

The biology of *Penstemon tenuiflorus* Pennell (Scrophulariaceae section *Graciles*). I. Taxonomy and geographic ecology.

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ABSTRACT

A taxonomic study of *Penstemon tenuiflorus* and the closely-related species *Penstemon hirsutus* (L.) Willd. was done using information obtained from herbarium specimens, field and greenhouse observations, and the literature. The geographic distribution of both species was established from herbarium records and literature reports, and county dot distribution maps were prepared. The geographic ecology of *P. tenuiflorus* was described from field observations and the use of topographic, geologic, and physiographic maps; county soil surveys; literature and herbarium specimen data; and climatic records.

A total of 701 herbarium sheets initially labelled and/or annotated as *Penstemon tenuiflorus* or *P. hirsutus* were examined and annotated; 207 them were determined to be other species of *Penstemon* within Section *Graciles*. Closing of the corolla orifice by the lower corolla lobes separates *P. tenuiflorus* and *P. hirsutus* from other taxa which exhibit either a non-pleated and inflated distal corolla tube with flaring lobes or a strongly-pleated tube and forward-projecting lower corolla lobes. Leaves of *P. tenuiflorus* are distinctly pubescent on both surfaces. This character readily separates the species from *P. hirsutus*, whose leaves have sparse pubescence on the lower surface when young but become glabrous with age. This character is consistent for plants in the field, on herbarium sheets, and on those grown from seeds under identical conditions in the greenhouse. Flowers of *P. tenuiflorus* are pure creamy-white (very rarely with faint purple nectar guides), while those of *P. hirsutus* have purple-violet corolla tubes with white lobes. However, this character is extremely difficult to detect in dried specimens because flowers of *P. hirsutus* nearly always fade to white when dried. The literature suggests that the ratio of sepal length to capsule length can be used to distinguish between these species, but this character is so variable that it is essentially useless. *Penstemon tenuiflorus* and *P. hirsutus* also appear to differ in habitat requirements; even though their ranges overlap I have not observed them growing together in the field.

A. Koelling suggested (unpublished Ph.D. dissertation, University of Illinois, 1964) that *Penstemon tenuiflorus* may be a variety or subspecies of *P. hirsutus*, because they produce fertile hybrids of intermediate characteristics when artificially crossed. However, there has been no attempt to merge these taxa, and the relevant literature and technical manuals published since *P. tenuiflorus* was described in 1919 maintain them as separate species. Based on the apparently stable taxonomic characters of flower color and leaf pubescence and on distinct habitat preferences and geographic ranges these two taxa are accepted as separate species.

Penstemon tenuiflorus ranges from southwest central Kentucky south through middle Tennessee to northern Alabama and east-central Mississippi. With the exception of seven counties west of the Tennessee River in Tennessee and a few counties in the Black Belt, its range is in the Interior Low Plateaus Physiographic Province. Within the Interior Low Plateaus, *P. tenuiflorus* occurs in the Shawnee Hills Section (Ohio River Hills and Lowlands Subsection, Mammoth Cave Plateau Subsection); the Highland Rim Section (Pennyroyal Plain, Western Highland Rim, Southwestern Highland Rim, Southern Highland Rim, and Moulton Valley subsections); and all subsections of the Central Basin Section (Cumberland River Basin, Harpeth River Basin, Duck River Basin, and Elk River Basin). Outside of the Interior Low Plateaus, *P. tenuiflorus* occurs in the Coastal Plain Province (Black Belt Section) of Mississippi and Alabama.

This species grows primarily at the edges of cedar glades, with some plants occurring in the adjacent open woodlands. In the Land Between the Lakes, *P. tenuiflorus* occurs on open limestone bluffs above Kentucky Lake (Tennessee River) and is common along the (disturbed) shoulders of the Trace. In the Black Belt of Mississippi, *P. tenuiflorus* occurs on disturbed sites including "prairie patches."

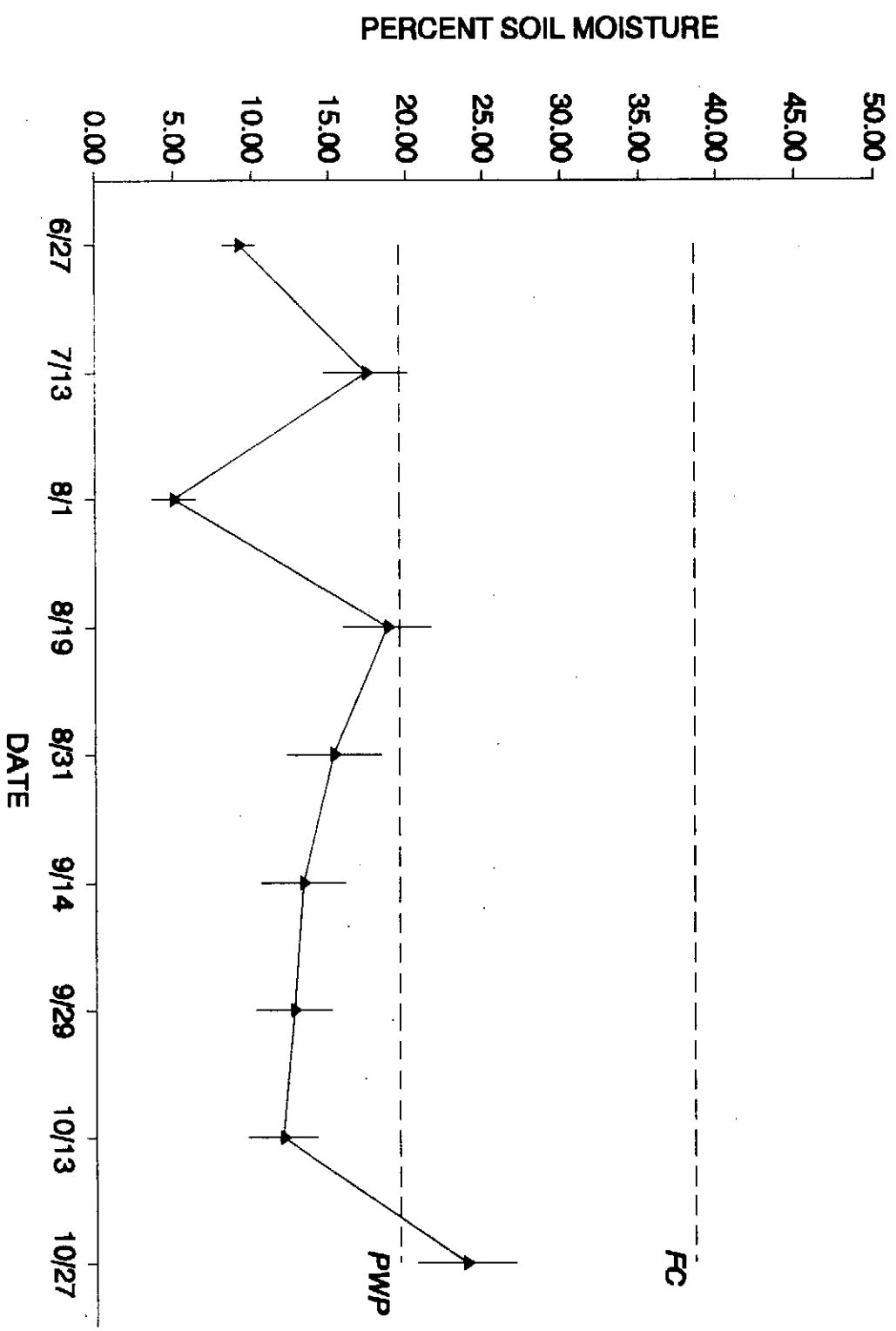
Penstemon tenuiflorus grows on soils derived primarily from calcareous bedrock: Mississippian limestones in the Shawnee Hills and on the Highland Rim, Ordovician limestone in the Central Basin, and Cretaceous chalk in the Black Belt. Soils are generally shallow rocky silt loams, with some populations occurring on silty clay and clay soils. Soil reaction varies from strongly acid (pH 5.1-5.5) to moderately alkaline (pH 7.9-8.4); most soils are in the medium to slightly acid range.

Mean annual precipitation throughout the range of *Penstemon tenuiflorus* exceeds 1100 mm, and is generally well distributed during the year. Mean annual temperatures range from 13.6°C in southwest central Kentucky to 16.9°C in the Black Belt of Mississippi. The frost-free season averages about 190 days in the northern part of the range and about 225 days in the southern part. The range of *P. tenuiflorus* falls within U.S.D.A. Hardiness Zones 6a (-20.6 to -23.3°C) in the north to 7b (-12.3 to -15.0°C) in the south.

J. Baskin and C. Baskin (Distribution and geographical/evolutionary relationships of cedar glade endemics in southeastern United States. *Bulletin of the Association of Southeastern Biologists* 33: 138-154, 1986; Cedar glade endemics in Tennessee, and a review of their autecology. *Journal of the Tennessee Academy of Science* 64: 63-74, 1989) listed *Penstemon tenuiflorus* as an endemic of the cedar glades of the southeastern United States. Although the primary native habitats of the species are cedar glades and glade-like areas, it also grows on limestone cliffs and in Black Belt prairies. Thus, in the strict sense, *Penstemon tenuiflorus* is not a cedar glade endemic.

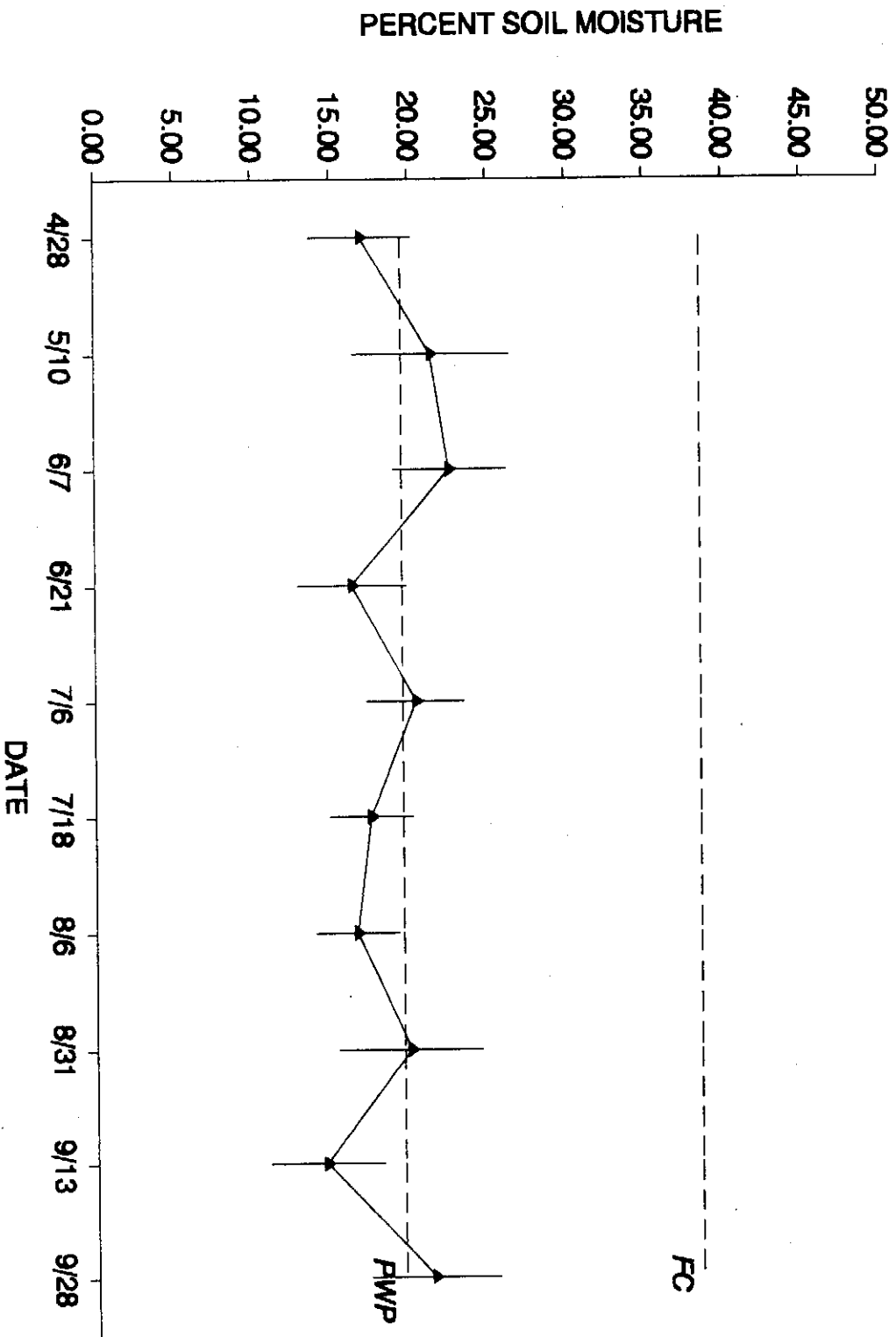
SOIL MOISTURE 1991

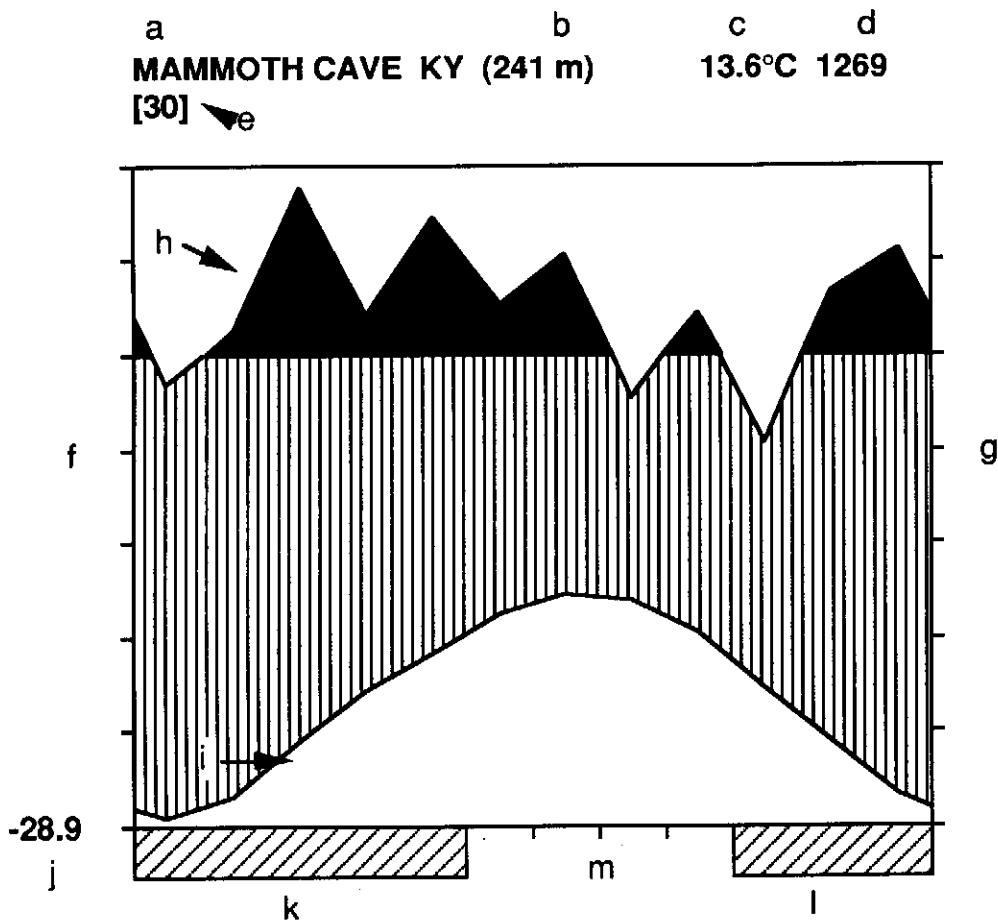
MAMMOTH CAVE NATIONAL PARK, EDMONSON COUNTY, KY



SOIL MOISTURE 1992

MAMMOTH CAVE NATIONAL PARK, EDMONSON COUNTY, KY



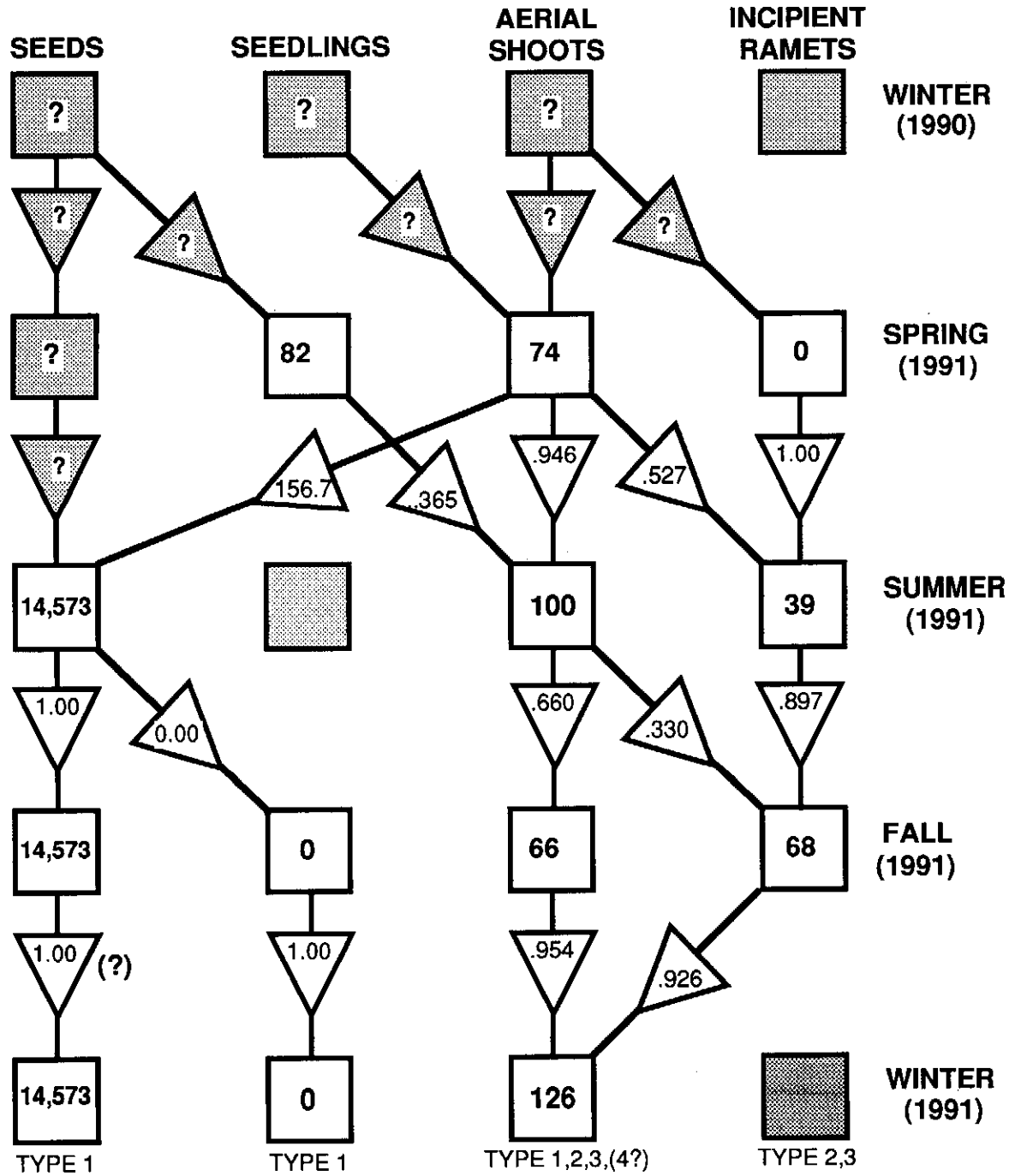


This is a Walter Climate diagram for Mammoth Cave based on data from 1960-1990. Explanations for each part of the diagram are as follows:

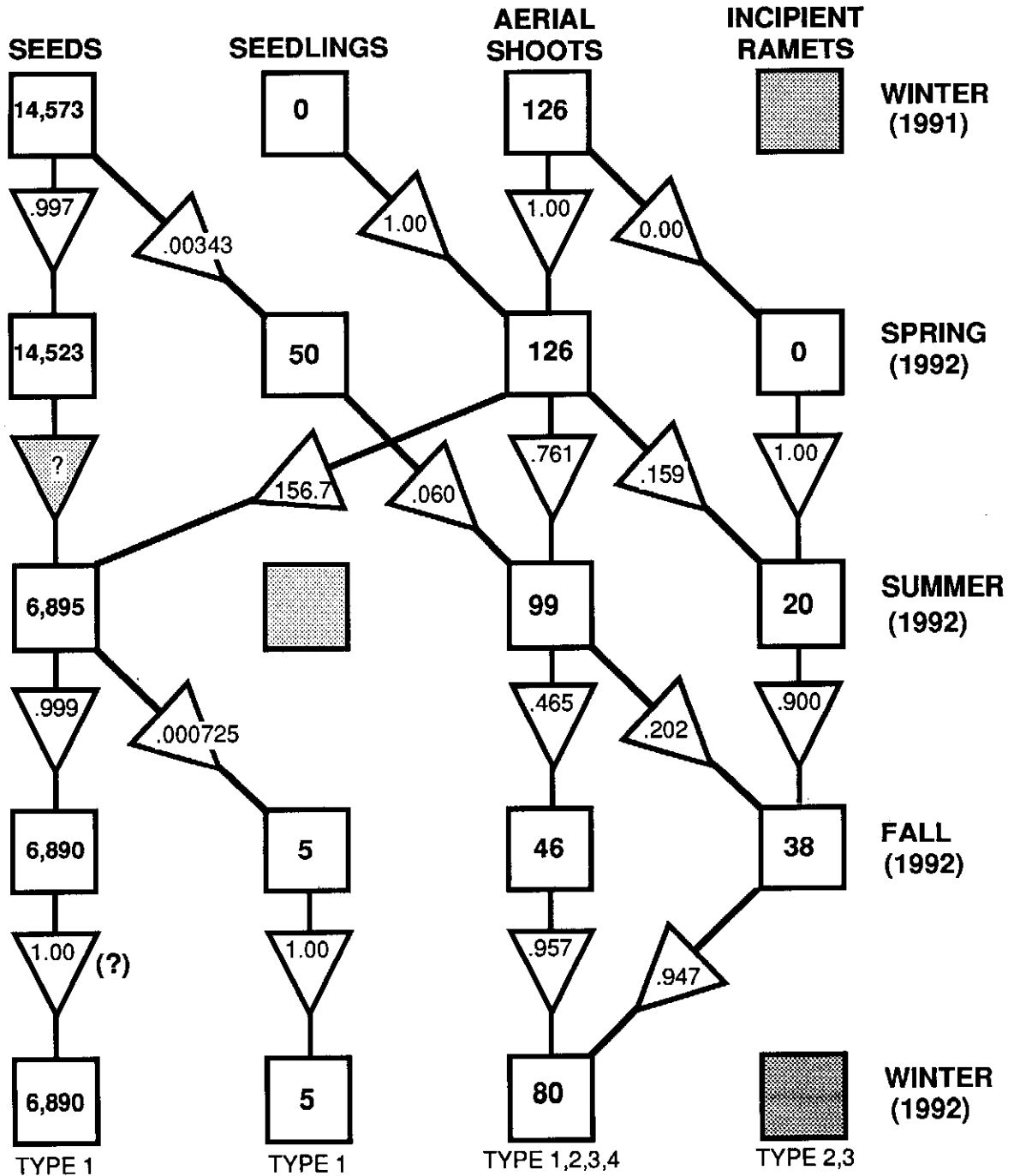
- a= Site name
- b= Elevation in meters
- c= Mean annual temperature
- d= Mean annual precipitation
- e= Number of years of data
- f= Temperature, 0-70°C in 10° increments
- g= Precipitation, 0-140 mm in 20 mm increments
- h= Precipitation curve. Black areas indicate precip. > 100 mm
- i= Temperature curve. Vertical hatch indicates 'humid' season
- j= Record low temperature
- k= Months with at least one frost (last frost in spring)
- l= Months with at least one frost (first frost in fall)
- m= Months (January - December)

**NOTE: This diagram is not complete;
a complete version will be included with
the FINAL REPORT in 1994.*

LIFE TABLE FOR *PENSTEMON TENUIFLORUS*
AT
MAMMOTH CAVE NATIONAL PARK
EDMONSON COUNTY, KENTUCKY
1991



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The biology of *Penstemon tenuiflorus* Pennell (Scrophulariaceae section *Graciles*). II. Ecological life history.

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ABSTRACT

Penstemon tenuiflorus is a C₃ herbaceous perennial hemicryptophyte apparently without vegetative reproduction. The inflorescence of *Penstemon tenuiflorus* is an indeterminate panicle of two to five verticels. Flowering progresses upward from the base of the inflorescence, with the oldest buds of a verticel opening first. Two pairs of anthers and the stigma are located on the dorsal surface and the bearded staminode on the ventral surface. Flowers are protandrous. At the beginning of anthesis, the distal pair of stamens dehisce, but the stigma is not receptive. By the third day, the proximal pair of anthers has dehisced and the stigma has become receptive. Flowers are insect pollinated. To effect pollination, an insect must land on the lower lip of the flower, which causes the corolla orifice to open. The pollinator's head and thorax are dusted with pollen, which is rubbed against the stigma when the insect visits another flower. The primary pollinators are bumblebees (*Bombus* spp., Apidae), but small solitary bees (Megachilidae) also pollinate the flowers. Pollinators do not systematically work individual inflorescences, but randomly visit flowers of different plants in the immediate vicinity. Carpenter bees (*Xylocopa* sp., Apidae) slit the base of the floral tube and rob nectar from the flower. Honeybees (*Apis mellifera*, Apidae) and a small wasp (Vespidae, Eumeninae) visit these slits. Bee flies (Bombyliidae) and hawk moths (Sphingidae) visit the flowers for nectar, but they do not assist in pollination.

Penstemon tenuiflorus is a facultative outcrosser; a small number of seeds are produced agamosperously. In a field experiment, significantly more seeds were produced by cross-pollinated flowers (mean = 783.9 per treatment) than by self-pollinated flowers (mean = 141.2 per treatment) (PLSD = 295.66, $p < 0.05$). Seed production in *P. tenuiflorus* was not pollinator-limited. The mean number of seeds produced was not significantly different between pollinator-assisted flowers (mean = 817.1 seeds per treatment) and non-assisted flowers (mean = 717.8 seeds per treatment) (PLSD = 295.66, n.s.). A small number of (apparently) asexual seeds were produced (mean = 6.0 per treatment). Weight per seed was significantly higher in sexually- than in asexually-produced seeds (mean = 119.5 μg vs 18.9 μg , PLSD = 88.5 μg , $p < 0.05$), as was seed viability (mean = 62.3% vs 17.3%, PLSD = 16.9%, $p < 0.005$). However, there was no significant difference in seed weight (mean = 134.3 μg vs 109.6 μg , PLSD = 88.5 μg , n.s.) or viability (65.8% vs 58.8%, PLSD = 16.9%, n.s.) between outcrossed and selfed seeds.

Penstemon tenuiflorus produces a septicidal capsule that matures in late August. Lepidopteran larvae consume the seeds in some of the capsules. Seed dispersal begins in late August or September and continues throughout winter. Seeds have no specialized dispersal structures. They are shaken from the capsules by wind, and perhaps rain, and fall near the base of the plant.

About 90% of freshly-matured seeds are dormant and 10% conditionally dormant. About 10% of seeds sown on soil in flats in an unheated greenhouse germinated in fall and 40% germinated in early spring. Cold stratification broke dormancy, and nondormant seeds germinated over a wide range of temperatures in light. Seeds buried in pots of soil in a nonheated greenhouse did not survive for more than one year, and no seedlings germinated in soil samples collected in the field after the spring germination season. Thus, *P. tenuiflorus* does not appear to produce a persistent seed bank.

Most seeds do not germinate. Of those that do only a small percentage of seedlings become established. Survival rates were higher in fall-germinated than in spring-germinated seedlings. Seedlings marked in spring 1991 had formed only small rosettes (< 2.5 cm diameter) by the end of their first growing season, and they were less than 5 cm in diameter at the end of their second year. Thus, plants do not reach reproductive maturity until the third year or later. Reproductive plants bolt and flower in spring; rosettes must be vernalized to flower. Bolting begins in March and flowering occurs in April and May. Timing of flowering is controlled by temperature and not by photoperiod. Most reproductive plants produce offshoot rosettes from early summer (after flowering) until fall. Larger non-reproductive rosettes may produce offshoot rosettes from the woody caudex throughout the growing season. In a cedar glade population in Cedars of Lebanon State Park, Tennessee, and in a population in a glade-like area in Mammoth Cave National Park, Kentucky, the total number of rosettes has remained nearly constant during the first two years of a study on the autecology and population biology of *Penstemon tenuiflorus*.

*Presenting paper