I also harvested 5 capsules per stalk and calculated mean seed number per capsule.

Ninety-five percent confidence intervals were used to assess whether there were differences between the 2005 and 2007 cohorts, and to identify differences between the natural and transplanted populations in height, flower number, capsule number, percent fruit set, seeds per capsule, and total seed number. The intervals were also used to assess whether inflorescences excluded from pollinators differed in reproductive attributes compared to open inflorescences.

## RESULTS

Total population size from 2005 to 2010 varied from 12 to 37, with variation in recruitment among years (Table 1). In 2007, 26 new individuals were recruited into the population, resulting in a total population size of 37 individuals, the largest recorded in the 6 years of monitoring. Only 3 new individuals were recruited in 2006, zero in 2008, and 7 in 2010 (Table 1).

Percent survival of the original 2005 cohort decreased over time from 91% to 46%, while the percentage of individuals flowering over the same time varied from 0% to 38% (Table 2). Percent survival of the 2007 cohort also decreased over time, from 78% to 50%, with percentage of individuals flowering ranging from 33% to 20% (Table 2). Nonflowering individuals all persisted as basal rosettes. I did not detect differences in measured plant attributes between the 2005 and 2007 cohorts (Table 3).

TABLE 2. Percent survival and flowering over 5 years for 2 cohorts of a natural population of tube penstemon, *Penstemon tubiflorus*, at Camp Dodge, Iowa Army National Guard, Johnston, Iowa. Percent flowering is based on surviving individuals. One plant from the 2005 cohort and 3 plants from the 2007 cohort could not be relocated because of troop training in the area. These plants were excluded from calculations of percent survival.

	2006	2007	2008	2009	2010
Survival					
2005 cohort	10/11 (91%)	8/11 (73%)	6/11 (55%)	5/11 (46%)	5/11 (46%)
2007 cohort	—	—	18/23 (78%)	13/20 (65%)	10/20 (50%)
Flowering					
2005 cohort	2/10 (20%)	3/8 (38%)	0/6 (0%)	1/5 (20%)	1/5 (20%)
2007 cohort	—	—	6/18 (33%)	3/13 (23%)	2/10 (20%)

TABLE 3. Performance attributes compared between 2 cohorts (2005, 2007) and between natural and transplanted populations of tube penstemon, *Penstemon tubiflorus*, at Camp Dodge, Iowa Army National Guard, Johnston, Iowa. Numbers in parentheses are  $\pm 95\%$  confidence intervals.

	Height (cm)	Flower number	Capsule number	% Fruit set	Seed number per capsule <sup>a</sup>	Total seed number per individual (estimated) <sup>a</sup>
Cohort comparison						
2005	80.8 (10) <i>n</i> = 11	54 (25) <i>n</i> = 11	24 (16) <i>n</i> = 11	42.8 (10) <i>n</i> = 11	65 (20) <i>n</i> = 11	1871 (1870) <i>n</i> = 11
2007	83.1 (4) <i>n</i> = 24	71 (15) <i>n</i> = 24	28 (7) <i>n</i> = 24	39.4 (6) <i>n</i> = 24	79 (27) <i>n</i> = 11	2310 (1533) <i>n</i> = 11
Transplant comparison						
Natural	83.1 (4) <i>n</i> = 24	71 (15) <i>n</i> = 24	28 (7) <i>n</i> = 24	39.4 (6) <i>n</i> = 24	77 (25) <i>n</i> = 12	2285 (1387) <i>n</i> = 12
Transplant	54.5 (7) <i>n</i> = 26	151 (37) <i>n</i> = 26	30 (11) <i>n</i> = 26	21.0 (6) <i>n</i> = 26	56 (19) <i>n</i> = 12	2384 (1655) <i>n</i> = 12

<sup>a</sup>Due to subsampling, sample size for seed number per capsule and total seed number were 11 for the cohort comparison and 12 for the transplant comparison.

In 2007, I compared the flowering individuals of the large first-year transplants to the natural population. The transplanted populations were substantially shorter than the natural population. Transplanted populations also produced twice as many flowers as the natural population; however, this higher flowering was offset by lower fruit set and fewer seeds per capsule in the transplanted populations (Table 3). Thus, estimated total seed number produced per individual was nearly identical between the natural and transplanted populations.

Twenty-nine of the 30 large transplants and all 30 of the small transplants survived until the end of the first growing season (2007), and 25 of these 29 large transplants flowered, while only 6 of the 30 small transplants flowered. By 2009, only 6 of the 30 large transplants and 5 of the small transplants had survived.

The low survival of transplants was very site-specific and was due to human and natural disturbance. At the old-field site, only one of the large transplant plots survived pond construction activity in the area. However, the surviving large

transplants performed exceptionally well, with 4 of the 5 individuals surviving and flowering in 2009, the third year after transplant. In addition, these individuals produced a mean of 101.5 seeds (range 29–245), much greater than the mean for the natural population (Table 3). The mean height of these plants (98.0 cm) also exceeded the mean values for the natural population in 2005 or 2007 (Table 3). No transplants survived at the former borrow site due to flooding in 2008 and 2009. At the natural population site, one large transplant and 5 small transplants survived to year 3.

In the pollinator study, excluded inflorescences had lower percent fruit set and had far fewer seeds per capsule compared to open inflorescences (Fig. 1). Plants flowered from around 3 June, when flowers were visible above the sepals, to 28 June, when flowers had dried and capsules were forming.

## DISCUSSION

*Penstemon tubiflorus* appears to be a short-lived perennial, with mean survival within both

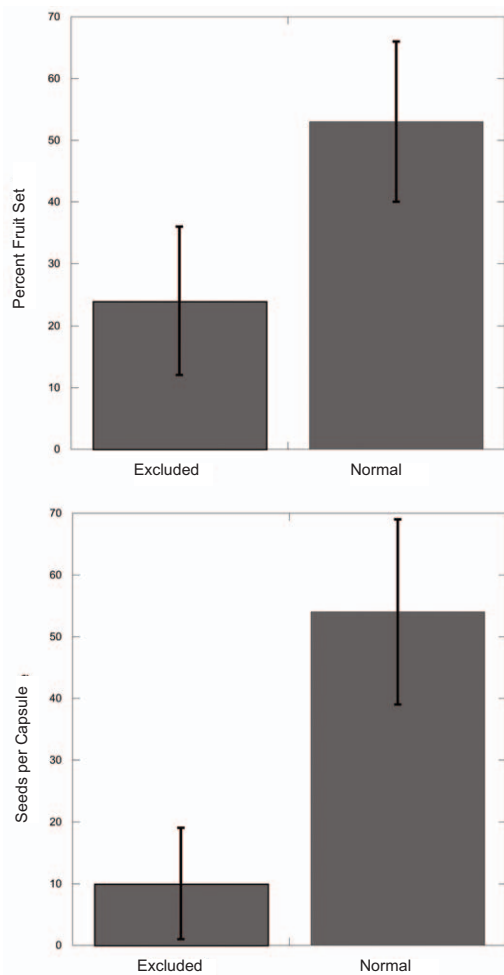


Fig. 1. Percent fruit set and mean number of seeds per capsule of *Penstemon tubiflorus* inflorescences excluded from pollinators and left open to normal pollination, Camp Dodge, Iowa Army National Guard, Johnston, Iowa. Bars are 95% confidence intervals.

cohorts showing yearly declines. Thus, it would appear that continuous recruitment of new individuals is needed to maintain population size. In addition, percentage of individuals that flowered in a given year was variable, leading to highly variable reproductive output. Nonflowering individuals persisted as basal rosettes.

A variety of factors that limit recruitment potentially contribute to the sparse population sizes of tube penstemon, including lack of pollinators, dispersal limitation, and lack of suitable microsites for establishment. A literature review of the pollination of other *Penstemon* species, in conjunction with the transplant data from this study,

suggests that a combination of dispersal and microsite limitation may explain the sparse distribution of tube penstemon, rather than factors related to reproductive output.

Comparison of tube penstemon to the more common *Penstemon digitalis* (foxglove penstemon) suggests that lower reproductive output in tube penstemon does not explain the difference in abundance between the 2 species. Tube penstemon, in the current study, produced a nearly identical number of seeds per capsule compared to a population of foxglove penstemon from Ohio (tube penstemon:  $n = 36$ ,  $\bar{x} = 71.9$ ; foxglove penstemon:  $n = 39$ ,  $\bar{x} = 71.2$ ; Mitchell and Ankeny 2001). However, tube penstemon produced more capsules per plant compared to foxglove penstemon (tube penstemon:  $n = 22$ ,  $\bar{x} = 26.7$ ; foxglove penstemon:  $n = 39$ ,  $\bar{x} = 9.7$ ). Because seed number was estimated by multiplying the number of capsules by seeds per capsule, tube penstemon also had a greater estimated seed number per plant (2921.9 vs. 754.5; R.J. Mitchell personal communication). Tube penstemon also had a higher percent fruit set compared to foxglove penstemon (tube penstemon:  $n = 35$ ,  $\bar{x} = 40.4$  percent; foxglove penstemon:  $n = 39$ ,  $\bar{x} = 225.6$ ; R.J. Mitchell personal communication). Heavy stem damage by lepidopteran larvae observed in foxglove penstemon in Ohio (Mitchell and Ankeny 2001) was not observed in tube penstemon. In Ohio, counts of mature capsules were based on the verified presence of seeds; however, in my study, I counted capsules as mature if they turned brown and were plump, but I did not open each one to verify presence of seeds. Thus, it is possible that my capsule count and therefore the estimated total seed output is somewhat inflated. Nevertheless, these data together suggest that lower reproductive output is not a factor in explaining the difference in abundance between the tube penstemon and foxglove penstemon.

Data from this study, as well as from 2 populations of rare western species, White River penstemon and blowout penstemon, provide evidence that all 3 species have limited ability to self-pollinate. However, data from White River and blowout penstemon suggest that they are not limited by pollinator shortages. The number of natural pollinator visits was sufficient to maximize reproductive output (Tepedino et al. 2006, Lewinsohn and Tepedino 2007), suggesting that lack of pollinators was not creating a bottleneck in reproduction. However, limited data suggest



that this may not be the case for a disjunct population of blowout penstemon (Tepedino et al. 2007). While the literature and data compiled so far do not indicate pollinator limitation, future work with tube penstemon is needed to investigate the possibility that pollinators are limiting, particularly for disjunct populations, such as those in Iowa. The possibility that floral tube morphology may restrict pollinators should also be addressed.

Plant population density may also contribute to variation in seed set, as sparse populations are often more pollinator-limited than dense populations (Kunin 1992), particularly for some prairie species (Hendrix and Kyhl 2000). However, this was not the case for the self-compatible foxglove penstemon, which showed no relationship between population density and the number of seeds per fruit, fruit set, or total seeds produced (Mitchell and Ankeny 2001). Again, this possibility should be investigated for tube penstemon.

Plant populations may also be limited by the inability of species to disperse to a suitable habitat (i.e., dispersal limitation) or by the failure of species to establish once seeds do arrive (i.e., establishment limitation) (Brudvig et al. 2011). If dispersal is limiting, new populations should establish in suitable habitat once propagules are introduced. In contrast, if suitable habitat is limiting, introducing propagules will still fail to result in new populations because site conditions are unfavorable (Brudvig et al. 2011). The transplant results provided evidence that recruitment in this Iowa population of tube penstemon is limited by dispersal because transplants survived at 2 of the 3 sites.

These data, while limited, suggest that there are suitable habitats, not yet colonized by natural seed dispersal, where new populations of tube penstemon can be established. Penstemon fruits are septical capsules with seeds that lack any specialized means of dispersal, reinforcing dispersal as a limiting factor.

Further study is needed to determine the extent to which unoccupied sites have suitable microsites for seed germination. The frequent location of this species in old fields, railroad right-of-ways, and roadsides suggests that some level of disturbance may be required for successful germination and survival of smaller seedlings. This study was not designed to address these aspects of site conditions, but they should be addressed through a seed addition study and

through further addition of transplants of various sizes under various degrees of disturbance.

Colonization of at least one other species of *Penstemon* appears to be limited by both dispersal and suitable habitat (microsites). Blowout penstemon depends, as the name suggests, on areas of sand exposed by active wind erosion for natural colonization. In addition, availability of this particular habitat needs to be coupled with adequate rainfall to allow for fruit production and for seeds to enter the long-term seed bank. A transplant study of this species found that the population size decreased 4 years after transplant, but a wet spring resulted in high seed germination and the population increased steadily over the following 10-year period, indicating successful short-distance dispersal (Stubben-dieck et al. 2007).

I found that tube penstemon produced abundant and easy-to-propagate seed, as is the case with the genus in general (Cullina 2000). If transplants are allowed to grow to sufficient size, reintroduction appears to have a high potential for establishing new populations on suitable sites. However, a number of key questions remain. In particular, it is necessary to know (1) whether tube penstemon has a persistent seed bank, (2) whether unoccupied sites have suitable microsites for germination, (3) the degree to which soil type and surrounding plant cover influence transplant survival at unoccupied sites and the degree to which these site conditions affect seedling survival, (4) the extent to which regular disturbance is needed to maintain populations, and (5) the possibility that fruit or seed set is pollinator-limited.

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#### LITERATURE CITED

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