BIOLOGY OF THE GEOPHYTIC LILY, TRITELEIA LAXA (THEMIDACEAE), IN GRASSLANDS OF THE NORTHERN SACRAMENTO VALLEY

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Abstract

Triteleia laxa (Themidaceae), a liliaceous geophyte common in California at lower elevations with mediterranean climate, was studied during 1998–2004 at four sites in the northern Sacramento Valley. New individual plants were randomly selected each year at one to four of these grassland or open savanna sites to provide a composite study of the biology and life history of the plant. A mature plant produced two leaves after fall rains begin, a new corm on top of the shrinking old corm in spring, and a scape with an umbel of large bluish flowers in late March or April. By seed production in May, above-ground parts were dead, and the new corm and seeds persisted through summer. Mean leaf lengths varied from 22 to 28 cm; no correlation was found with amount of precipitation. Mean scape lengths also varied, from 23 to 32 cm; overall, there was a negative correlation with spring precipitation. Corms of flowering plants had a mean volume of 1.30 cm³, and occurred at a mean depth of 7.27 cm; corm volume was correlated with scape height and with number of flowers. Dry mass increased linearly in the new corm during the spring growth period. Number of flowers per plant varied among sites and the mean varied highly significantly among 5 yr (range 8–12.6). Plants appeared to be largely self-incompatible, but produced a small number of selfed seeds when pollinated by hand. The pollen:ovule ratio was about 3100:1. Mean fruit set (range 50–74%) and mean seed set (range 40–58%) were low, and varied significantly among sites and years. Seed mass averaged about 1.7 mg, and seeds showed 100% viability. Germination time was about 4 wk after wetting, with up to 98% of seeds germinating. The seedling was carried downward from the seed by the elongating cotyledon, ultimately producing a single foliage leaf, a lateral contractile root that shortened in April (and in situ doubtless pulls the seedling deeper into the soil), and a corm <4 mm in diameter. Soils occupied in study sites were loams, with 20 to 39% clay particles. This study on T. laxa gives a reasonably complete picture of the biology for a common geophyte, and we hope that this work will provide impetus for additional studies of other widespread or local geophytes.

Key Words: Triteleia laxa, geophyte, mediterranean climate, annual grassland, corm, contractile root, low fruit and seed set.

Geophytes are perennial herbs that survive unfavorable periods for growth by dying back to underground storage organs such as corms, bulbs, tubers, or rhizomes (Rundel 1996). Dafni et al. (1981) have categorized geophytes as either "synanthous" (leaves and flowers produced in the same season) or "hysteranthous" (leaves and flowers appearing in separate seasons). Dafni et al. also point out that the underground storage organs of these perennial geophytes can be "annual" (that is, the old storage organ is completely replaced by a new organ each growing season) or perennial (with tissue added to the same organ over the years). In the two-season mediterranean climate, geophytes commonly dry up and become dormant aboveground during the dry summer and then renew growth from the storage organ when water becomes available during autumn, winter and spring (Rundel 1996; Parsons 2000). Thus, these geophytic species follow a phenological pattern similar to

that of most annual herbaceous species (which persist as seeds during summer) in California's savannas and grasslands (see especially Chiarello 1989).

The early, classic study of plant life forms (Raunkiaer 1934) noted that geophytes were well represented in areas with mediterranean climate. In (largely mediterranean) California, monocotyledonous geophytes constitute about 5% of native vascular plant species (Rundel 1996). Recent studies are still cataloging and making numerical comparisons of geophytic species occurring within different regions with this climate (Poches and Cowling 2004; Poches et al. 2005; Parsons 2000; Parsons and Hopper 2003). For geophytes of western Australia and some other regions with mediterranean climate, Pate and Dixon (1982) have provided detailed information on the morphology and anatomy of corms, bulbs and tubers, as well as on growth and phenology. There is a paucity of this type of information for California's geophytes. For example, no information on geophytes is in the book "California Annual Grasslands" (Huenneke and Mooney 1989).

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Many monocotyledonous geophytes of the "lily type" (Liliaceae *sensu lato*, as in Hickman 1993; FNAEC 2003) grow in grasslands and savannas of the northern Sacramento Valley of California and include species of *Calochortus, Chlorogalum, Fritillaria, Odontostomum, Zigadenus, Allium, Brodiaea, Dichelostemma,* and *Triteleia*. (*Triteleia* and several others of these genera are currently placed in families other than Liliaceae [e.g., see Pires and Sytsma 2002; FNAEC 2003].)

Several of the geophytic species that grow in California's low elevation grasslands have had limited information on features characterizing or affecting portions their life cycles (in these grasslands or elsewhere) published or presented in dissertations and theses. For example, reproduction and corm size in *Zigadenus fremontii* (Torrey) S. Watson was studied in relation to fire in southern California (Tyler and Borchert 2002), and its reproduction and survival have been studied in the northern Sacramento Valley (Mitchelson 1993). For *Calochortus luteus* Lindley, there are descriptions on floral phenology, pollen:ovule ratios and insect flower visitors/pollinators (Jokerst 1981), features of the pollen grains (Kannely 2003), and aspects of pollination in relation to evolution in the genus (Dilley et al. 2000). In *Chlorogalum angustifolium* Kellogg, floral biology was studied by (Jernstedt 1982), and the same author (Jernstedt 1984) published considerable detail on seed germination and the development of seedlings' contractile roots in *C. pomeridianum* Hoover. Jernstedt (1980) also studied flower development and anthesis in *C. pomeridianum*, and (Stockhouse and Wells 1978) presented information on pollination in this species. *Brodiaea californica* Lindley has had flower phenology, flower visitors, and seed production documented by (Doalson 1999). *Triteleia hyacinthina* (Lindley) E. Greene has had seedling development described by (Smith 1930; Putz 1992), and much earlier, *Dichelostemma pulchella* (Salisb.) E. Greene and several other geophytes had seedling development described (Rimbach 1902). *Fritillaria pluriflora* Benth. has had low fruit- and seed set described by (Witzman 1991). There is some basic life cycle information included in the mainly taxonomic papers for members of *Brodiaea, Dichelostemma* and *Triteleia* by (Keator 1987, 1989; Niehaus 1980), and especially in the biosystematic study of *Brodiaea* by (Niehaus 1971). Keator (1967) has amassed considerable information from field and garden studies for six species of *Dichelostemma* (e.g., on phenology, corms, flowering, seed production, and germination), but most of this work is unpublished. Despite all these studies for geophytic species that can be found in the area of the present study, we and others (Rundel 1996; Parsons 2000) believe that life cycle biology and

natural history in the field is incompletely known for geophytes in California.

To augment the sparse literature on California geophytes, *Triteleia laxa* Bentham was chosen for study. *Triteleia*, a mainly Californian genus, is composed of 15 species, all of which occur west of the Rocky Mountains (FNAEC 2003). *Triteleia laxa* (commonly called Ithuriel's Spear, Grass Nut or Walley Basket) is a synanthous geophyte occurring in the region with mediterranean climate in Western North America, ranging from San Bernardino County, California to Currey County, Oregon (Hoover 1941; Munz and Keck 1959; Keator 1993). This widespread species is found from sea level to 1500 m in elevation (Keator 1993), less commonly in open forest and chaparral, but more commonly in low elevation savanna and grassland ecosystems.

In *T. laxa*, the perennating corm first produces two long, grasslike leaves during the cool and rainy mediterranean winter season, and then a single scape 10–70 cm tall, bearing an umbel of large bluish trumpet-shaped flowers in the spring as the rainy season ends. After fruit and seed production, and formation of a new corm on top of the old corm, leaves and scape dry up, and aboveground activity ceases during the hot, dry summer months. With the fall rains, the corm initiates root growth and seed germination also occurs.

Triteleia laxa plants are notable for their morphological variability, as in height and in size and color of flowers (Hoover 1941; Keator 1993). The time of flowering also varies, with more-coastal variants flowering several months later than elsewhere (Hoover 1941). Corms of some variants have been successfully introduced into the horticultural trade, and are often listed in popular gardening catalogs.

Several environmental conditions of importance in the horticultural mass production of *T. laxa* for commerce, e.g., those promoting seed germination and cormel (vegetative corm) production, have been studied, but only in gardens and in laboratory experiments (e.g., Fortanier 1969; Han 1993; Han and Halevy 1993; Han et al. 1991). Anatomical development of the ovule, embryo sac, and endosperm has been described (Berg 2003), and polyploidy has been documented (n = 7, 8, 14, 16, 21, 24) among wild-collected populations (Lenz 1966; Davidson 1975; Keator 1993). According to (Han 1993), this species is self-incompatible, requiring pollen transfer between plants for seed production.

However, there are very few details published about this plant's biology where it is growing in the wild. Field studies of this plant are particularly warranted because it represents one of the most common geophytes of lowland mediterranean California. Its corms are almost certainly an important food source (e.g., Anderson and

Rowney 1998) that may be used by rodents and other animals. It also represents a large pollen and nectar food-source for insects.

The purpose of our study is to document aspects of the biology and ecology for *Triteleia laxa* in the northern Sacramento Valley. We provide basic information on three topics: 1) phenology and growth of leaves, scapes, and corms; 2) features of sexual reproduction; and 3) features of the seed and seedling stages in the life cycle.

STUDY AREAS

Areas with high densities of *Triteleia* were chosen for study near Chico, California, in the northern Sacramento Valley. The main study area, utilized 1998 through 2004 and referred to as "Vina" below, is located about 16 km north of Chico, east of Cana Pine Creek Road in extreme northern Butte County (39°52′46.6″N, 121°58′34.5″W), at the Vina Plains Preserve (owned and managed by the California Nature Conservancy). Grassland covers the gently rolling terrain of this preserve. This region is underlain with cemented materials of volcanic mudflow origin, washed down historically from the Tuscan Formation of the southern Cascade Range to the east (Broyles 1983, 1987). The soils are usually less than 1 m deep on top of this cemented hardpan (Gowans 1967). Soils where *Triteleia* is most abundant are clay loams, with clay particles ranging from 33–39% of total soil particles, according to analysis by (A. & L. Western Agricultural Laboratories, Modesto, CA). These soils will be classified as part of the Tuscan Series in the "Butte Area Soil Survey" being completed by the Natural Resources Conservation Service (Andrew Conlin, pers. comm.). These grasslands contain about 275 species of vascular plants, with about one third of these being exotic species (Broyles 1987; Mitchelson 1993; Oswald 1997). This main Vina site, at 52 m in elevation, had not been grazed by cattle since the study began in the spring of 1998 (Oswald 1997), although cattle were present for several weeks in April of 2003. The area was control-burned in early June 1997, the year before field study began, and again in 1998, 2002, and 2003; in each case; after the *Triteleia* growing season was over.

In 1998, 1999, and 2000, a second population of *Triteleia* was studied in the Preserve, about 2.3 km east of the main Vina study area, and east of Hwy 99 in southern-most Tehama County (39°53′38.6″N, 121°58′34.5″W). This site (referred to as "Barn"), at 62 m in elevation, has soils similar to those of the main Vina site. The region was control-burned in 1998, after the first year of study, and cattle grazed here several of the winter months each year of the study.

In 2003 and 2004, a "Park" study area was added, within Bidwell Park, on the east side of Chico (39°46′42.8″N, 121°45′10.8″W) at about 99 m in elevation. The *Triteleia* population here grows on a heavy loam of an ancient alluvial terrace above Chico Creek (Red Bluff gravelly loam), with about 25% clay particles (Andrew Conlin, pers. comm.). Vegetation is savanna, with a sparse overstory of *Quercus douglasii*. Neither burning nor grazing by cattle occurred immediately preceding or during the study years.

In 2003 and 2004, a "Road" study area was also utilized, just to the east of Chico along Humboldt Road (39°44′58.8″N, 121°45′10.8″W) at 131 m in elevation. Soils are derived from Tuscan Formation volcanic mudflows, and are gravelly loams with about 20% clay particles, classified as Typic Haploxeralfs (Andrew Conlin, pers. comm.). Vegetation is savanna, with a sparse overstory of *Quercus douglasii*. Neither burning nor grazing by cattle occurred immediately preceding or during the study years.

The climate at all sites is typical mediterranean, with cool, wet, winters alternating with hot, dry summers. Most (86%) precipitation (mean 55.5 cm) occurs as rain from November through April (Fig. 1; NOAA 2005).

METHODS

Sampling

Transects were established subjectively to cross through areas of abundant *Triteleia* plants. Two permanent 30–m transects were established at Vina, one mainly for observations on phenology and the other for measuring and/or destructive sampling of plant parts. Additional (temporary) transects were also set up at each study site for observations or for destructive sampling. For most aspects of study, plants were selected randomly on cross-transects (up to 6 m long) at right angles to the main transects every 1–2 m. Individual plants selected for whole-season observation had wire stakes with aluminum identification labels pushed into the soil 10 cm south of the plant base.

Phenology

Above-ground Shoots and Weather Data. Phenological measurements were made for 50–60 plants along a permanent 30-m transect at Vina for five years. Most plants selected for study could not be followed for more than one growing season due to the burrowing activities of pocket gophers (*Thomomys bottae*) dislodging the identification stakes and/or destroying the corms; thus, new individuals were chosen each season. In some cases gopher activity necessitated choosing
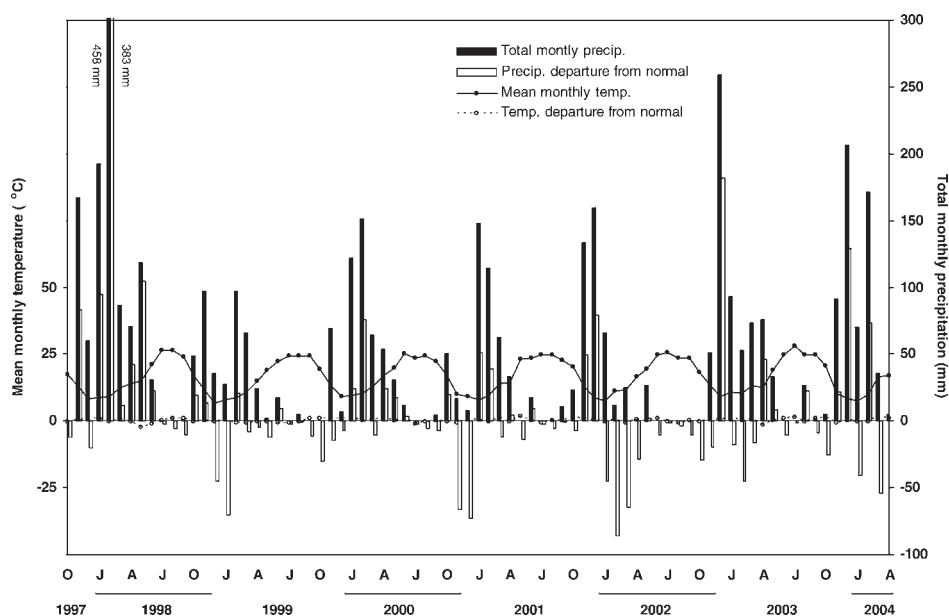
FIG. 1.   Approximated mean monthly temperature and total monthly precipitation for the Vina and Barn study areas, from a weather station in Orland, CA from October 1997 through April 2004 (NOAA 2005). Mean monthly temperature and precipitation departure is the amount deviating from a 30-yr mean.

several new individuals to measure during a growing season.

Start time for measurement varied during the years of study, but usually began soon after emerging *Triteleia* leaves were recognizable at the soil surface in February. In 1999, start time began in late March, when leaves were already approaching maximum length. Frequency of observation was weekly in 1998. Leaves and scapes were measured every four days in 1999. Leaves were measured every two weeks, but scapes weekly in 2000. Both leaves and scapes were measured weekly in 2002, 2003, and 2004. Length of both leaves was measured to the nearest 0.5 cm, from ground surface to leaf tip. Emerging scapes were measured from ground surface to the tip until the developing inflorescence was apparent, after which the scape length (=height) was measured from ground surface to the base of the umbellate inflorescence.

Phenological measurements on leaf and scape growth at Vina were not started at the same time each year, but were carried out until the marked plants reached maximum scape height at flowering in each of five years. The number of plants on which leaf growth was measured started out at 50 to 60 new individuals each year, but was usually lower (16–44 individuals) by the time of flowering because 1) gophers (and possibly rabbits and mice) herbivorized plants or dislodged/toppled identifying stakes, and 2) some individuals were mis-identified (i.e., *Dichelostemma, Chlorogalum,* and *Calochortus* leaves look much like *Triteleia* leaves initially). Also, the number of scape

measurements was lower on earlier dates because scapes did not start growth at the same time. Mean leaf length became *shorter* late in the growing season, because tips of the leaves shriveled and dried and broke off; thus, *maximum* leaf lengths were compared among the years.

Analysis of scape lengths was done only on four years (2000, 2002–2004), because data in 1999 could not be obtained randomly due to scapes dying before flowering. Leaf and scape length measurements were not made in 1998 or 2001.

Corms. In early March 1998, corms were excavated from randomly selected *Triteleia* plants commencing scape growth at Vina. Corm height and two diameters (widths) were measured with calipers to the nearest 0.5 cm, and corm volume was estimated as the volume of a sphere, based on the mean of the three measures. In latest April here, and also at the Barn site, additional corms were dug at randomly selected points, using pairs of the tallest and the closest, shortest flowering scapes, in order to determine if scape height, flower numbers, or soil depth of the corm was correlated with corm volume. All measurements were made with the corm coat still present.

In the growing season of 2002, random corms were excavated every two weeks at Vina to determine volume and mass. This time the corm coat was removed and the two parts of each corm (the plump, developing, new corm and the shrinking remains of the old mother corm producing the leaves and scape) were measured

separately. In December of 2004, non-randomly selected corms were dug at Vina to check volume and mass, and to determine extent of growth after the earliest rains of fall; again, the corm coat was removed and old and new parts were measured separately.

Breeding System and Pollination

At Vina in 1998, inflorescences were bagged with sheets of microscope lens tissue to exclude insect pollen vectors, and later examined for fruit and seed set. In 2000, individual flowers were bagged with strips of lens tissue for 48 or more hours. Bags were gently removed, and wooden toothpicks were used to transfer pollen in three types of pollinations within and between inflorescences: 1) pollen to stigma in same flower (autogamous), 2) pollen to stigma in separate flowers on same plant (geitonogamous), and 3) pollen to stigma in separate flowers on different plants (xenogamous). Treated flowers were re-bagged and examined for seed set in several weeks. Open-pollinated (marked, but not manipulated) flowers nearby were used as controls. At Vina in 2004, squares of tulle (a green net material with about 1 mm mesh) were gently tied around 30 inflorescences to exclude flower visitors; 30 nearby plants without tulle were marked to serve as controls. All flowers were examined for fruits and seeds in 2–3 wk.

To elucidate the period of stigmatic receptivity within individual flowers, a colorimetric assay was carried out at Park to test for the presence of stigmatic peroxidase enzymes. Four flower stages (n = 25 for each stage) were designated for the assay: a) flower buds nearly open (flowers collected), b) flowers recently opened (1–3 d old), c) flowers with anthers mostly dehisced and with the style bent towards the middle of the flower (2–4 d old), and d) flowers recently closed and most without any sign of seed formation yet (4–6 d old). Sampling was done between 2–4 pm (PDT) on 30 April 2003, and samples were placed in a freezer within twenty minutes of the last collection; the assay was carried out seven days after collection. Peroxidase activity was detected *in planta* with adoption of methods used by (Blee et al. 2003).

Pollen/ovule ratios were determined for 35 plants in the Vina population on 31 March 1998. Large flower buds with indehisced anthers were collected into botanical FAA. In the lab, one anther per flower was stripped of pollen with a needle in a 4 dram vial containing 1 ml FAA or 1 ml water. After vigorous shaking, an aloquat in a dropper was quickly transferred to a hemocytometer and a volume of 0.04 ml solution had pollen grains counted; this number was multiplied to represent the number of grains dispersed throughout the entire volume of solution. An-

thers from the upper and lower tiers were compared. Each flower that had pollen counted in one anther also had the ovules from the ovary counted under a dissecting scope. Pollen grains X 6 (6 anthers per flower) divided by the number of ovules gave the estimate of pollen:ovule ratio. Ratios were determined for each flower before being averaged.

In April 1998, unopened flower buds at Vina were bagged with strips of microscope lens tissue for 18 or more hours to provide samples of nectar. Nectar withdrawn from bagged flowers with 10 mu capillary pipettes had sucrose equivalents determined in the field with a Bellingham and Stanley pocket refractometer on 17 April. A few flowers (despite the bagging) had thrips present in the corollas that may have contaminated nectar with pollen; samples with suspected contamination were not used to calculate mean SUE. The volume of nectar varied, and although all samples were from separate plants, in 11 of 28 plants more than one flower had to be used to obtain a volume large enough to register on the refractometer.

Reproductive Output: Flowers, Fruits and Seeds

To determine variation among plants in flower, fruit, and seed production, flowers per plant, fruits per plant, and seeds per fruit were counted at each site in several years. Counts were made when plants were in fruit; number of flowers produced was ascertained by adding number of fruits and empty pedicels remaining—the latter indicating abortion of either a flower or a young fruit. Seeds per fruit were determined for two dried, indehisced fruits from each randomly-selected inflorescence. In several years, a dissecting microscope was used to also count aborted ovules remaining in the dried fruit.

Seed Weight, Viability, and Germination

A collection of mature seeds from about 200 inflorescences in the Vina population was made on 1 June 1997. Seed lots were stored in an indoor laboratory at ambient temperature and in an uncooled/unheated garage, where summer and winter outdoor (=field) temperatures of Chico were approximated. Forty seeds from both indoor- and garage-stored lots were weighed individually, on a Sartorius analytical balance in March 1998.

In 2003, collections of mature seeds, each from 100 or more inflorescences, were made at Vina (22 May), and at the Park and Road sites (27 May). Seeds from each site were stored in a garage in Chico where summer and winter outdoor temperatures were approximated, until viability tests and outdoor germination tests were made.

Seeds from each site, stored under outdoor temperatures, were subjected to viability tests in December 2003. For each site, 50 ''good'' seeds (dark-colored and unwrinkled) were placed in a Petri dish, on filter paper wetted with distilled water, and kept at ambient temperature in a cupboard for 45 hr. The viability of each seed was then tested with tetrazolium-chloride adjusted to pH 6.5 (Baskin and Baskin 1998).

To evaluate the proportion of seeds germinating, when they germinated, and when the shoot reached the soil surface, seeds collected at Vina and stored under outdoor conditions in 2003 were planted in a garden plot in Chico with prevailing outdoor temperatures and only natural precipitation. On 30 November, in a raised garden box with sandy loam soil, seeds were planted 8–10 mm deep, in 10 rows of 50 seeds spaced 20 cm apart, on a strips of moistened, non-inked newsprint paper 3 cm wide (so that recovery of germlings would be possible). The first row of germinating seeds was recovered in four weeks (28 December), and additional rows were exhumed every two weeks through 9 April 2004.

Climatic Data

Monthly climatic data for Orland, CA were used to approximate weather at the Vina study site, which is about 18.5 km northeast of Orland (NOAA 2005; Fig. 1). Daily measurements of precipitation, and minimum and maximum air temperatures at Orland and Chico were used with our phonological measurements and seed germination experiment, respectively (UCD 2005).

Data Analysis

Means for many traits measured (e.g., leaf length, scape length, flowers per plant) did not always have homogeneous variances, so non-parametric (Kruskal-Wallis, Dunnett T3, Tamhane or Games-Howell) analyses were used to test for differences in these cases. However, since we usually had large sample sizes, and the probabilities obtained from non-parametric tests were nearly identical to the P values obtained from ANOVA and Tukey HSD comparisons, we have usually reported the latter. Where its assumptions could be adequately satisfied, ANOVA followed by Tukey HSD comparisons was used to test differences. Repeated measures ANOVA was used to determine if scape growth rate during the logistic growth phase varied among years. Spearman's rho rank test was used to check for correlations. Most data analyses were preformed using SPSS software (Release 11.0.1, Chicago, IL), but some analyses were done using JMP IN 3.2.1 for Macintosh (SAS Institute, Inc. Cary, NC).

RESULTS

Phenology and Growth of Aboveground Parts

Mean maximum leaf and scape lengths differed among some years (Table 1). There was not an association between precipitation and leaf length, based on precipitation of the entire winter-spring growing season (1 October to date of maximum length) or on precipitation occurring only in the days of the (warmer) study period starting in February (Figs. 2 and 3). There was, however, a highly significant (P < 0.0001) negative correlation ($r_s = -0.408$, n = 153) of maximum scape length with precipitation of the study period (1 February to date of maximum length).

Raw data on lengths from four comparable sample dates in the logistic phase of scape growth in 2000 and 2002–2004 indicated that there was a significant affect of year on scape growth rate. The highest growth rate, in 2002 (10.4 cm per week) was highly significantly greater (P < 0.001) than in all other years (Table 1). The lowest growth rate was 5.5 cm per week in 2004. In these four years, flowering occurred a few days after maximum scape length was reached.

Leaf lengths, but not scape lengths, for 1999 are included in Table 1, because the scapes died just before flowering. By 7 April, effects of an unknown pathogen were first noticed as a downward bending of the scape several cm from the top. In a few days, the inflorescence and portion of the scape above the bend died, leaving the unopened, or barely-opened flower cluster dangling (Fig. 4a). By 2 May, 33 (94.3%) of the original 35 marked plants producing scapes at Vina had dead non-fruiting scapes due to this disease. A similar effect was observed in the Barn population, with dead scapes on 26 (76.5%) of the original 34 plants producing scapes. Phenology was not studied in 2001, but the same scape death phenomenon was observed in both Vina and Barn populations.

Corms

Corm volume comparisons, and corm depths in the soil. Corm volume (mean ± SE) in cm³, when first measured on 2 March 1998, at Vina, was 1.62 ± 0.131 (n = 30); all corms came from plants that had flowered the previous year. Paired corm volumes (longest and shortest flowering scapes) from Vina longest plants (1.76 ± 0.137; n = 30) and shortest plants (0.91 ± 0.059; n = 30) were highly significantly different (P < 0.0001) as were the paired corm volumes for Barn longest plants (1.56 ± 0.114; n = 30) and shortest plants (0.96 ± 0.080; n = 30). However, when long-plant corms from Vina and from Barn were compared, they did not differ significantly in volume, nor did the short-plant corms from the two sites (P = 0.589

TABLE 1. SUMMARY OF FIVE YEARS OF LEAF AND SCAPE PHENOLOGY FOR *TRITELEIA LAXA* AT A GRASSLAND SITE (VINA) IN THE NORTHERN SACRAMENTO VALLEY. See Figs. 2 and 3 for sample sizes. ANOVA and Tukey HSD comparisons were performed separately for leaf and scape lengths, and repeated measures ANOVA was performed for scape growth rate. Values within a column sharing the same superscripts are not significantly different. Leaf length differences are significant at $P < 0.025$ for 1999 vs. 2002 and 2003 vs. 2004, and $P < 0.001$ for 2002 vs. 2004. Scape length differences are significant at $P < 0.001$. Scape growth rate differences are significant at $P < 0.001$, except 2000 vs. 2003 at $P < 0.025$.

Year	Mean (1 SE) maximum length (cm)		Date of maximum length		Precipitation (mm)			Scape growth rate (cm/wk)
	Leaf	Scape	Leaf	Scape	1-Oct. to 1-Feb.	1-Feb. to date of max. scape length	1-Oct. to date of max. scape length	
1999	23.1 ± 1.0^{ab}	22.6 ± 2.5^{na}	3-Apr	20-Apr	220	174	394	na
2000	23.6 ± 1.2^{abc}	22.8 ± 0.9^{a}	27-Mar	10-Apr	181	266	447	6.0^{a}
2002	28.0 ± 1.5^{cd}	31.6 ± 1.3^{b}	12-Mar	18-Apr	348	30	378	10.4^{b}
2003	26.6 ± 0.7^{bcd}	24.9 ± 0.6^{a}	23-Mar	13-Apr	340	154	494	6.8^{c}
2004	22.1 ± 0.9^{a}	23.0 ± 1.3^{a}	24-Mar	7-Apr	290	102	392	5.5^{a}

in both cases). All of these corms combined from both sites at the end of the growing season in late April, showed an overall mean volume of 1.30 ± 0.061 cm^3 (n = 120).

Depths of these *Triteleia* corms in the soil were not significantly different in the paired longest and shortest plants dug in Vina and Barn populations (long-plant and short-plant corms combined at a site to compare Vina vs. Barn, $P = 0.112$; Vina and Barn corms combined to compare all long vs. all short corms, $P = 0.090$). Mean depth ($\pm$SE) for these combined corms (from soil surface to top of the corm) was 7.27 ± 0.29 cm (n = 120).

Corm volume correlated with scape length and number of flowers. The correlation coefficient for corm volume and scape length was 0.612, and for corm volume and numbers of flowers was 0.610 (both correlations significant at $P = 0.01$). In addition, at Vina and Barn in 1998, we found number of flowers per plant to be strongly correlated with scape length (Spearman's $r_s = 0.814$, $P = 0.001$, n = 120).

Corm volume and changes in mass through the spring. Only the 28 February volume was significantly different from each of the four volumes measured later ($P \leq 0.017$), and none of the March and April volumes differed significantly from each other (Fig. 5). There was close to a linear increase in volume through this 8-week study period, and the deviations of the sample means did not differ significantly ($P < 0.001$).

The preceding volume and depth data reported were obtained with the corm coat present on the outside. However, removing a *T. laxa* corm coat showed that the corm present at the beginning of the warm growing season (i.e., starting in February) had two parts. The first (referred to as the "old" corm), shrinks as leaves and scape lengthen on the growing plant; this older part was gradually replaced by an enlarging "new" corm on top of the old corm (not necessarily at the same rate in all plants of a population) (Fig. 4b). Dry mass for five dates measured starting in February 2002 (during the enlarging of the new corm, while leaves and scapes were growing), increased from about 210 to 547 mg (Fig. 5). Masses of the old corm, (not given in Fig. 5), were quite similar to each other, with means ranging from about 25 to 41 mg. An old corm is shown below the new corm in Fig. 4c.

New growth of corms in the wet season. In 2004, there was rain early in the wet season (67 mm from 17 to 26 October, when temperatures of air and soil were still warm, and 107 mm total by November 30). For corms dug at Vina on 1 December 2004, volume (mean $\pm$ SE) was 1.23 ± 0.08 cm^3. All these plants sampled in December
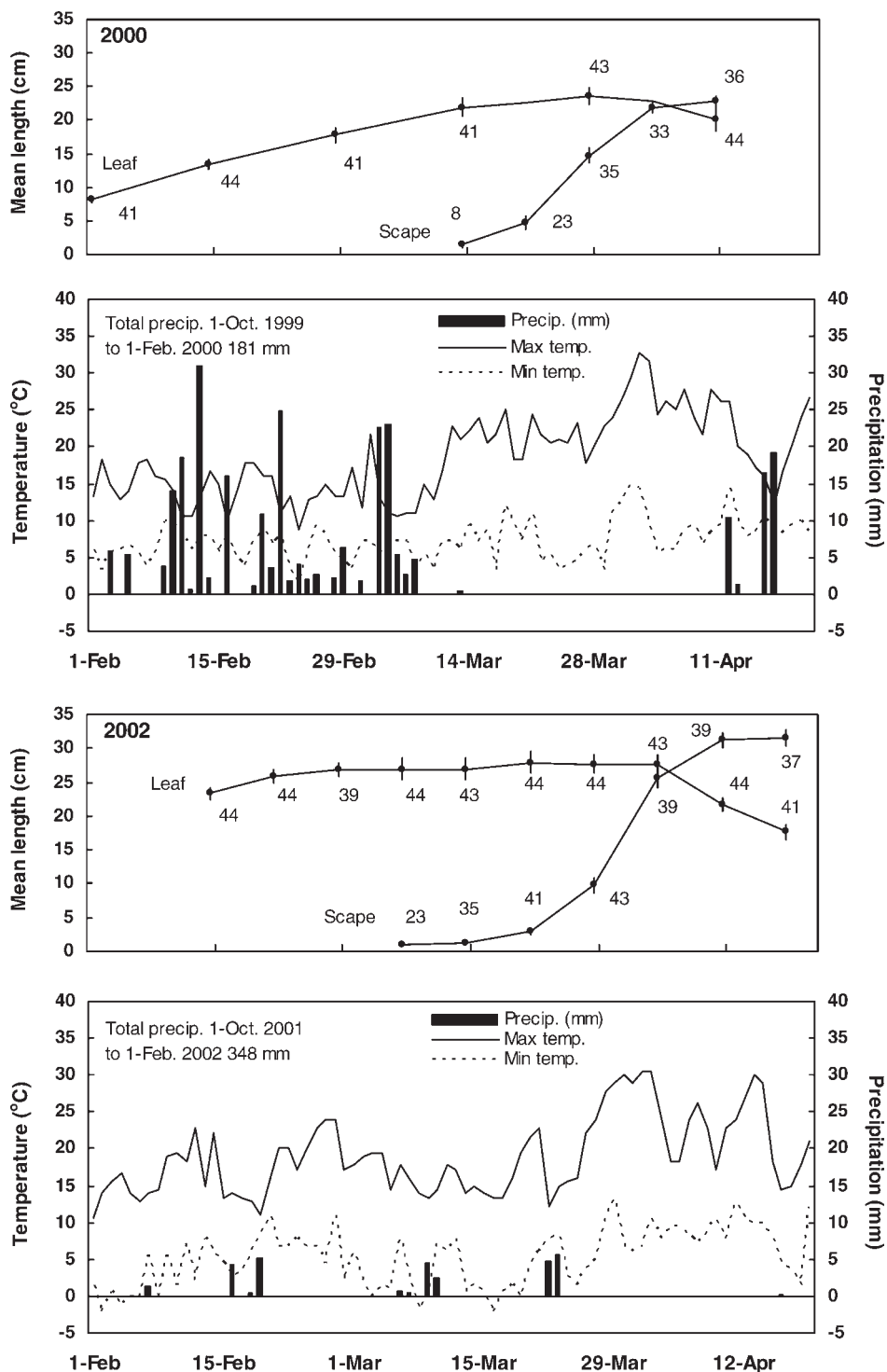
FIG. 2. Vegetative phenology for *Triteleia laxa* shown by mean (±SE) leaf and scape lengths at Vina during four years of the study. Daily precipitation and daily mean maximum and minimum temperatures at Orland, Glenn County (U.C. Davis 2005), are shown below each year's phenological data. Total wet season precipitation preceding 1 February is indicated in upper left corner for each year. N's are shown adjacent to the point of each sampling date.
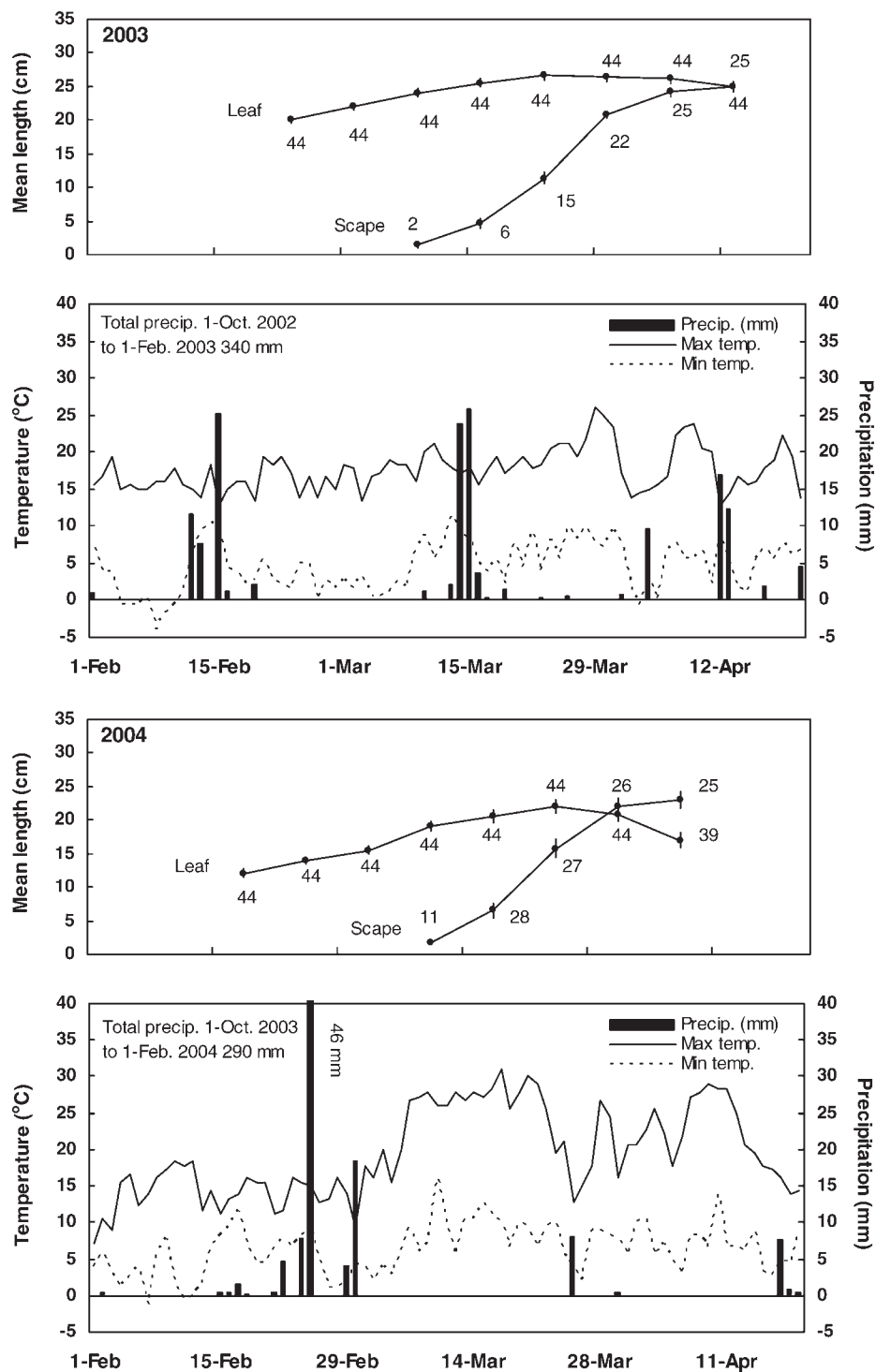
FIG. 2.   Continued.

(n = 30) had a new, green shoot extending upward from the corm (mean length = 6.6 ± 0.45 cm), but no shoots had reached the soil surface. Mean (±SE) dry mass for the 30 plump and turgid new corms was 150 ± 3.8 mg, and for the shrunken old corm still attached (i.e., functional during early spring plant growth in 2004), 31 ± 3.3 mg. Seven of the 30 corms had
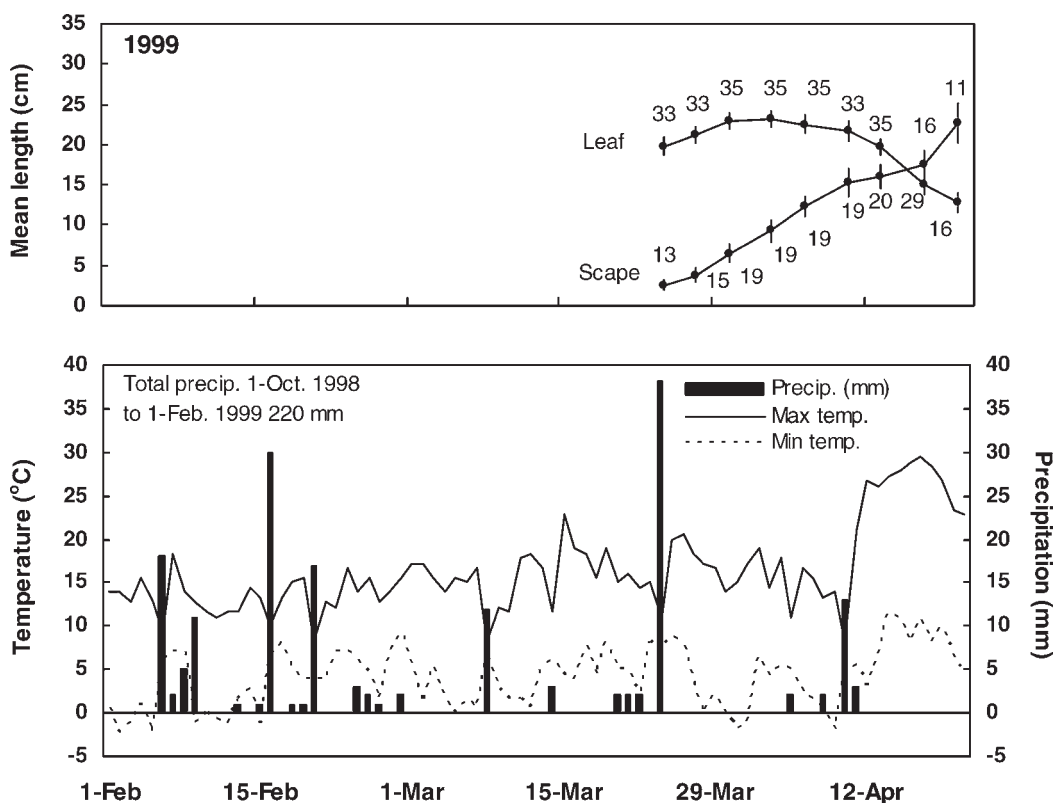
FIG. 3. Vegetative phenology for *Triteleia laxa* shown by mean (±SE) leaf and scape lengths at Vina in 1999 (a year scapes died before flowering). Daily precipitation and daily mean maximum and minimum temperatures at Orland, Glenn County (U.C. Davis 2005), are shown below the phenological data. Total wet season precipitation preceding 1 February is indicated in upper left corner. N's are shown adjacent to the point of each sampling date.

remains of the old corm from two years earlier (the corm functioning in 2003) still attached below the old corm.

None of the corms dug during any of the years of this study possessed additional small cormlets, derived vegetatively from the main corm, that have been reported elsewhere for *T. laxa* and have been used in horticultural propagation; however, geographical variation in cormlet production has been noted by (Hoover 1941).

Breeding System and Pollination

Compatibility. In 1998, a single flower was bagged on each of 37 plants; only 1 flower produced a fruit, whereas all plants produced fruits from unbagged flowers. Results are shown in Fig. 6. In 2000, a few seeds were produced in both types of hand self-pollinations, within flower (autogamous) and within plant (geitonogamous) (Fig. 6). Seed numbers did not differ statistically in these two types of selfings (P = 0.946); the few seeds observed suggests a high degree of self-incompatibility in this population. As indicated in Fig. 6, hand cross-pollinations (xenogamous) and open-pollinated controls did not differ from each other in seed number (P < 0.119). Both produced highly significantly more seeds than the self-pollinations (P < 0.0001). In 2004, among the 36 covered plants, 23 made one or more fruits. However, 26 of the 40 fruits total sampled from these plants had no seeds, giving a mean (±SE) of 1.1 ± 0.3 seeds set per fruit; the 14 plants with fruits that contained one to six seeds had a mean of 3.0 ± 0.4 seeds per fruit. The 39 uncovered plants produced a mean of 16 (±1; range 1–40) seeds per fruit (n = 78), and all of these plants had at least two fruits with three or more seeds. Seeds per fruit were very significantly lower in covered (autogamous) than uncovered (open pollinated) flowers (P < 0.0001).

Stigmatic receptivity and changes in floral morphology. Flowers remain open for up to four or five days. Anthesis occurs from the period when flowers are about to open to about one to two days old (flower phase A to C). Stigmas become receptive following anthesis; thus flowers are protandrous. Anthers are located towards the center of the flower during anthesis, after which point the stamens reflex towards the perianth, separating the anthers from the stigma. The
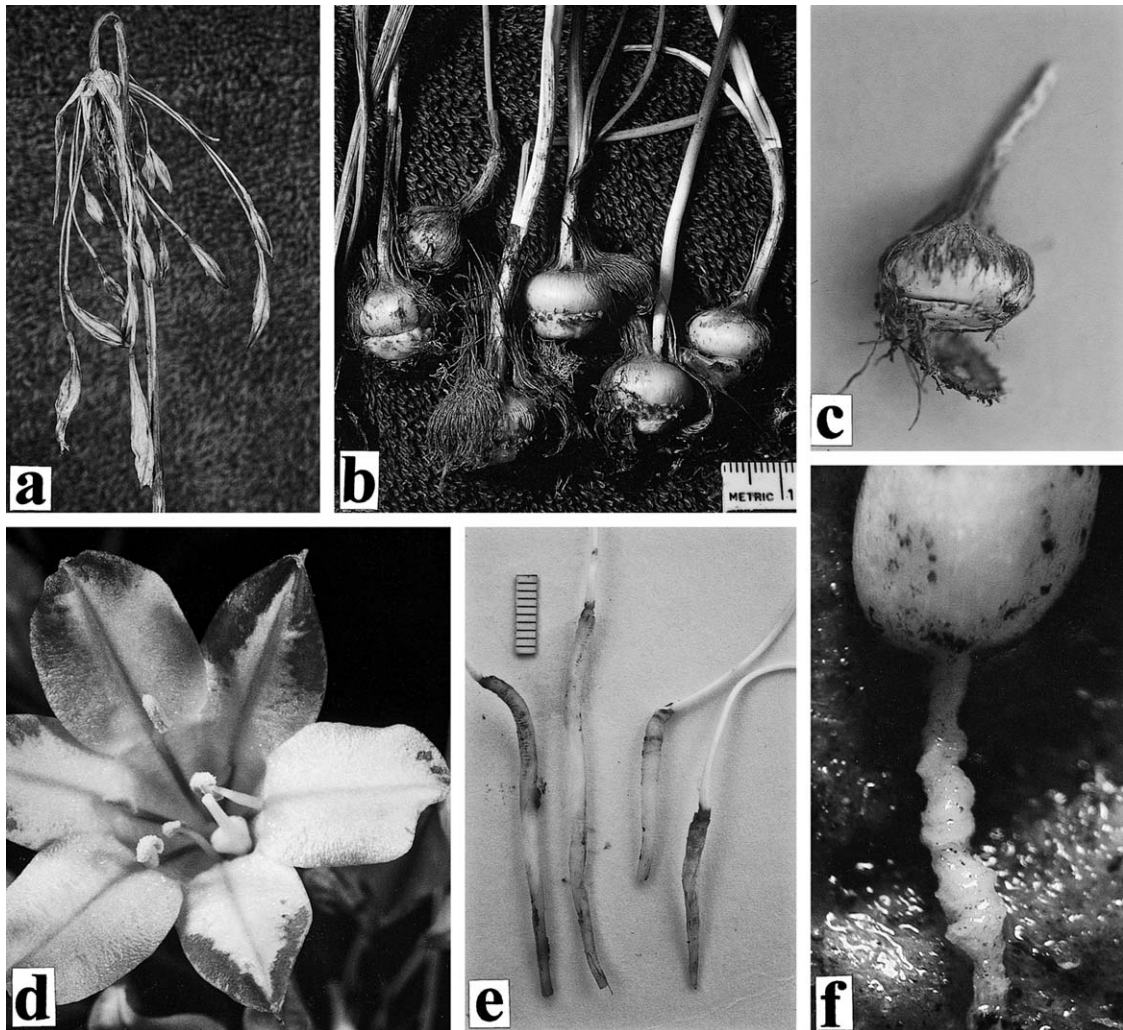
Fig. 4.   Portions of *Triteleia laxa* plants. a. Dead scape, which bent and dried before flowers fully opened (scape from base to bend ± 150 mm). b. Corms in mid-spring, with new corm developing on top of the old while leaves and scape still green aboveground (smallest increments on ruler in mm). c. New corm at end of growing season, with dried remnant of old corm pulled down (corm ± 16 mm diam.). d. Flower with an older pistil lying against the perianth, with style bent towards center of the flower and stamens empty of pollen (corolla ± 18 mm diam.). e. First-season seedlings, showing thick contractile roots which have replaced the fine primary roots; note transverse lines on several roots indicating areas of initial contraction (scale = 10 mm). f. Young corm (±4 mm diameter) on seedling at end of first growing season, with shortened (corrugated) section of the contractile root below it.

gynoecium lengthens from flower phase A to D, coming to rest on the lower-most tepals, and curves inward towards the center of the flower as the flower droops towards the ground (Fig. 4d). As flowers age the stigma becomes noticeably more glandular, presumably to promote pollen reception. As flowers reach phase D they begin to turn brownish due to loss of some pigmentation, and presumably become less attractive to visitors. Results of the peroxidase assay (Fig. 7) show an approximate linear increase in peroxidase activity in the stigma as flowers age. Peroxidase activity (PA) increased significantly from phase A to phase C, and phase D had greater PA than all other phases (P = 0.05). At the earliest flower phase (A), 96% of stigmas showed no PA (no blue color), but by phase D, 40% of stigmas had the highest ranking.

Pollen-ovule ratios. Counts of pollen grains and ovules in one flower bud from each of 35 plants showed (mean ± SE) 1) 20,500 ± 1760 pollen grains per anther, 2) no difference between upper-tier (n = 18) and lower-tier anthers (n = 17) (P = 0.64), and c) 40.1 ± 1.0 ovules per ovary. The mean pollen-ovule ratio was 3090 ± 260 (range
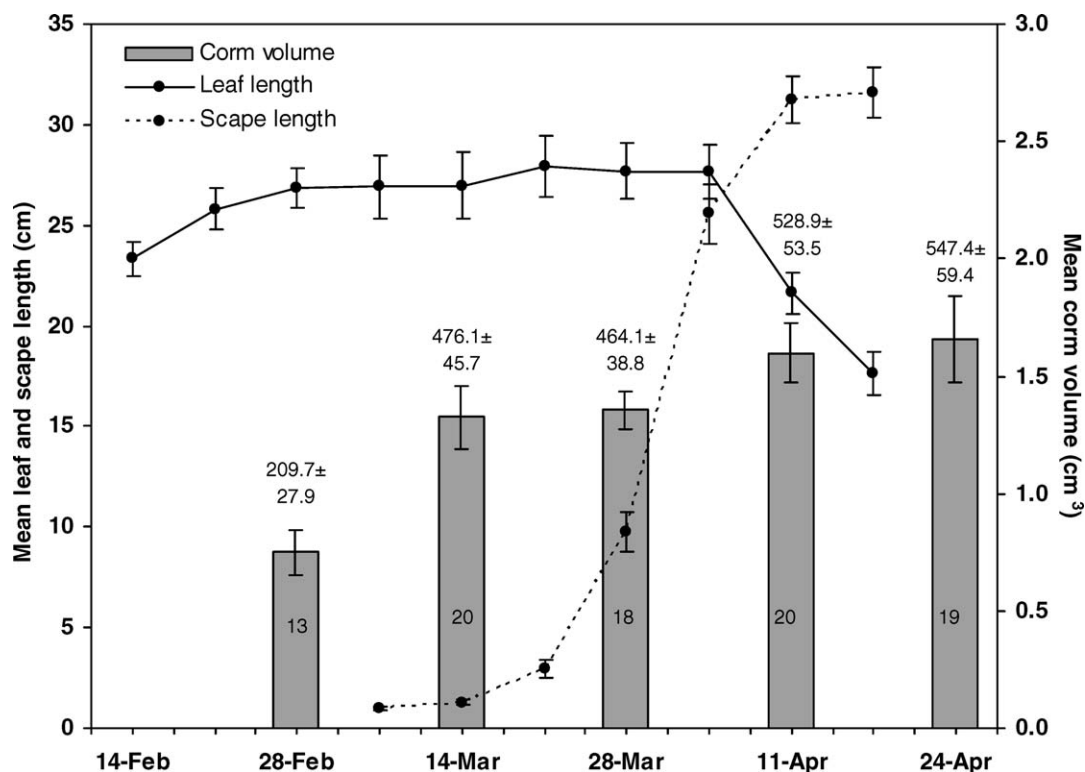
FIG. 5. Mean corm volume and mass in relation to mean leaf and scape length during the above-ground growing season in 2002 at Vina. Mean corm dry mass is given above each column. Sample size (n) for corm volume was 20 on every date; n's for corm dry mass are given inside columns; n's for leaf and scape length are given in Fig. 2. All error bars represent one standard error.

575–7250 grains per ovule); this result is consistent with the determination that flowers are outcrossing (Cruden 1977).

Nectar. A number of flowers tested had readings at the top of the refractometer scale (50% sucrose equivalents (SUE)), suggesting even higher SUE in these nectar samples. Mean ± SE of SUE was 44.1 ± 2.0%. Since readings were taken in the afternoon (4–6 pm DST), it is possible (but unlikely, due to the depth of corollas in bagged flowers) that there had been some evaporation of water from nectar, potentially biasing readings upward.

Reproductive Output: Flowers, Fruits and Seeds

Variation in numbers of flowers and fruits by year and by site. Significant differences in numbers of flowers were produced on the marked plants at the main study site at Vina during the five years they were available. Mean flowers per plant (±SE) in 2002 (12.6 ± 0.6; n = 50) was very significantly higher than all other years except 1998 (11.5 ± 0.9; n = 46) (P < 0.0001; Fig. 8). Fewer complete data sets on flowers per plant were available from our other sites, but we were

able to complete an ANOVA comparing different sites through several years (Vina 2002–2004 with Park 2003–2004 and Road 2003–2004). As noted in Table 2, Tukey HSD comparisons indicate many significant differences between these three sites in 2003 and in 2004 (and also between the two years for Park and Road sites).

Data on fruits per plant showed significant differences among the five years at Vina and also among sites in 2002, 2003, and 2004 (Fig. 8 and Table 2). Table 2 also shows comparisons of % fruit set (the proportion of flowers producing fruits). Additional determinations of % fruit set (mean ± SE, range, n) from Vina and Barn were not included in the ANOVAs: Vina in 1998 (75.7 ± 2.3, 40–100, 46) and in 2000 (69.1 ± 3.5, 16.7–100, 34); Barn in 1998 (60.0 ± 5.0, 0–100, 34) and in 2000 (68.8 ± 5.7, 0–100, 29).

Variation in numbers of ovules per ovary, seeds per fruit, and percent seed set. Ovules that did not develop into mature seeds were still present in mature fruits and distinguishable under a dissecting microscope. The vast majority of undeveloped ovules recorded appeared to have not developed at all, although there were also a number that reached nearly full seed size but
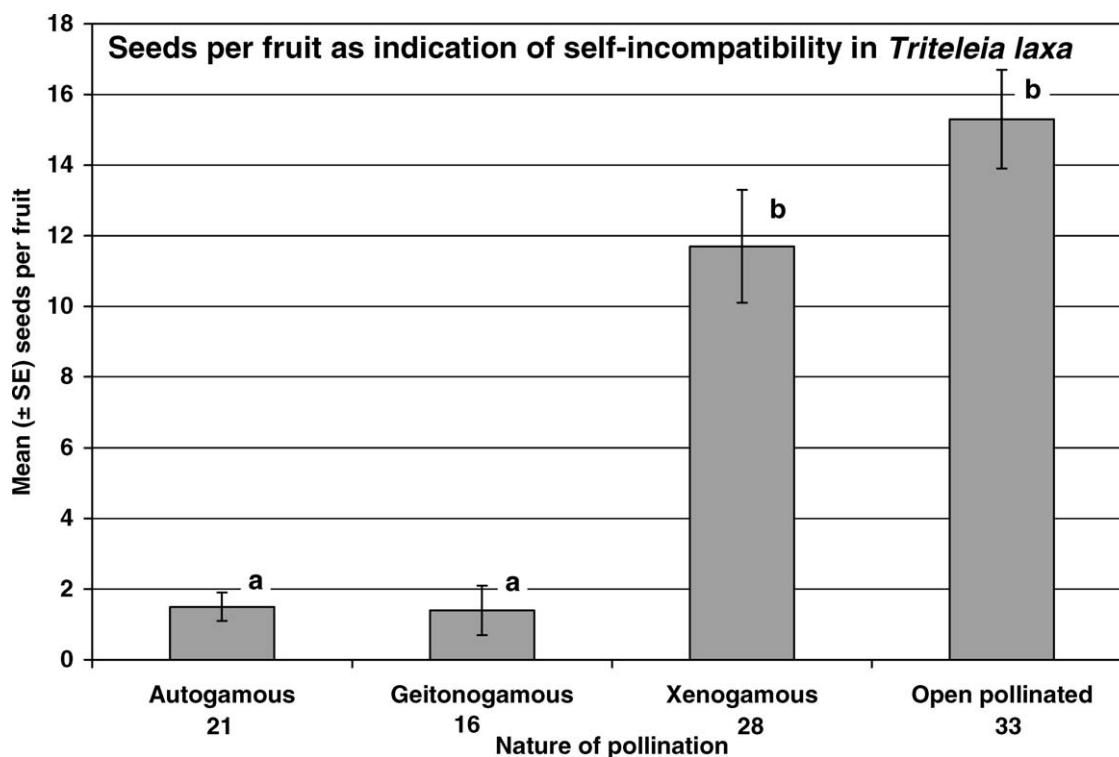
FIG. 6. Seeds per fruit (mean ± SE) in *Triteleia laxa*, resulting from three types of hand pollinations, compared with open-pollinated (control) plants at Vina in 2000. Sample sizes are shown below the x-axis labels. ANOVA and Tukey HSD comparisons were performed, and seed means with the same superscript letters at tops of columns do not differ significantly.

were pale and shrunken or caved-in. Counts from the largest samples of ovules and seeds are shown for three years at Vina (Table 3) and also in a comparison of three sites for 2003 (Table 4). Additional counts of seeds per fruit in earlier years at Vina and Barn (not included in these tables or the ANOVAs) are close to the 2004 count for Vina shown in Table 3. These earlier counts of seeds per fruit include (mean ± SE, range, n) Vina 1998 (14.8 ± 0.8, 1–33, 72); Vina 2000 (14.9 ± 1.1, 5–31, 33); and Barn 2000 (13.9 ± 0.9, 3–25, 39). Scapes that escaped the disease in 1999 were subjectively sought out, and showed lower numbers of seeds per fruit: Vina (11.3 ± 1.4, 2–26, 23), and Barn (11.0 ± 0.1, 0–24, 44).

Seed Mass, Viability, and Germination

Collected seeds showed no difference in mg per seed (mean ± SE): 1.660 ± 0.047 in garage and 1.753 ± 0.066 in lab (n = 40 each site; t = 1.154, P = 0.25). From all sites, collected seeds had 100% viability (n = 50 seeds each site).

Seed germination. Before the planting on 30 November 2003, 115 mm rainfall had already occurred in south Chico (U.C. Davis 2005). Fortuitously, 28 mm occurred in the first two

days after planting, and 191 mm total rainfall between planting and the first excavation of seeds on 28 December. There had been a total of 615 mm precipitation by the time these seedlings were drying up and the study was concluded (9 April 2004). Regional precipitation during this period was not obviously different from the preceding years (Fig. 1).

Table 5 shows that many seeds germinated in only four weeks. It was difficult to find the tiny seedlings among soil aggregates, and in four weeks after planting only 20 of the first 50 seeds were found as seedlings, along with 19 additional ungerminated seeds. Sizes of the seedlings in batches at 6 wk and later suggest that germination was well underway in four or five weeks after first wetting. Later batches of seeds showed germination percentages of 82–98%.

Seedling Growth. The sprout (cotyledon and rest of the seedling) continued to elongate, and in 8 wk the first foliage leaf of the seedling emerged from the somewhat sheath-like and still-elongating cotyledon. Leaf length of a seedling was measured from where it departed the cotyledon, to its tip. In 10 wk, leaves appeared green, some nearly above the soil surface; in 12 wk, most leaves extended above the soil surface, and by 18+

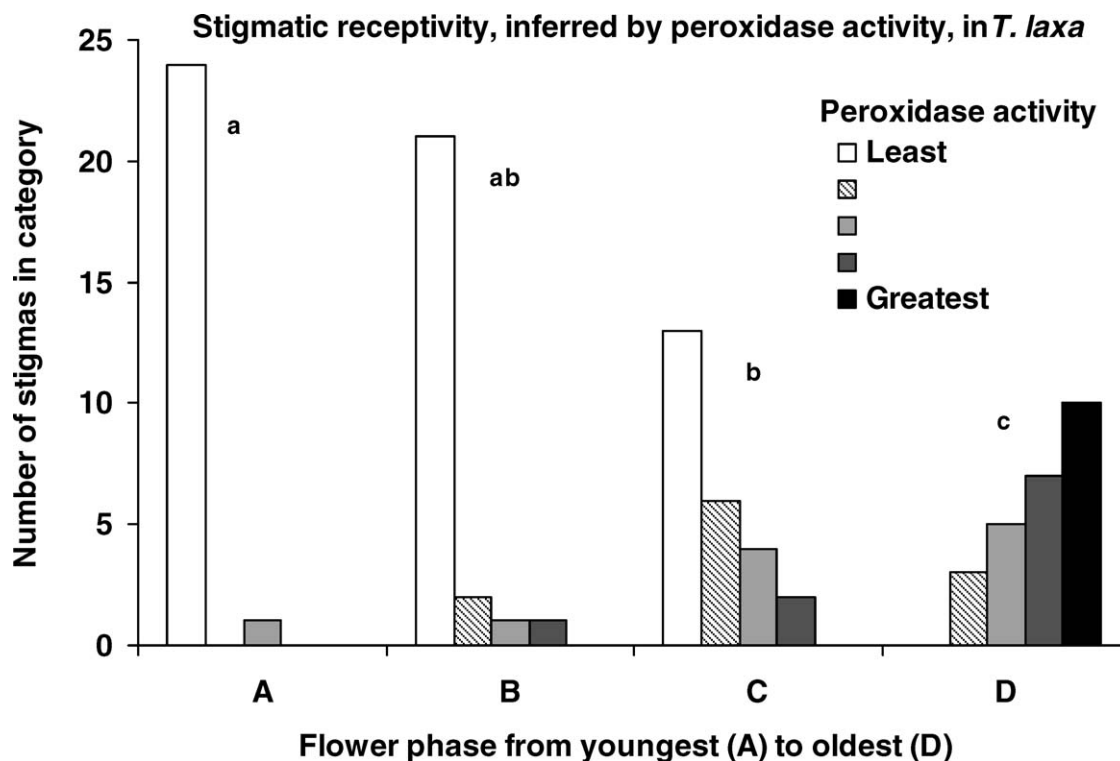## Stigmatic receptivity, inferred by peroxidase activity, in *T. laxa*

FIG. 7. Results of colorimetric assay in *Triteleia laxa* stigmas, showing increase in stigmatic peroxidase activity in relation to flower phase. Flower phases: (A) flower buds nearly open; (B) flowers recently opened and anthers dehisced (1–3 d old); (C) flowers with anthers empty, and with the style bent towards the middle of the flower (2–4 d old; Fig. 4d); and (D) flowers recently closed and most without any sign of seed formation yet (4–6 d old). Stigma coloration was ranked on a 0–4 (least to most) scale, based on the amount of stigmatic area covered and intensity of the color (n = 25 for each flower phase). ANOVA and Tukey HSD comparisons were performed; flower phases with the same superscript letter above their columns do not differ significantly (alpha = 0.05).

weeks (9 April) most leaves were yellowing and dying—representing the end of their winter/spring growth.

As the sprout continued to lengthen downward a thick lateral root emerged. A "pinching in" was discernible on the sprout by week 14, from which it was possible now to separately measure root (extending distally from this point), and shoot (the rest of the sprout extending back to the seed).

Two noteworthy features were observed from week 14 through week 18. At the base of the shoot by week 14, a slight swelling occurred, which later developed into the seedling's corm, the only part of the seedling to remain alive during the up-coming summer drought (Fig. 4e). Diameter of the corm (mean ± SE, at its widest, to the nearest 0.5 mm) increased from 2.4 ± 0.1 (n = 43) on week 16 to 3.2 ± 0.1 (n = 41) on week 18. On these weeks the thick lateral root, along the 2 or 3 cm immediately below the developing corm, appeared corrugated or twisted and thickened (Fig. 4f), and appeared to have a loose, transparent sheath around it in this region. Internal anatomy was not investigated, but this region certainly represents the "shorten-

ing" part of a contractile root, shown for other monocotyledonous geophytes, where growth changes in root cortex cells permit collapse of layers in cortex tissues, and cause the epidermis to loosen and become sheath-like (see Rimbach 1902; Smith 1930; Jernstedt 1984; Putz 1996). Table 5 shows that this root (below the corm) was indeed shorter in week 16 than in week 14. The degree that the contractile root helped move the seedling deeper into the soil was not investigated.

DISCUSSION

Phenology and Growth of Leaves, Scapes, and Corms

In the five years we observed vegetative phenology, we found that flowering plants each produced two leaves during the winter; leaves continued to elongate until mid March or early April. We did not find a correlation between yearly maximum leaf lengths and the amounts of precipitation. We have numerically documented that at maximum leaf length, the old corm, which
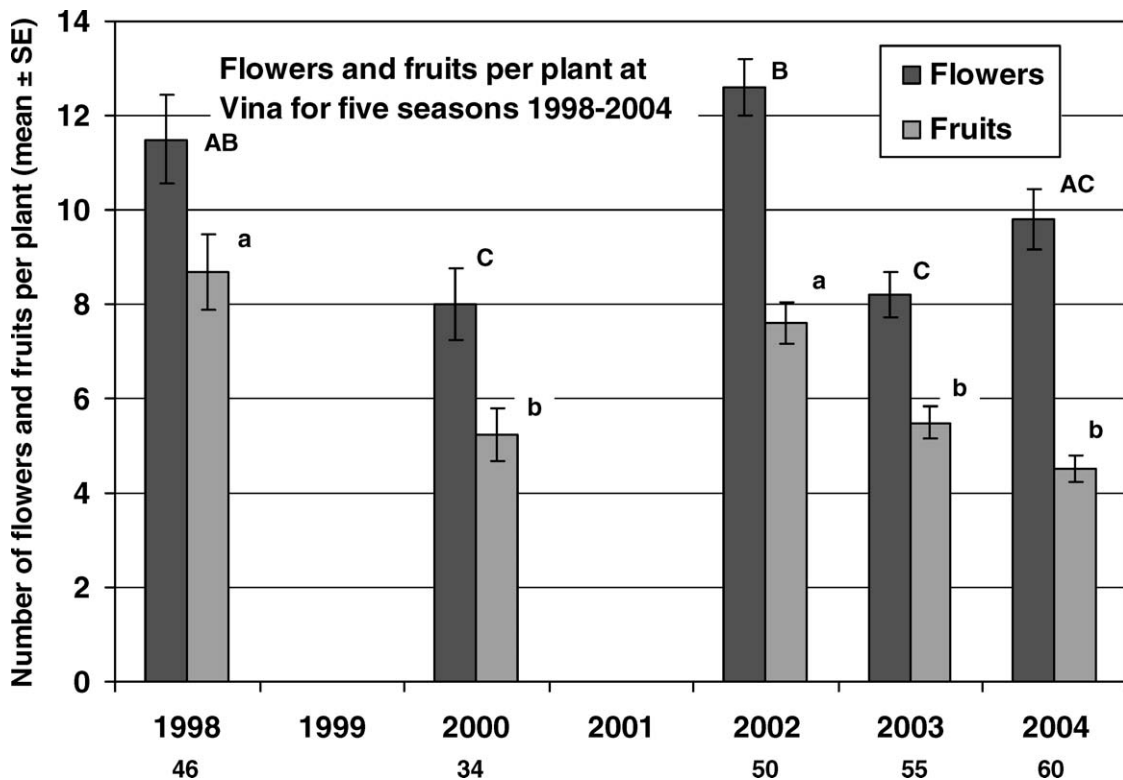
FIG. 8.   Mean (±SE) numbers of flowers and fruits per plant in *Triteleia laxa* at Vina, for the five years of successful reproduction from 1998 through 2004. N, the number of plants, is shown below the year. ANOVA and Tukey HSD comparisons were performed; means with the same superscript letters (flowers per plant, upper case; fruits per plant, lower case) do not differ significantly. Blank areas are left for 1999 and 2001 to emphasize the essential lack of flower, fruit and seed production in these two of the seven years of this study, due to the scape disease described in the text.

was giving rise to the leaves, had already produced a new corm on top of itself—before the plant had even flowered. Niehaus (1971) has described similar timing of new corm growth for species of *Brodiaea*.

The old corm also produced the flowering scape (for the anatomical site of scape origin in the old corm, see diagram for *Triteleia hyacinthina* in Smith 1930). Scape growth and maximum length (=height), and also the start of flowering may be influenced by daylength, as well as by the photosynthates produced by the leaves and the green scape itself. Maximum length was reached in a relatively narrow time period (about two weeks). It is not clear how many environmental factors influence maximum scape length, but the negative correlation between total amount of spring rain and scape length suggests that in some years (e.g., 2002; Table 1) scapes may be taller with *less* rain, and that air and soil temperatures and/or timing of the rain all have important influences. However, Niehaus (1971) reported that length of scape in species of *Brodiaea* varied according to the amount of moisture during the growing season, with the

scape 50% shorter in drier years (no measurements were given).

We have not studied summer dormancy in *T. laxa* corms, but have excavated corms at different times of the year. Rees (1989) described a ''physiological advantage'' existing in geophytes, in that corms that appear ''dormant'' may be producing primordia and early tissue growth well before environmental conditions promote expansive growth. Niehaus (1971) stated that corms in California species of *Brodiaea* show some underground growth, with both shoot and root emergence, even prior to the first winter rains. Keator (1967) reported that species of *Dichelostemma* vary in initiating root growth, most species only after several rains, and with only the early-flowering *D. capitatum* Alph. Wood showing any shoot growth after the first rains. We have provided quantitative information on early growth in *T. laxa*, on corm mass and volume, and on length of shoots after several rains, but still early in the wet season (e.g., by 1 December 2004, green shoots from 30 corms averaged 6.55 cm long, all still below the soil surface). More study on this topic could be

TABLE 2. YEAR AND SITE COMPARISONS OF MEAN ± SE (AND RANGE) FOR FLOWERS PER PLANT, FRUITS PER PLANT AND % FRUIT SET IN *TRITELEIA LAXA* AT THREE SITES IN 2002–2004. ANOVA and Tukey HSD comparisons were performed separately for each parameter listed. In each column means with the same superscript letters do not differ significantly. For flowers, P < 0.001 for all significant differences except Park vs. Road in 2003 with P < 0.05; for fruits, all significant differences at P < 0.001 except Park vs. Road in 2003 with P < 0.005, and Vina 2002 vs. Vina 2003 with P < 0.05; for percent fruit set, all significant differences with P < 0.001 except Vina 2002 vs. Vina 2003 with P < 0.05.

Year and site	n	Flowers per plant	Fruits per plant	% fruit set
2002				
Vina	50	12.6 ± 0.6[acd] (5–25)	7.6 ± 0.4[de] (3–14)	60.7 ± 2.0[bcd] (33.3–87.5)
2003				
Vina	55	8.2 ± 0.5[ab] (2–19)	5.5 ± 0.3[abc] (2–16)	69.6 ± 2.7[de] (33.3–100)
Park	51	12.6 ± 0.8[cde] (3–29)	8.6 ± 0.6[def] (3–22)	70.1 ± 2.3[def] (33.3–100)
Road	53	15.7 ± 1.1[df] (3–37)	11.5 ± 0.8[ef] (2–27)	74.4 ± 2.1[def] (43.5–100)
2004				
Vina	60	9.8 ± 0.7[abc] (4–28)	4.5 ± 0.3[ab] (1–12)	49.8 ± 2.6[a] (16.7–100)
Park	52	7.9 ± 0.4[a] (4–14)	3.9 ± 0.3[a] (0–10)	52.2 ± 2.8[ab] (0–85.7)
Road	52	14.1 ± 0.8[def] (3–30)	7.4 ± 0.5[cd] (1–19)	54.7 ± 2.4[abc] (7.8–85.7)

interesting, especially in determining if late dry season/early wet season growth also occurs in *T. laxa* or other geophytes occurring at considerably higher (colder) elevations in mediterranean California.

Corm depth did not differ significantly when large numbers of shorter and longer flowering scapes were compared; this may be the "standard" depth to which the corms are delivered by several seasons of contractile root activity (see below) in the clay loam soils here.

Although depths did not differ, the corm *volumes* were highly significantly different, with the longest scapes attached to the largest corms. Surprisingly, Han (2001) reported that heights of scapes were not related to corm sizes for (mainly garden-grown) *T. laxa* and several other California geophytes (*T. bridgesii* (S. Watson) E. Greene, *T. ixiodes* (S. Watson) E. Greene, and *Dichelostemma ida-maia* (Alph. Wood) E.Greene). However, number of flowers per scape in *T. laxa* was found to be positively related to corm size by us and also by Han (2001). According to (Han and Halevy 1993) these new corms can gain up to about 90% of their final weight even before flowering. Han (2001), who was growing live corms, indicated that *T. laxa* corms with a fresh weight of 1.1 g or more do flower in greenhouse studies, but that typically

commercial-sized corms weigh 2.5 g or more—a mass reached in three or four growing seasons. We expect that it also takes that long in the field to reach good flowering size, and expect that larger *T. laxa* plants seen in the field generally are older and have heavier corms. But in the related geophytic genus, *Dichelostemma*, Keator (1967) has noted that large corms do not guarantee flowering, and that environmental features of the current growing season (as well as stored reserves) may affect formation of flowers.

We have documented a feature of phenology and growth that seems to be un-recorded in literature about geophytes in the field. In two of the seven years of this study (1999 and 2001), most *T. laxa* plants at Vina and Barn produced apparently normal leaves, but failed to flower due to a disease causing death of the elongating scapes. We have recorded external symptoms caused by this pathogen (Fig. 4a; unpublished information), but have not determined the cause or found matching symptoms in the literature on wild plants. Superficial similarities in the disease referred to as "neck rot" (due to the fungus *Botrys allii*) can occur in the cultivated onion *Allium cepa*, where infection just below the umbel can result in "blasting of flowers" (Voss 1979). Also (Han and Halevy 1993) noted that *T. laxa* grown in Holland for commercial distribution

TABLE 3. YEARLY COMPARISONS OF MEAN ± SE (AND RANGE) FOR TOTAL OVULES PER OVARY, SEEDS PER FRUIT AND % SEED SET IN *TRITELEIA LAXA* AT VINA IN 2002, 2003, AND 2004. Total ovules includes undeveloped ovules as well as those maturing into seeds. ANOVA and Tukey HSD comparisons were performed separately for each parameter. In each column, means with the same superscript letter do not differ significantly (P < 0.001 for seeds, and P < 0.0001 for seed set).

Year, at Vina	n	Total ovules per ovary	Seeds per fruit	% seed set
2002	100	33.3 ± 0.6[a] (15–46)	19.0 ± 0.8[a] (3–39)	56.3 ± 1.8[a] (10–91.7)
2003	98	31.5 ± 0.6[a] (20–47)	18.4 ± 0.8[a] (1–40)	57.7 ± 2.0[a] (3–90.9)
2004	120	32.2 ± 0.5[a] (14–49)	13.1 ± 0.7[b] (0–36)	40.1 ± 1.9[b] (0–94.7)

TABLE 4. SITE COMPARISONS OF MEAN ± SE (AND RANGE) FOR TOTAL OVULES PER OVARY, SEEDS PER FRUIT AND % SEED SET IN *TRITELEIA LAXA* IN 2003. ANOVA and Tukey HSD comparisons were performed separately for each parameter. Total ovules includes undeveloped ovules as well as those maturing into seeds. In each column means with the same superscript letter do not differ significantly ($P < 0.009$ for ovules, $P < 0.001$ for seeds, and $P < 0.032$ for seed set).

Site, in 2003	n	Total ovules per ovary	Seeds per fruit	% seed set
Vina	98	31.5 ± 0.6^a (20–47)	18.4 ± 0.8^a (1–40)	57.7 ± 2.0^a (3–90.1)
Park	102	34.0 ± 0.6^b (18–50)	13.5 ± 0.7^b (2–31)	$39.1 \pm 2/0^b$ (6–92.6)
Road	106	34.4 ± 0.5^b (21–47)	17.5 ± 0.8^a (4–43)	50.3 ± 2.2^c (10.8–97.1)

can be infected by three pathogens (*Corynebacterium fascians*, *Rhizoctonia tuliparum*, and *Sclerotinia bulborum*), but no symptoms were listed. Our discovery emphasizes the value of observing the same populations in the field for a series of consecutive years, to note possible stochastic events in the life cycle, as when sexual reproduction is prevented.

Features of Sexual Reproduction

As with many plants in mediterranean areas, the flowers, fruits, and seeds are produced as vegetative growth is completed near the start of the hot and dry summer season. By the time *Triteleia laxa* produces a scape with flowers in late March or April, air temperatures are higher, and flying insects are available for vectoring pollen among flowers. Our tests suggest that *T. laxa* is self-incompatible (Fig. 6), or has a degree of self-compatibility but relies on insects to vector pollen and promote out-crossing. According to comments by (Cruden 1977) features that we observe in *T. laxa* are often associated with self-incompatible and out-crossing flowers, such as a large, showy floral display well up and above associated plants, a relatively high pollen:ovule ratio, and the presence of nectar. Berg (2003) has shown that nectaries in *T. laxa* are in the three septae that separate locules of the ovary, and that nectar is secreted into three nectar channels on the ''shoulders'' of the ovary. It would be interesting to determine if the tongues of any insects we observed visiting flowers, are able to extract nectar from these channels rather than strictly sucking it up from the pool that collects around the stipe at the base of the ovary. Outcrossing may be facilitated by these insect flower-visitors, and also by the protandry seen in these hermaphroditic flowers (Fig. 7).

Male and female functions in hermaphroditic flowers can be selected for by different mechanisms, and it is often found that factors that select for increases in male function in turn decrease female function, and vice versa (e.g., Charlesworth and Charlesworth 1987; Burd 1994). Protandry, the temporal separation of sexual functions in plants wherein the male function precedes the female function, may have evolved for reasons other than promoting self-incompat-

ibility, such as increasing male function. In contrast, self-incompatibility decreases male function (due to need for self pollen to travel elsewhere) while increasing female function (avoidance of potentially fitness depressing self pollen). Lloyd and Yates (1982) suggested that one advantage to separation of sexual functions in hermaphroditic flowers may be increased opportunity for floral features to evolve via sexual selection. The protandrous flowers of *T. laxa* suggest the opportunity for female choice and male-male competition. Furthermore, stigmatic receptivity schedules can affect the density and diversity of pollen, and increased pollen tube density and pollen donor diversity can encourage sexual selection via male-male competition and female choice (Galen et al. 1986). However, we have not examined pollen density and diversity in this species; the opportunity for sexual selection may be minimized if sexual reproduction is pollen-limited (Willson 1979; Galen et al. 1986). Lastly, stigmatic receptivity schedules can play a strong role in reproductive output due to affecting density and diversity of pollen received (Galen et al. 1986) as well as rate of pollen germination and pollen tube growth (Yi et al. 2006).

Relatively low reproductive output has been found in both fruit set and seed set for *T. laxa* in our region (well documented with large sample sizes, in several sites, and over several years). There are generally two main factors likely to cause low fruit set and seed set: pollen (including pollinator) limitation, and abiotic resource limitation (Stephenson 1981). Slightly more seeds per fruit were found in our open-pollinated flowers than in our hand cross-pollinated flowers, suggesting that pollen limitation is not occurring. Although we have no direct measurements on abiotic features like local temperature and precipitation, the study period in spring of 2003 had high amounts of rain regionally, which we expect would rule out moisture as a limiting resource in that year. The highest proportion of fruit set was indeed in 2003, but that was still only between 69.6 and 74.4% at the three sites measured. Our data from 2004 are in agreement: fruit set at these same three sites (this time with unusually low spring rainfall in 2004) were lower, and may

TABLE 5. SEED GERMINATION AND GROSS MORPHOLOGY OF SEEDLINGS IN *TRITELEIA LAXA*, BASED ON SEEDS COLLECTED AT VINA ON 22 MAY 2003 AND PLANTED OUTDOORS IN GARDEN SOIL IN CHICO ON 30 NOVEMBER 2003. Length of "sprout to primary root tip" refers to the entire seedling length from seed coat to tip of the primary root before additional organs were discernible; at week 14 the primary root was shriveled and no longer measured. Length of "lateral contractile root" refers to the thick, new (lateral) root from its point of emergence near the seed to its tip; this contractile root had not yet "replaced" the primary root. Length of "contractile root below new corm" refers to the contractile root (which has replaced the primary root) from its base at the developing corm, to its tip (see Fig. 4e,f). Length "sprout to base of new corm" refers to length of seedling, from the seed coat to the base of the new corm. Lenth "leaf" refers to the leaf from its point of emergence from the sprout to its tip. Diameter of corm was measured at its widest point. Lengths (mean ± SE) are in mm. [a] Germinating seeds were difficult to discern among the soil aggregates and pebbles. N is probably low here because ungerminated seeds were simply not detected. Numbers recovered (of 50) in later batches are as high as 42 (82%) to 49 (98%). [b] Since only 20 seedlings were recovered, but additional seedlings from outside the 50-seed batch were available for this one date, an additional 23 seeds with sprouts were measured. [c] N is lower because specimens broken during excavation could usually not be measured with accuracy. [d] Seedlings were too breakable to extract intact from soil, and leaves were yellowing and drying; only corms were able to be measured well.

Date seeds excavated (weeks since planting)	Number seedlings recovered (50 seeds)	Length sprout to primary root tip	Length lateral contractile root	Length contractile root below new corm	Length sprout to base of new corm	Length leaf	Diameter corm
28 Dec 2003 (4 wk)	20[a]	1.5 ± 0.1 n = 43[b]	—	—	—	—	—
11 Jan 2004 (6 wk)	37	3.8 ± 0.3 n = 37	—	—	—	—	—
25 Jan (8 wk)	42	7.9 ± 0.6 n = 42	—	—	—	—	—
8 Feb (10 wk)	49	19.6 ± 0.8 n = 45[c]	—	—	—	2.3 ± 0.3 n = 30[c]	—
22 Feb (12 wk)	46	23.9 ± 1.0 n = 42[c]	8.4 ± 1.0 n = 29	—	—	15.5 ± 0.6 n = 48	—
7 Mar (14 wk)	46	44.1 ± 1.7 n = 44[c]	—	29.8 ± 1.2 n = 44[c]	14.4 ± 0.8 n = 44[c]	29.4 ± 1.2 n = 38[c]	—
21 Mar (16 wk)	43	—	—	20.1 ± 1.5 n = 32[c]	20.1 ± 1.5 n = 32[c]	50.7 ± 1.3 n = 45[c]	2.4 ± 0.1 n = 43
9 Apr (18+ weeks)	41[d]	—	—	—	—	64.6 ± 1.4 n = 43	3.2 ± 0.1 n = 41

reflect plant reproduction suffering from drought of an "early mediterranean summer."

A possible cause for the relatively low proportion of ovules developing into seeds (Tables 3 and 4) could be a polyploid condition in the populations studied. Davidson (1975), using *Triteleia laxa* plants previously collected from different localities, but then growing at the Rancho Santa Ana Botanical Garden, documented diploid, tetraploid, and hexaploid conditions in this species. Source localities were not given, but he found percent of "good pollen" (as opposed to empty grains) varied somewhat in populations according to ploidy level. Although most diploid (2n = 16) as well as most polyploid (2n = 28, 32, or 48) plants produced 85 to 98% good pollen, one population with 2n = 28 and one with 2n = 48 produced only about 60% good pollen, associated with "lagging" meiotic chromosomes. In addition to affecting microspore formation, such meiotic irregularities could also cause some ovules to be inviable, and could account for the many tiny, white ovules, that did not seem to have grown at all, found among ripe seeds in mature fruits in our study.

Features of the Seed and Seedling Stages in the Life Cycle

We found that 100% of the plump and black *T. laxa* seeds were viable, and that 80–90% of these seeds germinated (Table 5). While Emery (1988) noted that no specific conditions are needed to get germination in this species, Han (1993) noted that eight weeks of cold stratification is needed to get high percentages of the seeds to germinate. We found that four weeks of ambient temperatures outdoors in December produced high percentages, possibly due to our storage methods having subjected seeds to alternating temperatures during both summer and fall.

Most of the early seedling growth occurs underground during the winter; several of the features we have found for *T. laxa* have been briefly described for other geophytes a century ago by (Rimbach 1902). The seedling of *T. laxa* has a contractile root, a structure now listed as widespread in geophytic monocots (Putz 1992, 1996) and that probably functions best in winter, when the soil is wet and is most penetrable. We suspect that the "channel effect" described for contractile roots of seedlings and also for older stages of geophytes including *T. hyacinthina* (Putz 1992, 1996) pertains to *T. laxa*. That is, the space or channel provided by the contractile root first growing wide and thick will later permit passageway (a channel) for the sinking of the developing corm as this root shrinks and pulls the rest of the growing seedling deeper into the soil. The increased depth of a seedling's corm (or bulb) achieved during the wet months by a contractile

root, presumably promotes survival during the intensely hot and dry conditions occurring nearer the soil surface during the mediterranean summer. Possession of deep-seated corms is usually considered an advantage of the geophytic habit (e.g., Rees 1989). Putz (1996) noted that second-year (or even older) plants of many geophytes (including *Brodiaea*, according to Niehaus 1971) can produce new contractile roots that help seat the corms even deeper.

Seedlings of some California geophytes have been described earlier with relatively little detail (e.g., Rimbach 1902; Keator 1967; Niehaus 1971), or occasionally with considerable anatomical detail (Jernstedt 1984). We have documented the size and behavior of *T. laxa* seedlings more quantitatively (Table 5), and show that a single green leaf extends aboveground 5 or 6 cm, and that a tiny corm forms, averaging 3.2 mm wide, before the seedling goes into a dormant state with the approach of mediterranean summer. This production of a small over-summering corm during the wet season is certainly a signature of survival in a geophyte seedling.

We have documented many aspects of the field biology for *T. laxa*, but gaps in our knowledge remain. We do not know how long it takes in the field for a seedling to produce a plant that flowers, or for how many years a plant flowers or persists. It also would be interesting to investigate the extent to which corms and aboveground organs are consumed by animals. We believe our data do provide ample background information to stimulate field studies on other species of *Triteleia* and other mediterranean geophytes.

Literature Cited

ANDERSON, M. K. AND D. L. ROWNEY. 1998. California geophytes: ecology, ethnobotany, and conservation. Fremontia 26(1):12–18.

BASKIN, C. C. AND J. M. BASKIN. 1998. Seeds. Academic Press, New York, NY.

BERG, R. Y. 2003. Development of ovule, embryo sac, and endosperm in *Triteleia* (Themidaceae) relative to taxonomy. American Journal of Botany 90:937–948.

BLEE, K. A., J. W. CHOI, A. P. O'CONNELL, W. SCHUCH, N. G. LEWIS, AND G. P. BOLWELL. 2003. A lignin-specific peroxidase in tobacco whose antisense suppression leads to vascular tissue modification. Phytochemistry 64:163–176.

BROYLES, P. 1983. A flora of the Nature Conservancy's Vina Plains Preserve, Tehama County, California. M.A. Thesis. California State University, Chico, CA.

———. 1987. A flora of Vina Plains Preserve, Tehama County, California. Madroño 34:209–227.

BURD, M. 1994. Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. Botanical Review 60:83–139.

CHARLESWORTH, D. AND B. CHARLESWORTH. 1987. The effect of investment in attractive structures on allocation to male and female function in plants. Evolution 41:948–968.

CHIARELLO, N. R. 1989. Phenology of California grasslands. Pp. 47–58 *in* L. F. Huenneke and H. A. Mooney (eds.), Grassland structure and function: California annual grassland. Kluwer Academic Publishers, Dordrecht, The Netherlands.

CRUDEN, R. W. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in plants. Evolution 31:32–46.

DAFNI, A., D. COHEN, AND I. NOY-MEIR. 1981. Life cycle variation in geophytes. Annals of the Missouri Botanical Garden 68:652–660.

DAVIDSON, C. 1975. Pollen size and polyploidy: a review with studies in *Dichelostemma* and *Triteleia* (Liliaceae). Los Angeles County Museum of Natural History Contributions in Science No. 262.

DILLEY, J. D., P. WILSON, AND M. R. MESLER. 2000. The radiation of *Calochortus* generalist flowers moving through a mosaic of potential pollinators. Oikos 89:209–222.

DOALSON, M. 1999. Morphological variation and reproductive biology of a native Californian geophyte, *Brodiaea californica* (Liliaceae). M.S. Thesis. California State University, Chico, CA.

EMERY, D. E. 1988. Seed propagation of California native plants. Santa Barbara Botanic Garden, Santa Barbara, CA.

FORTANIER, E. J. 1969. The influence of temperature, light energy and photoperiod on flowering of *Brodiaea laxa* Wats. Netherlands Journal of Agricultural Science 17:176–182.

FNAEC (FLORA OF NORTH AMERICA EDITORIAL COMMITTEE) (eds.). 2003. Flora of North America North of Mexico. Vol. 26, Magnoliophyta: Liliidae, Liliales, and Orchidales. Oxford University Press, New York, NY.

GALEN, C., J. A. SHYKOFF, AND R. C. PLOWRIGHT. 1986. Consequences of stigma receptivity schedules for sexual selection in flowering plants. American Naturalist 127:62–76.

Gowans, K. D. 1967. Soil survey of Tehama County, California. United States Government Printing Office, Washington, DC.

Han, S. S. 1993. Chilling, ethephon, and photoperiod affect cormel production of *Brodiaea*. HortScience 28:1095–1097.

———. 2001. Flowering of three species of *Brodiaea* in relation to bulb size and source. Scientia Horticulturae 91:349–355.

——— and A. H. Halevy. 1993. *Triteleia*. Pp. 611–116 *in* A. A. De Hertogh and M. Le Nard (eds.), The physiology of flower bulbs. Elsevier Science, Amsterdam, The Netherlands.

———, ———, R. M. Sachs, and M. S. Reid. 1991. Flowering and corm yield of brodiaea in response to temperature, photoperiod, corm size and planting depth. Journal of the American Society of Horticultural Science 116:19–22.

Huenneke, L. F. and H. A. Mooney (eds). 1989. Grassland structure and function: California annual grassland. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Hickman, J. C. (ed.). 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, CA.

Hoover, R. 1941. A systematic study of *Triteleia*. American Midland Naturalist 25:73–100.

Jernstedt, J. A. 1980. Anthesis and floral senescence in *Chlorogalum pomeridianum* (Liliaceae). American Journal of Botany 67:824–832.

———. 1982. Floral variation in *Chlorogalum angustifolium* (Liliaceae). Madroño 29:87–94.

———. 1984. Seedling growth and root contraction in the soap plant, *Chlorogalum pomeridianum* (Liliaceae). American Journal of Botany 71:69–71.

Jokerst, J. D. 1981. The reproductive ecology of *Calochortus* (Liliaceae). M.A. Thesis. California State University, Chico, CA.

Kannely, A. 2003. Pollen output in the first and second flower of the geophytic lily *Calochortus*. M. S. Thesis, California State University, Chico, CA.

Keator, G. 1967. A taxonomic and ecological study of the genus *Dichelostemma* (Amaryllidaceae). Ph. D. Dissertation, University of California, Berkeley, CA.

———. 1987. Differentiating California's Brodiaeas. Fremontia 14(4):20–24.

———. 1989. The brodiaeas. Four Seasons 8:4–11.

———. 1993. *Triteleia*. Pp. 1206–1208 *in* J. C. Hickman (ed.), The Jepson manual: higher plants of California. University of California Press, Berkeley, CA.

Lenz, L. W. 1966. Chromosome numbers in the Allieae (Liliaceae). Aliso 6:81–82.

Lloyd, D. G. and J. M. A. Yates. 1982. Intrasexual selection and the segregation of pollen and stigmas in hermaphrodite plants, exemplified by *Wahlenbergia albomarginata* (Campanulaceae). Evolution 36:903–913.

Mitchelson, S. R. 1993. Factors affecting fruit set and survival of *Zigadenus fremontii* (Liliaceae) growing in a northern California annual grassland. M.S. Thesis. California State University, Chico, CA.

Munz, P. A. and D. D. Keck. 1959. A California flora. University of California Press, Berkeley, CA.

NOAA (National Oceanic and Atmospheric Administration). 2005. Monthly station climate summaries. Available at: http://www5.ncdc.noaa.gov/pdfs/cd/california.

Niehaus, T. F. 1971. A biosystematic study of the genus *Brodiaea* (Amaryllidaceae). University of California Studies in Botany 60.

———. 1980. The Brodiaea complex: genera *Brodiaea*, *Triteleia*, *Dichelostemma*; family Amaryllidaceae. Four Seasons 6:11–21.

Oswald, V. H. 1997. Vascular plants of the Vina Plains Preserve, Wurlitzer Unit. Department of Biological Sciences, California State University, Chico, CA. Unpublished.

Parsons, R. F. 2000. Monocotyledonous geophytes: comparisons of California with Victoria, Australia. Australian Journal of Botany 48:39–43.

——— and S. D. Hopper. 2003. Monocotyledonous geophytes: comparison of south-western Australia with other areas of mediterranean climate. Australian Journal of Botany 51:129–133.

Pate, J. S. and K. W. Dixon. 1982. Tuberous, cormous and bulbous plants. University of Western Australia Press, Perth, Western Australia.

Pires, J. A. and K. Sytsma. 2002. A phylogenetic evaluation of a biosystematic framework: *Brodiaea* and related petaloid monocots (Themidaceae). American Journal of Botany 89:1342–1359.

Poches, S. and R. M. Cowling. 2004. Cape geophytes: putting the pieces together. Pp. 1–10 *in* M. Arianoutsou and V. P. Papanastasis (eds.), Proceedings 10th MEDECOS conference, April 25-May 1, 2004, Rhodes, Greece. Millpress, Rotterdam, The Netherlands.

———, ———, and D. R. Du Preez. 2005. Patterns of geophyte diversity and storage organ size in the winter-rainfall region of southern Africa. Diversity and Distributions 11:101–109.

Putz, N. 1992. Measurement of the pulling force of a single contractile root. Canadian Journal of Botany 70:1433–1439.

———. 1996. Development and function of contractile roots. Pp. 859–874 *in* Y. Waisel, A. Eshel and U. Kafkafi (eds.), Plant roots: the hidden half. Marcel Dekkar, Inc., New York, NY.

Raunkiaer, C. 1934. The life forms of plants and statistical plant geography. Oxford University Press, London, England.

Rees, A. R. 1989. Evolution of the geophytic habit and its physiological advantages. Herbertia 45:104–110.

Rimbach, A. 1902. Physiological observations on the subterranean organs of some Californian Liliaceae. Botanical Gazette 33:401–420.

Rundel, P. W. 1996. Monocotyledonous geophytes in the California flora. Madroño 43:355–368.

Smith, F. H. 1930. The corm and contractile roots of *Brodiaea lactea*. American Journal of Botany 17:916–927.

Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. Annual Review of Ecology and Systematics 12:253–279.

Stockhouse, R. E., II and H. Wells. 1978. Pollination ecology of *Chlorogalum pomeridianum* (DC) Knuth. (Liliaceae). Bulletin of the Southern California Academy of Science 77:124–129.

Tyler, C. and M. Borchert. 2002. Reproduction and growth of the chaparral geophyte, *Zigadenus fremontii* (Liliaceae), in relation to fire. Plant Ecology 165:11–20.

U.C. DAVIS (UNIVERSITY OF CALIFORNIA, DAVIS). 2005. Integrated Pest Management Website http://www.ipm.ucdavis.edu/calludt.cgi/WXDATAREPORT

VOSS, R. E. 1979. Onion production in California. Agricultural Sciences Publications, University of California, Berkeley, CA.

WILLSON, M. F. 1979. Sexual selection in plants. American Naturalist 113:777–790.

WITZMAN, J. 1991. The biology of *Fritillaria pluriflora* (Liliaceae): a rare endemic of the California flora. M.S. Thesis, California State University, Chico, CA.

YI, W., S. E. LAW, D. MCCOY, AND H. Y. WETZSTEIN. 2006. Stigma development and receptivity in almond (*Prunus dulcis*). Annals of Botany 97: 57–63.