

SEXUAL AND APOMICTIC PRAIRIE FLEABANE  
(*ERIGERON STRIGOSUS*) IN TEXAS: GEOGRAPHIC  
ANALYSIS AND A NEW COMBINATION  
(*ERIGERON STRIGOSUS* VAR. *TRAVERSII*, ASTERACEAE)

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ABSTRACT

The reproductive mode (sexual diploid vs. apomictic polyploid) of prairie fleabane (*Erigeron strigosus* Muhl. ex Willd.) in Texas was estimated through the analysis of pollen quality for herbarium specimens from the Botanical Research Institute of Texas (BRIT) and the University of Texas (TEX). The approximate geographic coordinates for 285 unique collections were determined and geographic distributions of sexual vs. apomictic plants were plotted using Geographic Information System (GIS) software. The species as a whole occurs throughout the eastern half of Texas, although one outlying specimen was recorded from the northern Panhandle. Apomictic plants were far more common than sexual plants (245 vs. 40 specimens), and exhibited greater ecological amplitude with respect to natural area, precipitation, and soil. Sexual plants were restricted to Pineywoods and Post Oak Savannah habitats in extreme eastern Texas, and correspond to *Erigeron traversii* Shinnery. This taxon was described in 1964 but subsequently included as a synonym of *E. strigosus*. This geographical pattern is similar to that recorded for other taxa that include sexual and apomictic populations. The new combination *E. strigosus* var. *traversii* (Shinnery) Noyes is proposed.

RESUMEN

El modo de reproducción (diploide sexual vs. poliploide apomíctico) de *Erigeron strigosus* Muhl. ex Willd. en Texas se estimó mediante el análisis de la calidad del polen en especímenes de herbario del Botanical Research Institute de Texas (BRIT) y de la Universidad de Texas (TEX). Se determinaron las coordenadas geográficas aproximadas de 285 colectas y se representaron las distribuciones geográficas de plantas sexuales contra apomícticas usando un software de Sistemas de Información Geográfica (GIS). La especie en conjunto está por la mitad este de Texas, aunque se registró un espécimen del norte de Panhandle. Las plantas apomícticas fueron mucho más frecuentes que las sexuales (245 vs. 40 especímenes), y mostraron mayor amplitud ecológica con respecto al área natural, precipitación, y suelo. Las plantas sexuales estuvieron restringidas a hábitats de pinares y robledales en el extremo este de Texas, y corresponden a *Erigeron traversii* Shinnery. Este taxon se describió en 1964 pero después fue incluido como sinónimo de *E. strigosus*. El patrón geográfico es similar al registrado para los otros taxa que incluyen poblaciones sexuales y apomícticas. Se propone la nueva combinación *E. strigosus* var. *traversii* (Shinnery) Noyes.

Many plant taxa in temperate regions include both sexually and apomictically reproducing populations (Gustafsson 1946–1947; Grant 1982; Asker & Jerling 1992). These taxa occur predominantly in the Asteraceae, Rosaceae, and Poaceae, and include diplosporous apomicts (the unreduced gametophyte arising di-

rectly from divisions of the megaspore mother cell) as well as aposporous apomicts (the unreduced gametophyte arising from a vegetative cell of the ovule). Apomictic taxa are almost always polyploid, and though they produce genetic clones through maternal function, they also usually produce reduced pollen that can function in crosses with facultative apomicts and sexual plants. The latter are frequently restricted to the diploid level. Apomictic populations and sexual populations may have different distributions, a pattern that is referred to as geographic parthenogenesis. Apomicts, relative to sexuals, have larger ranges, range into higher latitudes, range to higher altitudes, and have a greater tendency to colonize once-glaciated areas (Bierzychudek 1987).

In plants, pollen quality is highly diagnostic for mode of reproduction (Gustafsson 1946–1947). Sexual plants typically produce pollen of uniform size and high viability as estimated with pollen vital stains. Apomictic plants, on the other hand, produce pollen that is of relatively low quality, with high variation in size, a high proportion of aborted grains, and often including miniature aborted pollen grains (i.e., micrograins). These distinguishing features are readily observed from pollen samples obtained from fresh pollen samples as well as from herbarium specimens.

*Erigeron strigosus* Muhl. ex Willd., the prairie fleabane, is abundant in the United States from the Atlantic coast to the Great Plains and occurs sporadically in the West (USDA, NRCS 2005). The species has been considered to be uniformly apomictic in monographs (Cronquist 1947) and floristic treatments (e.g., Barkley 1986; Hickman 1993). Diplospory was documented cytologically (Holmgren 1919) and most of the published chromosome number counts for the species are triploid ( $2n = 27$ ; 14 / 38 counts = 37%), tetraploid ( $2n = 36$ ; 6 / 38 counts = 16%), or hexaploid ( $2n = 54$ ; 4 / 38 counts = 11%) (Compiled from Index to Plant Chromosome Numbers, 1955–2000). Nesom (1978), however, based on diploid counts ( $2n = 18$ ) from Alabama, Louisiana, and Florida, considered the strong likelihood of sexual populations of *E. strigosus* in the southeastern United States. Sexual reproduction was subsequently verified cytologically for diverse diploid populations in the southeastern United States (Noyes & Allison 2005). Sexual diploid populations included *E. strigosus* var. *calcicola* J. Allison, principally restricted to cedar glades in Tennessee and Alabama, *E. strigosus* var. *dolomiticola* J. Allison, restricted to a single dolomite glade in Bibb Co., Alabama, and plants occurring on the piedmont and coastal plain of South Carolina, Georgia, Florida, and Alabama. In contrast to apomicts, all sexual populations investigated were characterized by tetrasporic ovule development.

The coastal plain is continuous from the Atlantic states to east Texas, and although *Erigeron strigosus* is abundant throughout, biosystematic analysis has been wanting. In addition, *E. traversii* Shinnars was described to include subtly distinct plants in the Pineywoods of Texas and adjacent Louisiana that flowered earlier than typical *E. strigosus* (Shinnars 1964). Although accepted in the

Manual of the Vascular Plants of Texas (Correll & Johnston 1970), the taxon was later provisionally listed as a synonym of *E. strigosus* owing to the absence of conspicuous morphological characteristics (Johnston 1990). That precedent has been followed in checklists (e.g., Kartesz 1992; Hatch et al. 2001; USDA, NRCS 2005) and floras (Flora of North America, Asteraceae 2006, G.L. Nesom, BRIT, pers. comm.).

The objective of this work was to investigate the occurrence of sexual vs. apomictic plants of *E. strigosus* in Texas based on analysis of herbarium specimen pollen samples. Further, detailed geographic distribution and phenological patterns were analyzed, as was the relationship between reproductive mode and those plants previously identified as *E. traversii*.

#### METHODS

Specimens were loaned to the University of Colorado (COLO) from the Botanical Research Institute of Texas (BRIT) and the University of Texas (TEX). Pollen was removed from each specimen to estimate mode of reproduction. Five to ten florets that had newly opened or were 1–2 days (estimated) from anthesis were removed from single capitula for each specimen. Florets were placed on a standard microscope slide with ca. 15  $\mu$ l Cotton blue in Lactophenol (Stanley & Linskens 1974) and allowed to saturate 2 days–1 week. Pollen was released from the softened florets as necessary by tearing a longitudinal slit into the corolla tubes using dissecting needles. Floral debris was removed, a cover slip was applied, and pollen was allowed to stain for ca. 1 week prior to observation. The stained pollen was evaluated visually using bright-field microscopy at 400 $\times$ . A pollen sample was identified as being produced by a polyploid apomictic plant if it included a high proportion of aborted grains, large grains (usually some grains > 17  $\mu$ m diam), and / or micrograins. Conversely, a pollen sample was identified as being produced by a sexual plant if it generally included a low proportion of aborted grains, was uniformly small (ca. 12–15  $\mu$ m diam), and lacked micrograins. Measurements of grains, as required, were performed on pollen images captured and analyzed using AnalySIS (v.3.1; Soft Imaging System, GmbH 1989–2001).

The longitude and latitude of each collection location was determined from the data provided on the herbarium specimen label. This was accomplished initially using the mapping software TOPO! Texas (Copyright 2004, National Geographic Maps, Evergreen, CO) and later using TOPO USA (version 5.0, DeLorme, Yarmouth, ME), facilitated on occasion with text web inquiries using Google (Google, Inc, Mountain View, CA). Locality data were compiled in Excel (version 10.0.4, Microsoft Corp.). If not explicitly stated, distances and directions from towns given on herbarium specimen labels were assumed to lie along existing roads. In most cases, the collection data were sufficient to estimate co-

ordinates with a high degree of confidence. For a few older specimens, only a county or town was provided, in which case coordinates were selected at the geographic center of the county or town. To evaluate differences in the phenology of apomictic vs. sexual plants, collection dates were compared statistically using Excel. This test assumed that the herbarium specimen collection dates, taken as a whole, accurately reflected the duration of flowering in the species.

Localities were mapped using Geographical Information System (GIS) software ESRI ArcInfo (v. 9.0, copyright 1999–2004; <http://www.esri.com>). Duplicate specimens within or between herbaria were removed from the database so that subsequent analyses were performed only on unique collections. As a check on locality coding, county names for data plotted in ArcInfo were extracted and compared with the original data set. In addition, ca. 20% of the herbarium specimens were selected at random and plotted localities were evaluated for accuracy. Geographic distributions of sexual and apomictic plants were analyzed visually and statistically with respect to rainfall, natural areas, and soils using GIS data layers for Texas available from the Texas General Land Office (<http://www.glo.state.tx.us/gisdata>), the Texas Park and Wildlife Department ([http://www.tpwd.state.tx.us/landwater/land/maps/gis/map\\_downloads](http://www.tpwd.state.tx.us/landwater/land/maps/gis/map_downloads)), and the United States Department of Agriculture (<http://www.ncgc.nrcs.usda.gov/products/datasets/statsgo/data/tx.html>), respectively. The soil classification employed followed the taxonomy proposed by the United States Department of Agriculture that recognizes 12 soil orders and 64 soil suborders (Soil Survey Staff 1999). Specific environmental point data for collections were obtained using the Intersect Point Tool (Beyer 2004), and statistical analyses were conducted using Excel.

## RESULTS

A total of 311 Texas collections were studied. These included 184 specimens from BRIT and 127 specimens from TEX. In addition, floral material from the holotype of *Erigeron traversii* Shinnery (C.L. Lundell 11,093, 11 Apr 1942, BRIT) was obtained via special arrangement with curators (185 BRIT Texas collections analyzed, 312 collections total). Twenty collections were duplicated between BRIT and TEX, one collection was represented by two separate sheets at TEX, and three collections were represented by two separate sheets at BRIT. In total, there were 288 unique collections between the two institutions. Three collections (1%), all from TEX, were excluded from subsequent analyses: *G.L. Fisher* 38,018 (1938) and *W.R. Carr* 11,924 (1992) lacked capitula at a suitable age from which pollen could be obtained, and the locality (even to county) could not be determined for *A. Gieseuschlags.n.* (1928). The earliest collection (*F. Lindheimer* 6978) was made near Austin in 1844, and the largest portion of specimens (113, 40%) was collected in the 1940s (Fig. 1). Although there were specimens prepared by 95 principal collectors, the majority (52%) was collected by just seven

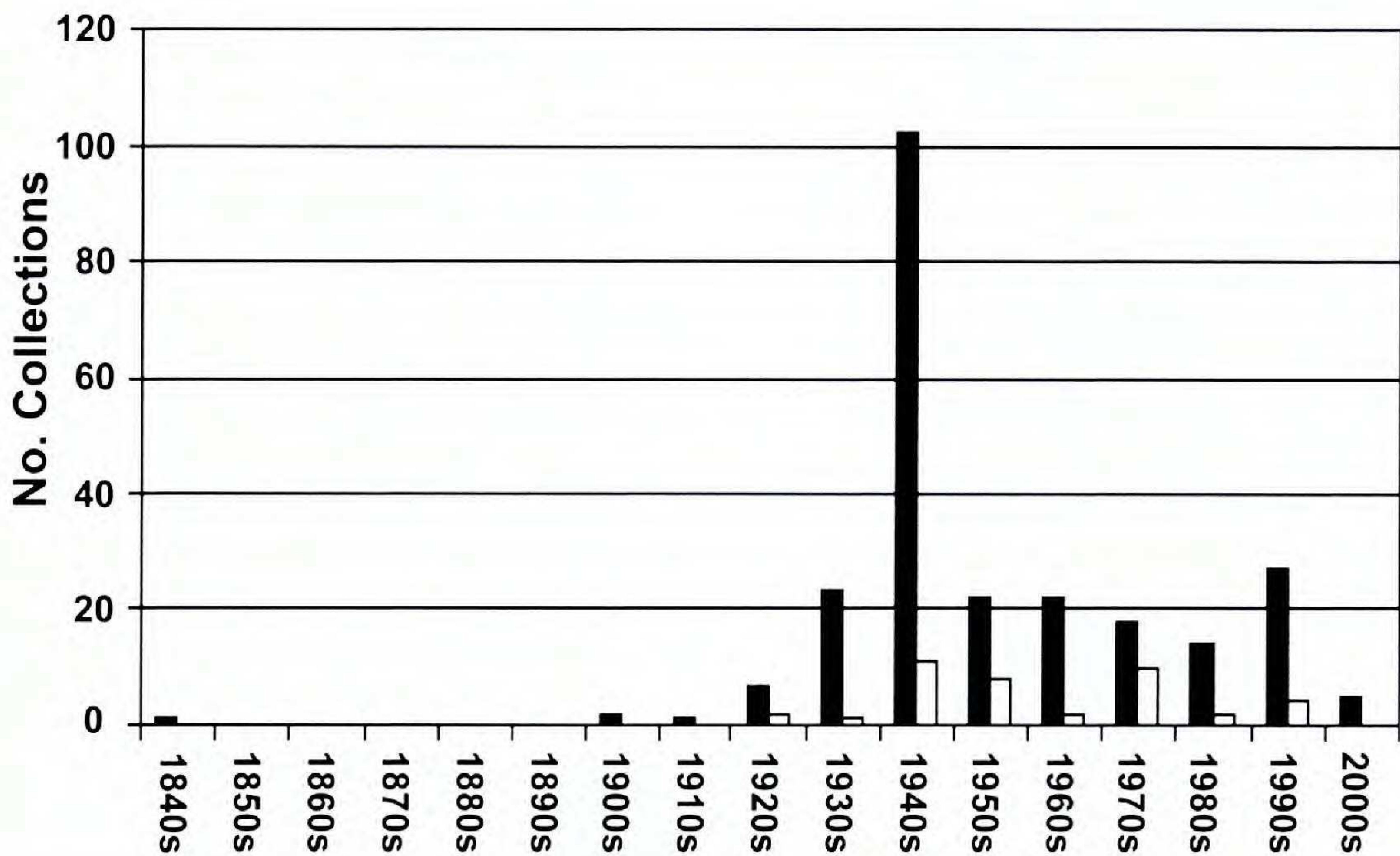


FIG. 1. *Erigeron strigosus* collections by decade in Texas. Solid bars = apomictic ( $n = 245$ ); open bars = sexual ( $n = 40$ ).

botanists: L. Shinnars, 40 (14%); E. Whitehouse, 29 (10%), V.L. Cory, 27 (9.5%), D.S. Correll, 13 (5%); B.C. Tharp, 13 (5%), and C.L. Lundell, 11 (4%), who were prolific in the middle decades of the 20th century, and W.R. Carr, 14 (5%), whose collections were prepared in the 1990s.

The 285 specimens were collected in 87 of 254 Texas counties (Fig. 2A), which are concentrated in north central and east Texas. Most of the collections (87%) were restricted to Pineywoods (88, 31%), Post Oak Savannah, (87, 31%) and Blackland Prairie (73, 26%) (Fig. 2B). The remaining 37 collections (13%) occurred in adjacent regions to the west (Edwards Plateau, 12; Rolling Plains, 14; Llano Uplift, 4) or to the south (Gulf Coast Prairies and Marshes, 5; South Texas Brush Country, 1). Additionally, one specimen occurred in the extreme north Panhandle in Lipscomb County. It was the only specimen to occur in the High Plains region of the state. No specimens were collected in the Trans Pecos region or Coastal Sand Plain of southern Texas. The western boundary of *Erigeron strigosus* in Texas occurs abruptly at ca. 99°W in the central part of the state. This corresponds approximately to the 28 in. precipitation isohyet (Fig. 2C). The Lipscomb county outlier is exceptional in longitude and rainfall, occurring at 100°W in a region with approximately 23 in. annual rainfall.

Of the 285 specimens, 40 (14%) were determined to possess pollen characteristic of sexual diploids, and 245 (86%) were determined to possess pollen characteristic of polyploid apomicts (Fig. 3). Polyploid apomicts occur throughout the range of the species in Texas. Sexual diploid plants, however, were restricted to Pineywoods (34 / 40, 85%) and Post Oak Savannah (6 / 40, 15%).

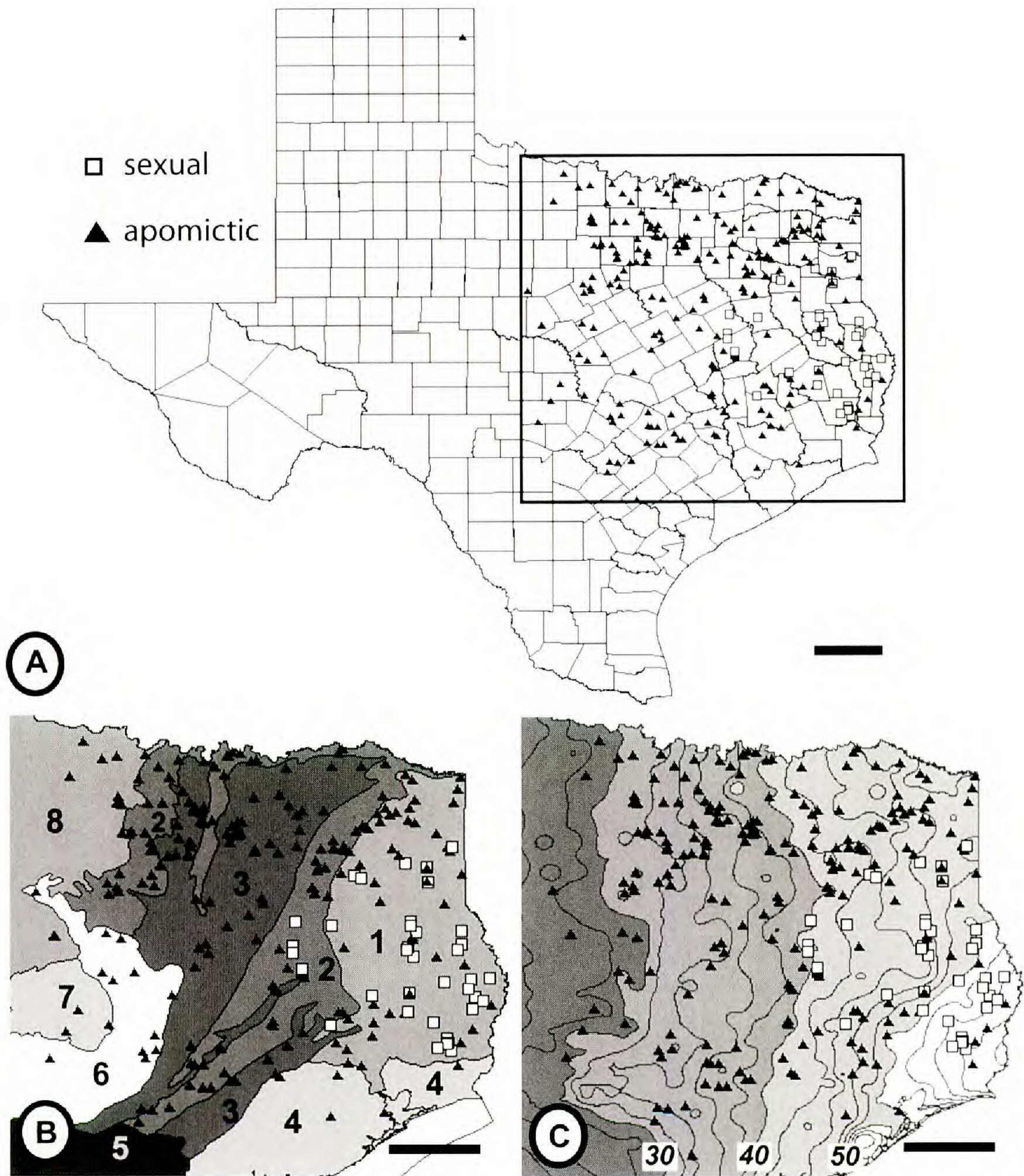


FIG. 2. Geographic distribution of *Erigeron strigosus* in Texas. **A.** Distribution by county. **B.** Distribution by natural area. **1:** Pineywoods; **2:** Post Oak Savannah; **3:** Blackland Prairie; **4:** Gulf Coast Prairie and Marshes; **5:** South Texas Brush Country; **6:** Edwards Plateau; **7:** Llano Uplift; **8:** Rolling Plains. Regions according to Hatch et al. 2001. **C.** Distribution by precipitation. Isohyet values in inches. Scale bars = 100 km.

Sexual plants were collected in 17 counties within these two regions. In six of these counties, only sexual plants have been collected. However, in the other 11 counties, both sexual and apomictic plants have been collected. The oldest sexual specimen was collected by C.L. York in 1928 (s.n., Gregg Co.). There is no significant trend in the proportion of sexual plants collected by decade in the 20th century ( $r = 0.19$ ,  $P = 0.58$ ). This indicates that both sexual and apomictic

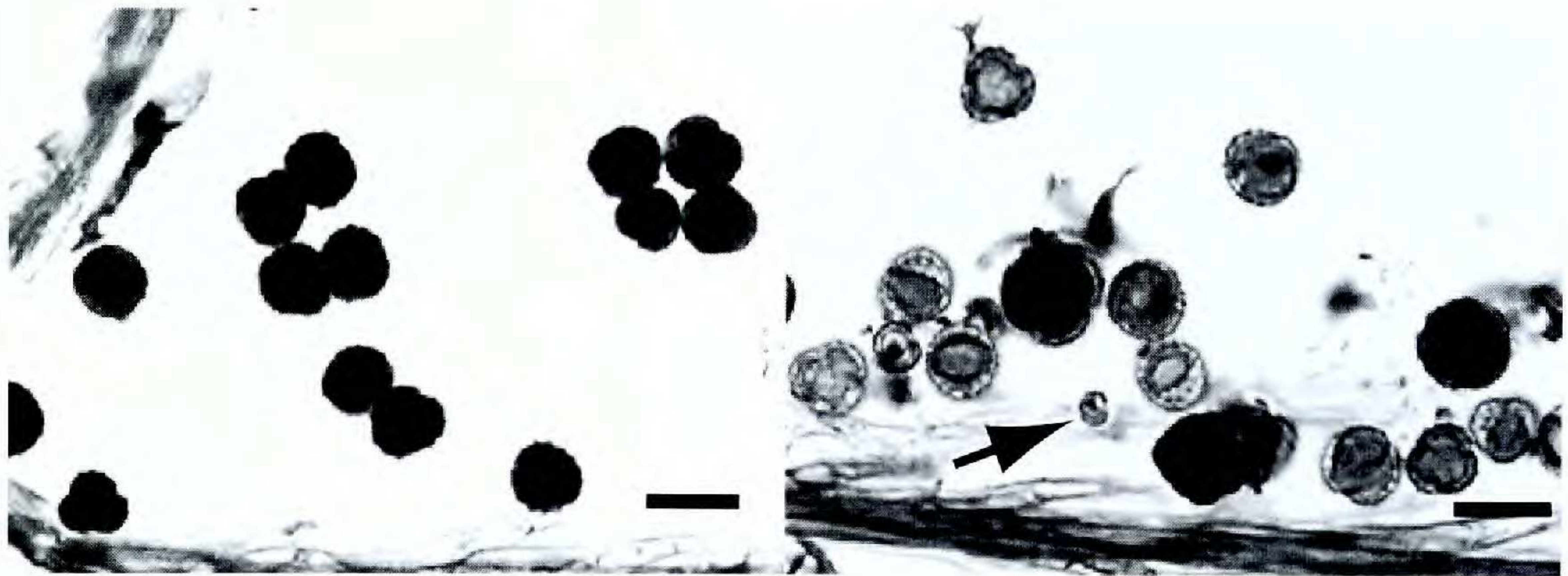


FIG. 3. Pollen from herbarium specimens of *Erigeron strigosus*. A. The holotype of *E. traversii* (C.L. Lundell 11,093, Nacogdoches Co., BRIT), sexual. B. L.H. Shinnery 32,543 (Morris Co., BRIT), apomictic. Arrow indicates a micrograin. Scale bar = 20  $\mu$ m.

plants have coexisted in Texas since at least the 1920s, and that their relative proportions have not changed dramatically. The holotype of *Erigeron traversii* was determined to have pollen characteristic of sexual diploids, as did the specimens L. H. Shinnery 7618 (BRIT), 18,387 (BRIT), 18,402 (BRIT), 18,450 (BRIT), 18,503 (BRIT), and B.L. Turner 4377 (TEX), which were cited in the original description of *E. traversii* (Shinnery, 1964). *E. Whitehouse* 20,861 (BRIT), the eighth specimen cited by Shinnery for Texas, was not present among the loan materials.

Precipitation at sites where sexual plants were collected ranged from 41 to 57 in. / year (mean = 48.2 in., SD = 4.9), while values at apomictic sites ranged from 23 to 57 in. / year (mean 39.1 in., SD = 6.3). Precipitation values for apomictic plants, though overlapping, were significantly lower than those for sexual plants (Student *t*,  $P = 6.04E-17$ ). Sexual plants predominantly occurred on leached forest soils with subsurface clay (alfisols, 18 collections; ultisols, 18 collections). Four sexual collections occurred on poorly developed entisols. Apomictic plants in Oak Savannah and Pineywoods regions also occurred on alfisols (72 collections) and ultisols (28 collections), but also were found on clay-rich vertisols (11 collections), and dark grassland mollisols (12 collections). Six apomictic collections corresponded to entisols.

Collections dates of specimens of *Erigeron strigosus* (Fig. 4) indicate that flowering commences in March, peaks in April and May, and continues sporadically at reduced levels until October or early November. One exceptional apomictic specimen (*R.J. Fleetwood* 10,050, Nacogdoches Co., TEX) was collected 5 Jan 1972 (the collector noted the presence of ice on the plant). The average collection date for sexual plants (for 39 collections made from March to June) was 22 April (SD = 23.3 days). The average collection date for 210 apomictic plants made during the same time period was significantly later (10 May, SD =

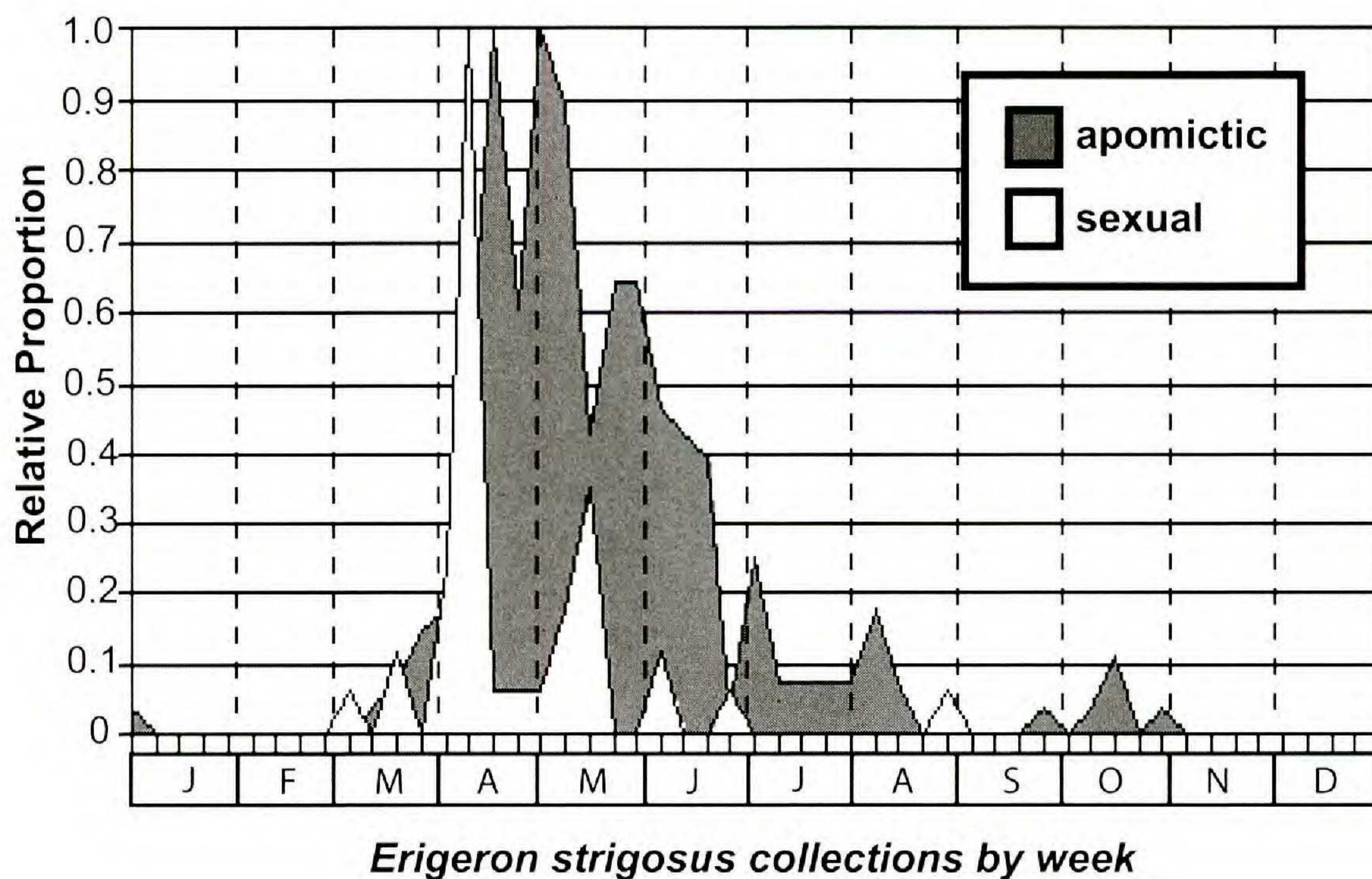


FIG. 4. *Erigeron strigosus* collections in Texas by date. Dates from herbarium specimens grouped by week.

22.5 days, Student *t*,  $P = 2.5E-06$ ). The same tendency was observed for asexual plants occurring in only those counties where sexual plants also occurred ( $n = 22$ , avg. = 9 May, SD = 20.4 days; Student *t*,  $P = 0.006$ ).

## DISCUSSION

### **Sexual and apomictic *Erigeron strigosus* in Texas**

The greater range of habitat, precipitation, and soils tolerated by apomictic *Erigeron strigosus* in Texas is consistent with the hypothesis (Baker 1965; Lynch 1984) that asexual lineages, through polyploidy, hybridization, and genome level selection, evolve general-purpose genotypes that are capable of exploiting diverse habitats. However, this pattern is also consistent with the hypothesis that apomictic reproduction may be favored in fragmented marginal habitats because it circumvents the deleterious effects of inbreeding depression and mate scarcity (Haag & Ebert 2004). Detailed, fine-scale analysis of populations, especially in regard to population size, habitat, and disturbance, will be required to differentiate between these two hypotheses. Superficially, the geographic pattern for *E. strigosus* is similar to that for *Taraxacum officinale* in Europe. Sexual diploid populations of that taxon are restricted to low-elevation habitats in south central and southeastern Europe, while apomictic populations are found throughout northern Europe (Den Nijs & Menken 1994).

The historical record indicates that sexual and apomictic *Erigeron strigosus* have co-existed in Texas at least since the early 20th century, and that there-



fore, the two different forms might be in stable equilibrium. Investigations of *E. strigosus* in Georgia document that gene flow from apomicts to sexual diploids may occur, such that progeny of the latter may include a significant proportion of apomicts (Noyes unpublished). Whether or not sexual and apomictic plants occur simultaneously at the same sites in Texas, and hybridize, is unknown. However, because the phenology of the two forms overlaps, hybridization is likely. Hybridization between sexual and apomictic plants has been thought to be important as a source of novel apomictic genotypes (Stebbins 1950) and has been hypothesized to be an important part of the dynamics between apomictic and sexual *Taraxacum* in Europe (Menken, Smit, & Den Nijs 1995; Verduijn, van Dijk, & van Damme 2004). However, in theory, apomictic plants should ultimately replace sexual populations through reproductive advantage (Maynard Smith 1978) or by unidirectional gene flow via pollen from apomictic to sexual plants (Mogie 1992). To determine if apomictic and sexual *Erigeron strigosus* are in dynamic equilibrium in Texas, or if replacement is occurring, detailed demographic study will be required.

#### **Status of *E. traversii* and a new combination**

Although not known by Shinnars at the time he published the species, pollen evidence indicates that *Erigeron traversii* is a sexual diploid taxon. It is therefore distinct from other *Erigeron strigosus* in Texas, which, based on pollen, is apomictic and polyploid. The analysis of collection dates supports Shinnars (1964) observation that *E. traversii*, on average, flowers earlier than *E. strigosus*. Although Shinnars documented *E. traversii* in Pineywoods habitats, our data also document the existence of sexual diploids in Post Oak Savannah. According to Shinnars, *E. traversii* was distinct in the field from *E. strigosus* in producing showier plants. Whether that difference is due to features of the capitulum (colors, shapes, presentation) or shape and structure of the inflorescence has not been evaluated. These traits, as well as geographic variation among sexual plants, require further study.

The question of whether or not *E. traversii* should be resurrected based on the available evidence is not without controversy. *Erigeron traversii* is distinct from *E. strigosus* in ploidal level and mode of reproduction but the two taxa are sympatric and likely hybridize. However, the sexual taxon appears to be a consistent component of forested habitats of east Texas. To recognize the distinctiveness of *E. traversii* yet acknowledge the close relationship between *E. strigosus* and *E. traversii*, the following combination is proposed:

***Erigeron strigosus* Muhl. ex Willd. var. *traversii* (Shinnars) Noyes, comb. & stat. NOV.** *Erigeron traversii* Shinnars, Sida 1:376. 1964. TYPE: U.S.A. TEXAS. Nacogdoches Co.: off US 59, ca. 8 mi S of Nacogdoches, 11 Apr 1942, C.L. Lundell and A.A. Lundell 11,093 (HOLOTYPE: BRIT).

The holotype of *E. strigosus* var. *traversii* shows strong morphological similarity to sexual diploid plants from South Carolina, Georgia, Florida, and Alabama

(Noyes & Allison 2005). In particular, these plants are distinguished by narrowly spatulate rosette and lower stem leaves that bear small, alternate, mucronate lobes along the petiole margin. Thus it is possible that *E. strigosus* var. *traversii* extends continuously from east Texas to South Carolina on the coastal plain and piedmont. Molecular phylogenetic analysis indicates that sexual diploid southeastern populations of *Erigeron strigosus* are distinct from sexual diploid edaphic endemic populations of *E. strigosus* var. *calcicola* and *E. strigosus* var. *dolomiticola* (Noyes 2006a). On the other hand, ongoing geographic mapping for *E. strigosus* indicate that sexual diploid populations occur in western Louisiana, where they are contiguous with those in East Texas, and also in scattered localities in the Ozarks of western Arkansas and adjacent Oklahoma (Noyes 2006b). Detailed biosystematic analyses will be required to determine if these geographically disparate sexual populations constitute a single taxon, or several distinct taxa.

The precise leaf morphology observed in sexual plants of *Erigeron strigosus* has not been observed for apomictic polyploid *E. strigosus*, which may entirely lack petiole lobes, or exhibit larger, more irregular lobing. Variability in apomictic *E. strigosus* is complex, extending from *E. strigosus* var. *septentrionalis* (Fernald & Wiegand) Fernald, which includes plants approaching *E. annuus* (L.) Pers., to apomictic *Erigeron strigosus* var. *strigosus*, which can be very similar to *E. strigosus* var. *traversii*. In addition, the closely related species *E. tenuis* Torr. & A. Gray, also occurs in Texas and adjacent states. The likelihood of hybridization and morphological similarity between early flowering *E. strigosus* (likely corresponding to *E. strigosus* var. *traversii*) and *E. tenuis* was discussed by Van Vleet (1951). Further, based on consideration of published chromosome counts, *E. tenuis* also likely includes sexual and apomictic plants, but the geographic distribution of mode of reproduction in the species is unknown. Thus, elucidation of evolutionary relationships for *Erigeron strigosus* must also include detailed study of *E. tenuis*.

The recognition of *E. strigosus* var. *traversii* brings to three the number of recognized sexual taxa related to the widespread apomictic taxa *E. strigosus*, *E. annuus*, and *E. tenuis* and contributes to our understanding of the evolution and dynamics within the species complex.

The following key is provided to aid in distinguishing *Erigeron strigosus* var. *traversii* from its close relatives in Texas:

1. Pappus of ray and disc florets of numerous conspicuous capillary pappus bristles; the species including both sexual and apomictic plants and in need of taxonomic study \_\_\_\_\_ **E. tenuis**
1. Pappus of ray florets a low crown-like series of scales, lacking conspicuous capillary pappus bristles, disc florets with capillary bristles.
  2. Plants relatively tall (to 1.5 m) with broad usually pliable leaves; dense, long, flattened trichomes present along the main stem and on the involucre; apomictic and usually triploid; relatively uncommon and restricted to eastern Texas \_\_\_\_\_ **E. annuus**

2. Plants relatively shorter (to 0.7 m) with narrower, stiffer leaves; flattened trichomes if present, restricted to the base of the plant or relatively sparse or absent; sexual or apomictic.
3. Plants generally lacking flattened trichomes throughout; plants sexual, diploid; pollen of high quality, relatively uniform in size, grains  $< 15 \mu\text{m}$  diam; restricted to Pineywoods habitat in East Texas and adjacent Louisiana \_\_\_\_\_ **E. strigosus** var. **traversii**
3. Plant stems and involucres sometimes possessing spreading flattened trichomes; plants polyploid, apomictic, highly variable in morphology; pollen of poor quality, highly variable in size, largest viable grains  $> 17 \mu\text{m}$  diam; relatively widespread.
4. Hairs of involucres flattened, mostly 0.5–1.2 mm; hairs of stems 0.5–1 mm, appressed to spreading \_\_\_\_\_ **E. strigosus** var. **septentrionalis**
4. Hairs of involucres terete, mostly 0.1–0.5 mm; hairs of stems mostly 0.1–0.4 mm, appressed to ascending \_\_\_\_\_ **E. strigosus** var. **strigosus**

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