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Population biology of Gilia tenuiflora ssp. Arenaria (Polemoniaceae)

Joan Dorrell-Canepa
San Jose State University

POPULATION BIOLOGY OF *GILIA TENUIFLORA* ssp. *ARENARIA* (POLEMONIACEAE)

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Joan Dorrell–Canepa

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APPROVED FOR THE DEPARTMENT OF BIOLOGY

Dr. Michael Foster

Dr. Jim Harvey

Dr. Robert Patterson

APPROVED FOR THE UNIVERSITY

ABSTRACT

POPULATION BIOLOGY OF GILIA TENUIFLORA SSP. ARENARIA (POLEMONIACEAE)

by Joan Dorrell–Canepa

Gilia tenuiflora ssp. arenaria, sand gilia, is an endangered annual plant endemic to coastal dunes of Monterey Bay, California. The population biology of the plant was investigated using field seeding, lab germination, and outplanting in 1992-1994. Size, success (seeds produced) and mortality were compared between two of the largest populations. There were 100,000 individuals in ten populations in 1993, but abundance fluctuated yearly. Individual sand gilias produced 200-6000 seeds depending on plant size, which differed significantly between sites. At one site, 77% of the naturally occurring sand gilia produced seed. Herbivory caused most pre-reproductive mortality. Germination from field seeding was 7-15%, and 53% of the sand gilias that germinated, produced seed. Germination was 34-80% in lab experiments, and seed burial improved germination. Three-year-old seed was viable. Of the seedlings outplanted from lab to field, 76% produced seed. Results suggest that rainfall, herbivory, and seed burial, limit natural and established populations.

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INTRODUCTION

Gilia tenuiflora ssp. arenaria, sand gilia, is a purple-flowered annual of the phlox family (Polemoniaceae), that occurs on coastal sand dunes in Monterey County, California. A slender, decumbent herb with a basal rosette of serrate leaves, the plant grows in open, yet wind-sheltered areas surrounded by more dominant dune vegetation (Natural Diversity Database, 1985a; Fig. 1). Sand gilia also has been recorded in sandy openings of oak woodland and maritime chaparral (U.S. Army Corps of Engineers, 1994).

Loss of dune habitat, disturbance by humans, and invasion by non-native plants, particularly Carpobrotus spp., may threaten existing populations of sand gilia (Natural Diversity Database, 1985a). There are ten separate populations identified in dunes around the Monterey Bay, ranging from Moss Landing to Spanish Bay (Fig. 2). Because of limited distribution and low abundance, the U.S. Fish and Wildlife Service listed sand gilia as an endangered species on June 22, 1992 (Federal Register, 1992).

Current knowledge of sand gilia ecology is limited to status reports from the California Department of Fish and Game (Endangered Plant Program) and rare plant surveys. An Element Preservation Plan (Natural Diversity Database, 1985b) provides historically valuable, but outdated information regarding distribution. Zoger and Pavlik (1987), Pavlik et al. (1987), and Arnold (1991), have mapped populations and counted sand gilia plants in Marina and Sand City. California Native Species Field Surveys provide maps of distribution and estimated abundance, as well as lists of associated species (Natural Diversity Database, 1990).

Sand gilia population size fluctuates considerably from year to year (Natural Diversity Database, 1990). In Sand City, abundance from 1986 to 1991 ranged from 5000 to 34,650 individuals (Natural Diversity Database, 1990; Arnold 1991; summarized in Table 1). Sand gilia at Salinas River State Beach also varied greatly in abundance, ranging from 1665 to 10,000 individuals during 1985 to 1990 (Natural Diversity Database, 1990; Dorfman 1990). My surveys at Marina State Beach indicated a consistent decline in sand gilia numbers, from 10,000 individuals in 1985 (Natural Diversity Database, 1990) to 325 individuals in 1993, to 61 plants in 1994. Year to year variability is not uncommon in annual species (Harper, 1977), but could lead to local extinction if a series of drought years exceeds the longevity of the seedbank in areas of low abundance.

In May 1993, I recorded ~100,000 sand gilias in ten populations around the Monterey Bay (Table 2). I counted previously undocumented populations at Mulligan Hill in Marina (T. Moss, State Parks ecologist, pers. comm.) and on Watertower Hill in Moss Landing (V. Harris, Thomas Reid Associates, pers. comm.). Another previously unknown population at Fort Ord may contain 50-70% of all the sand gilia in the Monterey Bay area (U.S. Army Corps of Engineers, 1994). On the eastern side of Fort Ord, Gilia tenuiflora ssp. arenaria intergrades into a non-endangered subspecies, Gilia tenuiflora ssp. tenuiflora (slender-flowered gilia), which is more common in sandy washes of woodlands in the Salinas Valley (U.S. Army Corps of Engineers, 1992). The two subspecies may intergrade slightly, but are distinct (A. Day, in Natural Diversity Database, 1985a).

To determine what may affect sand gilia distribution and abundance, it is necessary to understand the population biology of the plant relative to abiotic and biotic characteristics of dune habitats. Physical factors such as wind, high surface temperatures, and reduced levels of available nutrients affect all dune plants. Plants experience reduced soil moisture because of the low water-holding capacity of coarse-textured sands (Oosting, 1954). De Jong (1979) described various ways that dune plants obtain water, such as the use of long tap roots to penetrate the water table ~ 1 meter below the surface. Others form a diffuse and shallow root system that uses precipitation (including fog drip) and "internal dew," the condensation of water vapor on sand grains as a result of diurnal temperature fluctuations. Most dune annuals germinate in autumn or winter when precipitation increases, and complete their life cycle before summer drought begins (Pemadasa & Lovell, 1975). Barbour et al. (1985) suggested that patterns of precipitation may be at least as important as total annual precipitation.

Nutrients are scarce in dune soils, due to rapid leaching through the coarse substrate lacking clay and organic matter (Clayton, 1972). Aerosols in salt spray and fog droplets provide high concentrations of Na, Cl, Mg, and Ca, but N, P, and K are low compared to levels required for optimum plant growth (Morris et al., 1974). Supplementing beach stands with fertilizer results in significantly greater biomass production (Augustine et al., 1964). Sand gilia seems tolerant of reduced nutrients in the dunes, but whether nutrients are limiting has not been examined.

Large, daily fluctuations in surface temperatures and strong winds are common on the dunes (Barbour & Johnson, 1977), and may be important factors limiting sand gilia survival. Long periods of elevated soil surface temperatures raise the air temperature and the vapor pressure deficit at seedling height (Kramer, 1969). High transpirational demand superimposed upon low soil moisture availability likely increases mortality from desiccation (Selter et al.,1986). Associated vegetation and varied topography (i.e. depressions in the sand) may provide valuable protection for plants in stabilized dunes. A continuous plant cover of herbaceous perennials stills the sand, allowing dune sands to accrete (Barbour & Johnson, 1979). Accumulation of organic material increases with the presence of vegetative cover, because vegetation produces litter and traps wind-blown particles (Ranwell, 1972). The effect of associated vegetation and topography on sand gilia survival has not been determined.

In addition to physical factors, dune plants must survive herbivory. Peromyscus maniculata (deer mouse) and Sylvilagus bachmani (brush rabbit) burrow in the more stable soils of dune scrub habitat and feed on seeds and native vegetation (U. S. Army Corps of Engineers, 1992). Sometimes, grazing may have a positive effect on plants. Paige and Whitham (1987a) found that artificially grazed Ipomopsis aggregata (Polemoniaceae) produced 2.4 times as many seeds as ungrazed plants. In contrast, Bergelson and Crawley (1992) repeated the same experiment on 14 different populations of I. aggregata and found no such benefits, concluding that the advantages of grazing vary among populations and are presumably mediated by genetic and/or environmental factors. I have observed regrowth of sand gilia in the field after grazing, but effects of herbivory on the plant have not been documented.

In an initial attempt to understand the biology of sand gilia relative to management, Dorfman (1990) recorded plant associates and attempted germinating seed at Salinas River State Beach. His germination trials were unsuccessful, as were seed viability tests at the Rancho Santa Ana seedbank (O. Mistretta, pers. comm., 1993). Kreiberg (1990) reported germination of 80% (28 of 32 seeds) in nursery trials, despite freezing temperatures. She found the plants easy to cultivate and reported production of abundant flowers and seed.

Rarity is a phenomenon in time and space, and a function of the size, number, and carrying capacity of habitable sites, as well as the length of time sites remain habitable (Harper, 1981). Harper (1981) also mentioned the importance of propagules dispersing to habitable sites, and the effects of predators and pathogens on the plant. Pavlik (1986) stated that "data on survivorship and seed production are most important in the monitoring of rare plant species." Schemske et al. (1994) emphasized the importance of assessing the biological status of rare species, identifying critical life stages that affect reproductive potential, and defining the biological factors that cause variation in those critical life stages.

In this demographic study, I investigated the factors that make Gilia tenuiflora ssp. arenaria a rare species, by defining habitable sites and recording present distribution and abundance. Aspects of the population biology of sand gilia were defined to enhance propagation efforts that might facilitate recovery of the subspecies. Details of germination, survivorship, and seed production were studied because they are critical for management decisions regarding sand gilia. Because the ability to successfully establish experimental populations may reduce the probability of extinction, I also investigated techniques for lab germination, and tested transplantation and seeding in the field.

METHODS

Distribution

Surveys of all known sand gilia populations were conducted in April and May of 1993 to determine distribution and abundance. Coastal dunes from Spanish Bay to Moss Landing were walked in a slow, crisscrossing traverse, searching for sand gilia's bright purple corolla and characteristic basal rosette of serrate leaves. Surveys north of Moss Landing to the Pajaro River were conducted in April, 1994. Search was intensified in areas of bare open sand in mid-to-hind dunes where other annual species associated with disturbed areas occur (e.g., Chorizanthe spp. and Cryptantha leiocarpa). All sand gilias were counted and numbers rounded to the nearest 100 individuals, because small or crowded plants were difficult to count accurately. At high density, an outstretched hand at ground level covers the same area as ~25 sand gilias, allowing efficient estimation. Clusters of sand gilia less than 1 km apart were considered part of the same population and noted by letters following the population number (i.e. 9a, 9b, 9c; Table 2). These clusters were within probable seed dispersal range and were not separated by any major topographical barriers.

Natural history observations

This study of sand gilia ecology included four annual growing seasons, February through May, 1991-1994, and provided an opportunity to monitor survivorship during years of highly variable rainfall. General observations from monitoring of field plots, and surveys of all ten populations documented life history, habitat characteristics, and seed dispersal. To explore possible competitive effects of other plants on sand gilia, associated vegetation was noted within, and just outside the plots. Weekly photographs of each plot recorded any visible competition effects (i.e., spindly growth after shading by Abronia umbellata (pink sand verbena), or plant overgrown by Eschscholzia californica var. maritima (California beach poppy). There was constant vigilance for pollinator visits. Weather station records from Reservation Road in Marina and Fort Ord (Marina Coast Water District, 1970-1994; Naval Postgraduate School-Department of Meteorology, 1991-1994) were used to draw general conclusions about effects of rainfall on sand gilia germination and mortality.

Field Growth

To assess survivorship and growth of naturally occurring sand gilia in 1991, seventeen 100 x 50 cm plots were established at Sites 4 and 9 in the coastal scrub zone of the Monterey Bay dunes. These sites were 16 km apart and contained the two largest populations known in 1991; the extent of the Fort Ord population was not documented until 1993. Comparison of the two sites provided information on the natural variability between populations (Fig. 3).

Site 4 originally included 10 plots of naturally occurring sand gilia in the "East Dunes" of Sand City, just south of Tioga Avenue along the eastern edge of Highway One (Fig. 4a). Native dune vegetation provided 0-30% cover at this site, but the low profile of the foredunes to the west offered little wind protection, resulting in much sand movement. Stakes used to delineate the original plots at Site 4 were completely buried on two occasions, indicating sand burial of at least 10 cm in February and March, 1991. Four plots were irretrievably buried, leaving six plots distributed randomly on shallow slopes (< 5°) with an eastern aspect. The plots contained approximately 0.3% of the naturally occurring sand gilia population at Site 4. More protected dune swales at the site contained the largest individuals (basal diameter of 64 cm) seen during the course of the study. Plots were not placed in these stands of large sand gilia, because the plants seemed uncharacteristic.

Site 9a & b included 11 plots of naturally occurring sand gilia at Salinas River State Beach–Molera Road (Fig. 4b). These plots were located in open areas on a stabilized hind-dune with native vegetation covering 20 to 50% of the area. Topography of the natural dunes provided some shelter from wind and blowing sand. Plot stakes at Site 9a & b were never buried during 1991, indicating little sand movement in this area. Four plots were placed on the west side of Monterey Dunes Way (Site 9a). These plots were level, and the sand had been disturbed previously by road grading as indicated by its hardness and the presence of pebbles. Another seven plots were placed 0.4 km away, along a ridge of open sand (10-30% associated vegetation), where naturally occurring sand gilia was prolific (Site 9b). On this ridge, slope was < 5° and there was a slight eastern aspect. At the time, these areas included most of the known sand gilia at Salinas River State Beach, so randomization of plots was not attempted. Additional plants were found during the study; therefore, an estimated 6% of the total population was sampled at Site 9a & b.

The four corners of each plot were marked with wooden dowels that protruded five cm above the sand. A portable PVC frame was lowered onto the dowels, enclosing the naturally occurring sand gilia. The frame was marked with a reference grid for mapping each plant through time. Due to sand burial of the original plots, Site 4 was only measured for four weeks, whereas Site 9a & b was measured for nine weeks.

During March through May 1991, basal diameter (cm) of all sand gilia in plots was recorded weekly as a measure of vigor and reproductive potential. Diameter was chosen because reproductive output is highly correlated ($r = 0.90$) with plant size in annuals (Mack and Harper, 1977; Watkinson, 1982). Basal diameter was defined as the largest measurement across the basal rosette, from the tip of one leaf to the opposite leaf tip. As flower stems elongated from the basal rosette, basal diameter was measured from the tip of one decumbent flowering branch to the tip of the opposite flowering branch (Fig. 5). Thus, measurement of basal diameter changed from a measurement of basal leaves in March to a measurement of flower stems in April and May. This change was necessary because flower stems gave a more accurate determination of size than diameter of the basal rosette leaves, which became desiccated and died as flowering progressed.

To compare size through time between the two populations, the basal diameter of all sand gilia in plots was averaged weekly for each site. On 28 April 1991, the mean basal diameter between sites was compared using a Student's t-test. On that date, the greatest number of sand gilia were still alive and had reached maximum size. The relationship of density versus plant size was determined by regression for each site.

Reproductive success was defined as the completion of flowering, fruiting, and seed dispersal without destruction by herbivores (Fiedler, 1987). Every sand gilia that produced seed, regardless of size, was tallied as a success. Survivorship based on reproductive success was determined for all naturally occurring sand gilia in plots at Site 9a & b. Comparison with survivorship at Site 4 was not attempted because measurements began late in the season due to sand burial of the original plots.

To explore causes of mortality and critical life history stage(s), date and cause (if observed) of mortality were recorded for all sand gilia in plots at Site 9a & b. A survivorship curve was constructed to indicate number of survivors over time according to life stage. Stages were: cotyledons (1-7 days), seedling (4-8 leaves, 7-14 days), juvenile (rosette of 8-24 leaves, 14-56 days), and adult (budding and flowering, 56-126 days). Causes of mortality included desiccation, herbivory, and possible nutrient deficiency.

Herbivory was indicated by chewed leaves, as well as sand burial and root damage from hole digging. Desiccation was indicated by brown or withered sand gilia (plant present and no evidence of digging or burrowing by herbivores). Nutrient deficiency was indicated by pale or red leaves, although nutrient status was not confirmed. When plants disappeared with no evidence of herbivores (holes, mounds) in or around the plot, cause of mortality was listed as unknown.

Seed Counts

In May 1991, seeds were collected at Sites 4 and 9 to determine seed production and natural variation among individuals. Sixty mature, unopened seed capsules from separate, randomly selected plants were collected. Seeds were gathered from sand gilia inside and outside existing plots, and size of plant was recorded. Plants were divided later into three size classes: small (1-14 cm basal diameter), medium (15-24 cm), and large (25-64 cm). The number of seeds per capsule was regressed on plant size. To estimate seed capsule production, all the mature capsules were counted on fifty senescent sand gilias selected at random. These individuals were divided into the same three size classes, and number of seed capsules was regressed on plant size. To estimate mean seed production, the mean number of seeds per capsule was multiplied by the mean number of mature capsules per plant for small, medium and large plants. Because there was a wide variation in number of seeds produced within each size class, the full range of seed production was estimated by minimum and maximum values (minimum = ($\bar{X}$ - S.E) seeds per capsule multiplied by ($\bar{X}$ - S.E.) number of capsules; maximum = ($\bar{X}$ + S.E) seeds per capsule multiplied by ($\bar{X}$ + S.E.) number of capsules).

To collect, the ripe capsule was gently flicked with a finger to release seeds into an envelope. Seeds were passed through a kitchen sieve for cleaning (to reduce pest contamination), counted, and left at room temperature (18-20°C) to "after-ripen". Germination is often improved by this aging process, which results in physiological changes within the seed (Hulbert, 1955). Most of the seeds were stored at 4°C (cold-stored treatment) in tightly closed jars with silica packets (Hartmann et al., 1990) for 100 days before use in germination experiments. Approximately 500 seeds were stored at room temperature (16-20° C) for later comparison with cold-stored seed.

Soil Analysis

To assess soil fertility, a single soil sample from each Site (4 and 9b) was analyzed by Soil Control Labs (Watsonville, CA.) for available plant nutrients. The soil sample from Site 4 was taken within two meters of the largest sand gilia (64 cm) measured in 1991, and the sample from Site 9b was from the center of the 1991 plots of naturally occurring sand gilia. Each sample was excavated from 15 cm depth.

Field Seeding Experiments

Field seeding was attempted in 1992 to determine techniques and optimal habitat for the establishment of sand gilia. Seeding trials were conducted at Sites 4S and 9bS, just north of plots at Sites 4 and 9a & b monitored for growth and mortality of naturally occurring sand gilia in 1991 (Fig. 4). Basal diameter of the seeded plants was recorded as a measure of vigor and reproductive potential for 51 plots at the two sites. Effects of dune aspect and percent cover of associated vegetation on establishment were explored by measuring these variables, and recording germination, reproductive success, and mortality in the plots. These values were averaged by site to assess the variability between locations for two seeded populations. Aspect was determined by bisecting the plot with an imaginary line drawn in the direction of downward slope. Direction from north in degrees was measured by compass along the line (north aspect = 340° - 20°, east = 7°-110°, south = 160° - 200°, and west = 250° - 290°). Percent cover was estimated visually.

Site 4S was located on 3.1 ha at the Sand Dollar Habitat Preserve in Sand City (Fig. 4a). This habitat area was ~75 meters north of the naturally occurring sand gilia plots at Site 4, and was more protected from wind and sand burial. Fifteen seeded plots were located in open areas between existing and restored native vegetation.

Site 9bS was located at Salinas River State Beach (Fig. 4b), 100 meters to the north of Site 9b. Thirty-six seeded plots were placed on hind-dune bluffs and swales throughout the dune scrub habitat.

Seed was collected in May 1991 from randomly selected sand gilia at both sites. To maintain genetic integrity, Site 4 seed was used only at Site 4S, and seed from Site 9a & b was used only at Site 9bS. For maximum genetic diversity, seed was gathered from plants of all sizes and thoroughly mixed together. Seed was stored in a dry area at room temperature (16-20° C) and then cold-stored at 4°C for 100 days before seeding. The same seed treatment was used for all field seeding.

Seeded plots were scattered in sandy openings at the two sites wherever associated vegetation ranged from 0-50% cover (Fig. 6). The same PVC frame used for 1991 plots of naturally occurring sand gilia was used, delineating 100 x 50 cm plots. One hundred seeds per plot were dropped from a height of 2-3 cm through evenly spaced pegboard holes onto the sand. The pegboard grid provided an efficient way to verify the number of small seeds being dropped onto the plot. Seeding was easiest in the early morning when wind was low. Fingers were more effective than forceps in picking up the tiny, < 1 mm seeds. Rain followed the seeding within two to three days, often the same night. Seeds either fell naturally among sand grains or remained atop the sand for plots seeded in February 1992. When these seeds failed to germinate in March 1992, techniques were modified. Subsequent plots seeded in December 1992 were covered with a thin layer (< 1cm) of sand. Plots were marked with highly visible flags and aluminum nursery tags for future monitoring.

Plots with different dune aspects were established at both sites to explore optimum habitat for sand gilia establishment. At Site 4S in Sand City, one plot was seeded on 15 February 1992 and 14 plots on 23 December 1992. The plot seeded in February was a trial plot in a protected swale with a western aspect. The area seeded in December included 12 plots with three replicates of each aspect (north, east, south, and west), and two level plots. The 12 replicated plots at Site 4S were designed for comparison with the 12 plots seeded in December 1992 at Site 9bS.

At Site 9bS at Salinas River State Beach, 24 plots were seeded on 3 February 1992 and 12 plots on 11 December 1992. The 12 plots seeded in December 1992 at Site 9bS had different dune aspects similar to plots at Site 4S. To explore the competitive effects of other plants on sand gilia, I seeded 24 plots in February 1992 that included different aspects and associated vegetation cover. These plots contained three replicates each of 0-25% or 25-50% cover within 6 plots of each aspect. The vegetation in some plots increased dramatically in April and May due to fast growing annuals such as Eschscholzia californica var. maritima, Marah fabaceus, and Abronia umbellata. Because most sand gilia germination had occurred by this time, original estimates of associated vegetation cover were used in calculations.

All emerging sand gilias were mapped and basal diameter (cm) measured biweekly. Cause and date of mortality were noted as for naturally occurring individuals in 1991 plots. To detect differences from timing of seeding effort (February versus

December 1992), basal diameter (cm) was averaged biweekly by plot. Mean plot diameter on 26 March 1993 was compared between sites using a Student's t-test. At Site 9bS on the same date, sand gilia size in plots with cover treatments of 0-25% and 25-50% was also compared by t-test.

To determine the efficacy of field seeding and optimal habitat for sand gilia establishment, percentage germination, reproductive success, and mortality were averaged for each plot at both sites. Separate two-way, Model 1 ANOVA were used to compare the effects of aspect and site on mean percentage germination and mean percentage reproductive success for all plots seeded in December 1992. For Site 9bS, separate two-way, Model 1 ANOVA compared the effects of aspect and percent cover on percentage germination and success.

Slope in degrees was recorded but not used as a replicated variable. It proved difficult to find suitable sites with different aspect, associated vegetation cover, and slope. To determine any possible effects, percentage germination was regressed against slope.

Nursery Germination Experiments

To explore requirements for propagation, germination in containers was compared by measuring percentage germination (viability) and days to germination (vigor) for various treatments. Techniques for optimal germination of sand gilia were determined by comparing the effects of different seed storage methods, different seed collection years, and seed burial versus non-burial. Natural variability in germination was explored for two separate populations of Gilia tenuiflora ssp. arenaria, and the related subspecies, Gilia tenuiflora ssp. tenuiflora.

Germination failed in nursery experiments attempted in February and March of 1992. Originally, 50 seeds were dropped through a pegboard grid onto flats filled with

100% sand. No effort was made to cover the seed as this method had been successful in the past. Daily watering kept the deeper sand moist, while the top layer of sand dried, mimicking dune conditions. It was subsequently learned that sand gilia does not germinate well if the top layer of sand dries (P. Kreiberg, Sunset Coast Nursery, pers. comm.). In addition, the late seeding date may have caused poor germination (sand gilia naturally germinates in January and February). These failures lead to modification of the seeding technique used in December 1992.

Successful germination was achieved using trays of "stubby" supercells® (Stuewe and Sons, Inc., Corvallis, Oregon). Each supercell was 14 cm long and 4 cm in diameter, and 98 cells were arranged in a treatment tray (Fig. 7). The soil mix was McCalif's Sunshine Mix #3 mixed with 4 ounces of Nutracote® pelleted fertilizer (N-P-K of 14-14-14) per tray (McCalif Grower Supplies, Inc., Ceres, California), and it was kept uniformly moist. Each cell (one replicate) received 5 seeds, and treatments were randomly mixed within the tray. A continuous thin strip of copper eight cm tall surrounded the trays to discourage snail grazing.

Seed storage conditions and seed collection date (year) were varied within Tray 1 to define optimal storage methods and assess longevity of the seed. Seeds were collected at Site 4 in May of 1990, 1991 and 1992 from randomly selected, naturally occurring sand gilia of all sizes. The supercells were seeded on 19 December 1992, and covered with ~0.5 cm of soil mix. Storage conditions were: cold-stored (4°C), stored at room temperature (16-20°C), and seedbank (heat-sealed in polyfoil bags, stored at -20°C). For the cold-stored treatment, seeds were collected in May 1991, stored at room temperature for 455 days, then cold-stored for 100 days before seeding. For the room temperature treatment, seeds were collected in May of 1990 (stored 940 days), or in May of 1992 (stored 210 days). For the seedbank treatment, seeds were collected in June of

1990 and stored at the seedbank for 465 days. Effects of storage method and year of collection on percentage germination and days to germination were compared but not tested for significance.

In Tray 2, I explored the possibility of a darkness requirement for germination with two treatments, seed burial versus non-burial. Seeds from Site 9 were collected from randomly selected plants in May 1992, stored at room temperature for 210 days, and planted on 27 December 1992. Seeds were either buried to a depth of 0.5 cm, or remained atop the sand (non-burial).

In Tray 3, I assessed the variability in germination between two separate Gilia tenuiflora ssp. arenaria populations and Gilia tenuiflora ssp. tenuiflora. Seeds from Sand City (Site 4), Salinas River State Beach (Site 9), and Fort Ord were planted on 24 January 1993. The seeds from Fort Ord were collected from an inland population of G. t. ssp. tenuiflora, and grown to compare morphology between the two subspecies. All seeds were stored at room temperature (16-20°C) and buried to a depth of 0.5 cm.

Percentage and days to germination were noted for each supercell. Dates were averaged for the occasional supercell that did not have simultaneous germination. Percentage and rate of germination between the Sand City (Site 4) and Salinas River State Beach (Site 9) populations were compared using a Student's t-test. Germination differences between G. t. ssp. arenaria and G. t. ssp. tenuiflora were also compared by t-test.

Transplant experiments

Transplant experiments explored techniques for sand gilia establishment, and compared the efficacy and success of field seeding versus transplantation. Seedlings grown in containers to adult stage (budding) were transplanted at the Sand Dollar Habitat

Preserve in Sand City (Site 4S) on 20 February 1993, and at Salinas River State Beach (Site 9bS) on 27 March 1993 (Fig. 4). Seedlings growing together in a single cell were separated carefully when planted or left in a dense clump. Disturbing the roots by separating the seedlings was not ideal, but it was thought that five seedlings growing in one hole might be too competitive.

Each transplanted sand gilia was flagged and monitored for percentage success (produced seed), or mortality and cause, and final basal diameter (Site 4 only). These values were averaged for all transplants at each site to compare transplant success between sites.

RESULTS

Distribution

In 1993, approximately 100,000 sand gilias were counted in 10 separate populations in the Monterey Bay dunes (Table 2, Fig. 2). Rainfall was greater than average in late 1992 and early 1993 (Fig. 8), and not only were new locations discovered, but several populations were more numerous than ever recorded (Table 1). The largest populations occurred at Salinas River State Beach (10,000 individuals), in the "East Dunes" of Sand City (25,000), and at Fort Ord (45,590; Table 2). Known populations of sand gilia range from Spanish Bay to Moss Landing and inland to Fritzsche Field on Fort Ord. In 1994, surveys conducted north of Elkhorn Slough to the Pajaro River revealed suitable habitat for sand gilia, but no plants. Rainfall was generally lower than average when these surveys were done (Fig. 8).

Limited surveys indicate that sand gilia population size has varied by as much as a factor of seven from year to year (Table 1). After low rainfall in the winter of 1994, numbers recorded at Marina State Beach, Salinas River State Beach, and Sand City were 80-95% less than in 1993. Less than 100 individuals have been counted at Marina State Beach in four of seven years. Most of the other populations appeared to be maintaining or gradually increasing in number, except during years of low rainfall.

In 1993, five of the ten known sand gilia populations were fully or partially protected from human impact, either as parkland or in conservation easements (Table 2). These protected populations contained ~15,000-20,000 individuals, whereas the remaining ~80,000-85,000 sand gilia occur on property that may be developed.

Natural history observations

Life History: During the three years of this study, sand gilia in plots germinated in January, with sporadic germination continuing from February through April. The basal rosette of leaves increased in size February through March, when budding commenced. As flower formation continued in April and May, flower stems elongated from the rosette and basal leaves died (Fig. 5). Flowers of this annual plant bloom April through May (Munz and Keck, 1968), although variation in rainfall may shorten or delay the flowering period (pers. obs.). Fruit maturation and seed dispersal occurred in May and June, followed by death. Seed never germinated in nursery flats during the summer or fall, despite adequate soil moisture.

Habitat Characteristics: Sand gilia occurs on sands stabilized by a nearly continuous plant cover in the mid-to-hind dunes of coastal strand and dune scrub habitat (Natural Diversity Database, 1985a). Sand gilia also occurs in sandy openings of oak woodland and maritime chaparral, and on the cut banks of sandy drainages at Fort Ord (U.S Army Corp. of Engineers, 1994). Surveys indicated that the plant inhabits level areas and slopes up to 45° from the horizontal. Individuals were often found on north, west, and east slopes but were seldom on south slopes. Sand gilias were observed thriving in slight depressions where dead vegetative matter gathered, perhaps providing extra shade, moisture, and nutrients. Previous disturbance to the sand sometimes appeared to encourage germination. Healthy sand gilia populations were observed in old vehicle tracks (Sand City, Salinas River State Beach, Moss Landing), along old roads and firebreaks (Fort Ord; U.S. Army Corps of Engineers, 1994), and in areas where trenching occurred (Asilomar State Park; T. Moss, pers. comm.). These areas were once disturbed by tires or machinery, but were usually characterized by stable sands.

Observation of naturally occurring sand gilias suggested that sand covering the meristem of the basal rosette (> 1 cm), accelerated desiccation and mortality. The plant survived if sand was removed or blown away and sufficient moisture was available.

Associated Vegetation: Surveys indicated sand gilia was most common in areas where associated vegetation cover was low, usually less than 30%. In maritime chaparral, the plant survived in sandy openings between taller species such as Ericameria ericoides (mock heather) and Baccharis pilularis (coyote bush; U. S. Army Corps of Engineers, 1992). I have observed sand gilia in areas of dense plant cover (Carpobrotus spp., Bromus diandrus), but the plants were small and few in number.

Associated native species in the dunes include Chorizanthe spp. (spineflower), Cryptantha leiocarpa (popcorn flower), Camissonia cheiranthifolia (beach primrose) and C. micrantha (small primrose), Abronia umbellata (pink sand verbena), Dudleya caespitosa (bluff lettuce), Lessingia filanginifolia (beach aster), Cardionema ramosissimum (sandmat), Eschscholzia californica var. maritima (California beach poppy), Eriogonum latifolium and E. parvifolium (coast and dune buckwheat), Ericameria ericoides (mock heather), and Lupinus chamissonis (silver beach lupine; Natural Diversity Database, 1990; Dorfman, 1990; and pers. obs.). Cryptantha leiocarpa and Chorizanthe spp. may be indicator species for sand gilia because they also occur in sandy, open spaces, and usually are associated closely (Zoger & Pavlik, 1987; Dorfman, 1990). These annual species germinate at a similar time as sand gilia (pers. obs.). During its juvenile phase, Cryptantha leiocarpa can easily be mistaken for sand gilia, until the basal leaves become distinct (entire leaves versus sand gilia's serrate or once-pinnate leaves, Fig. 5).

Qualitative field observations indicated that naturally occurring sand gilia usually increased in size as the associated annual vegetation increased. In plots, sand gilia showed few visible signs of impact from associated vegetation, with the exception of fast growing species such as Eschscholzia californica var. maritima and Marah fabaceus. When these species grew nearby, they always outcompeted the sand gilia, which either wilted and turned brown (desiccation), or became pale and etiolated (shading). Sand gilia altered its growth habit when shaded by associated vegetation; either growing tall and spindly, or bending to reach the light. In some plots, associated vegetation provided shelter from herbivory or desiccation. Sand gilia isolated on bare sand was often damaged or destroyed by herbivores, or withered by the sun, while sheltered sand gilia survived.

Floral Characteristics: In plots, every sand gilia that grew past the cotyledon stage, regardless of size, produced at least one flower. It appeared that flowers and capsules produced early in the season were larger than those produced late in the season. Flowers opened fully by mid-morning, closed in late afternoon, and remained closed in foggy or stormy weather.

Seed Dispersal: The small (~1 mm) seed falls from ripened capsules to the sand beneath (pers. obs.), or is shaken from the capsule by wind, thus dispersing with blowing sand (U.S. Army Corps of Engineers, 1994). Evidence for wind dispersal includes observations of sand gilia populations moving gradually landward through time in the direction of prevailing winds (Marina State Beach; East Dunes, Sand City; pers. obs.). Sand gilia presence at the base of washouts, as well as germination downslope from seeded plots, indicated that seeds also may disperse in water rivulets.

Pollination: Although pollination was not confirmed, I observed a beefly (Oligodranes spp.) visiting 20 separate gilia flowers along Picnic Canyon Road at Fort Ord in May 1993. This particular population of gilia showed characteristics of both Gilia tenuiflora ssp. arenaria and Gilia tenuiflora ssp. tenuiflora. Plants were small and semi-decumbent (G. t. ssp. arenaria), but had well-exserted stamens and stigma (G. t. ssp. tenuiflora). A few collected specimens were identified as G. t. ssp. tenuiflora (A. Day, California Academy of Sciences, pers. comm.). Gilia tenuiflora ssp. tenuiflora is an outcrossing subspecies that has some ability to self-pollinate (Grant and Grant, 1965). This Fort Ord population may be an intermediate population between the two subspecies. No other pollinator visits were observed in coastal populations of sand gilia despite long hours in the field. A beefly was observed visiting sand gilia in containers during nursery trials, which occurred far from the dunes.

Rainfall: Rainfall in the Marina dunes (at a weather station mid-way between Sites 4 and 9) averaged 430 mm per year (24 year record), although quantity and timing varied considerably among years (Marina Coast Water District, 1970-1994). From 1992 through 1994, germination and survivorship of sand gilia appeared to be related to the quantity and consistency of rainfall received December through February (Fig. 8). Rain in December 1991 and February 1992 was average, but January rainfall was reduced (32 mm versus an average of 58 mm). Sand gilia seeded into plots in February 1992 failed to germinate, but germinated successfully the following year. Rainfall was twice the average from December 1992 through February 1993, and record numbers of sand gilia germinated. In December 1993, rainfall was below average (34 mm versus an average of 54 mm) and January 1994 had average rainfall (69 mm) but not until the end of the month. Thus, between 15 December 1993 and 22 January 1994, before and during the characteristic time for sand gilia germination, there was no substantial rainfall to imbibe the seed. In 1994, three populations were 80-95% less than in 1993 (total rainfall December through March 1994 was 204 mm, December through March 1993 was 513 mm; Table 1).

Field Growth

Plots of naturally occurring sand gilia at Site 4 (Sand City) contained a mean of 14 ± 1.5 (S.E.) sand gilias per square meter, whereas plots at Site 9a & b (Salinas River State Beach) had a mean of 25 ± 5.9 (S.E.) individuals per square meter. Plant size was negatively correlated with increasing density at Site 9a & b ($r = -0.7$, $n = 11$, $p < 0.05$), but there was no significant relationship at Site 4 ($r = 0.4$, $n = 6$, $p = 0.48$). On 28 April 1991, basal diameter of sand gilia at Site 4 was significantly greater than at Site 9a & b ($t = 2.28$, $df = 15$, $p = < 0.05$). The mean size of plants at Site 4 was also greater on all other dates measured (14 April 1991 through 5 May 1991; Fig. 9). Age was estimated because accurate identification of seedlings in this first year of study was uncertain until late juvenile stage (rosette) was reached at ~ 21- 48 days. Because sand burial delayed measurements at Site 4, survivorship and reproductive success were only measured at Site 9a & b.

In the 11 plots at Site 9a & b, 164 of 214 (77%) sand gilia produced seed. Fifty sand gilia (23%) died before reproductive maturity. Herbivory caused 74% of the mortality, possible nutrient deficiency 2%, and unknown causes 24%. A survivorship curve (Fig. 10) indicated the most significant decline in numbers occurred at 114 days (21 April 1991) as plants began to produce seed. All plants were desiccated and dying by 142 days (12 May 1991), although many were still dispersing seed. Because the first measurements at this site were not made until 9 March 1991 as plants were growing into adults (stem elongation), the survivorship curve does not reflect early mortality of seedlings and juveniles.

Herbivores occasionally stimulated thicker leaf growth and late flowering by "pruning" the basal rosette and "nipping" the flower buds. Sometimes flower stems were chewed in half and remained uneaten in the plot. A characteristic hole and mound (possibly a mouse or vole warren) was always found near damaged or missing sand gilia; however, trapping experiments were not conducted. If 25-50% of the basal rosette remained after grazing, I observed that sand gilia often recovered and eventually produced seed, but no increase in seed production was noted. Extensive grazing of all vegetation within a radius of 5-10 meters was assumed to be rabbit herbivory. No evidence of snail damage (mucus trails) was seen in the field, although snail grazing on sand gilia in the nursery was quite common and destructive.

Seed Counts

Sand gilia produces small, capsular fruits that contain many tiny seeds (Natural Diversity Database, 1985b). The seeds look like sand grains, and are approximately 1 mm at their widest point. Seed capsules are 5-6 mm long (A. Day, in Hickman, 1993), and are divided into three chambers. I observed that early seed capsules usually contained the largest seeds, and size of capsule (and seed) decreased as the fruiting season progressed. Shriveled, pale, or translucent seeds often were found in smaller capsules produced towards the end of the life cycle.

Naturally occurring sand gilia of all sizes produced a mean of 39 ± 2.5 (S.E.) seeds per capsule (n = 27 capsules) at Site 4, and 31 ± 1.3 (S.E.) seeds per capsule at Site 9a & b (n = 32 capsules). Larger individuals produced more seed capsules and more seed (Fig. 11). Potential seed production increased approximately fourfold for each size class (small, 1-14cm; medium, 15-24 cm; large, 25-64cm) with the largest plants producing an estimated 4000+ seeds (Table 3).

Soil analysis

Sites 4 and 9b were substantially lower in nutrients than a typically fertile soil. Results are only suggestive due to lack of replication, but gave a general impression of available nutrients at each site. Both sites had a similar pH (6.0-6.1). The sample from Site 4 had slightly more K_2O, CA, Mg, and SO_4 than Site 9b, but less Cl, Na, and soluble salts. Organic matter was greater in the sample from Site 9b (1.8%) than at Site 4 (0.8%; Table 4).

Field Seeding

Field seeding resulted in low germination, but provided valuable information on timing of seeding and techniques. The first seeding trials attempted in February 1992 were probably too late in the winter season for germination the same year. Germination was very low in 1992, but seeds at both sites germinated the following year in January 1993.

Timing of Seeding: In winter of 1992/1993, seeding trials began earlier and were more successful. Plots were seeded in December and germinated one month later in January 1993, along with sand gilia seeded earlier in February 1992. The advantage of seeding early in the year (February), rather than later (December), was apparent. Basal diameter (cm) of all plots measured on 26 March 1993 at Site 9bS indicated plants were significantly larger when seeded in February compared to December ($t = 3.62$, $df = 34$, $p < 0.001$; Fig. 12). At Site 4S, the mean diameter of the single plot seeded in February was not significantly larger than the mean diameter of all December seeded plots combined ($t = 0.55$, $df = 13$, $p = 0.29$).

Germination: In March 1992, the 24 plots seeded in February 1992 at Site 9bS produced only 57 sand gilia (2% germination; Table 5). Seeded plants were much smaller than naturally occurring sand gilia. No germination was seen in 1992 at the single plot seeded in February at Site 4S.

In 1993, germination in all plots combined (regardless of seeding date), was 15% at Site 4S (15 plots), and 7% at Site 9bS (36 plots). Of the plots seeded in December 1992, there was significantly greater germination at Site 4S (15%, 14 plots) than Site 9bS (8%, 12 plots; $t = 1.79$, $df = 19$, $p < 0.05$). Plots seeded in February 1992 also showed different germination between the two sites (14%, 1 plot at Site 4S; 6%, 24 plots at Site 9bS), but this was not statistically tested due to lack of replication at Site 4S (Table 5). At Site 9bS, there was no significant difference in germination between 24 plots with non-buried seed (seeded February 1992) versus 12 plots with buried seed (seeded December 1992; $t = 1.29$, $df = 16$, $p = 0.22$). It is likely that seed left in plots for one year before germination was naturally buried by blowing sand.

Success and mortality: In 1992, 21 of 57 sand gilia (37%) survived to produce seed in plots at Site 9bS, and the primary cause of mortality was desiccation. In 1993, 110 of 229 plants (48%) produced seed in 14 plots at Site 4S, and 51 of 101 (51%) produced seed in 12 plots at Site 9bS (Table 5). Percentage success was not significantly different between the two sites ($t = 0.23$, $df = 20$, $p = 0.82$). Mortality at Site 4S was due to herbivory (56%), desiccation (7%), possible nutrient deficiency (17%), and unknown (20%). Mortality at Site 9bS was due to herbivory (44%), desiccation (36%), competition (10% - a seeding accident), and unknown (13%). Greatest mortality at Site 4S occurred between 14 and 28 days when seedlings were just growing into basal rosettes (Fig. 13). Greatest mortality at Site 9bS occurred between 51 and 58 days (late juvenile = rosette) and between 78 and 92 days (adult = late budding-early flowering stage). Most plants were dead or dying by 130 to 143 days as seed capsules ripened and dehisced.

Aspect: Dune aspect had no significant effect on germination or success in 1993, however, the two sites had opposite results. At Site 4S, germination was greater on north aspects (34%) than all other aspects (10-13%), but results were only close to significant ($F = 2.53$, $df = 11$, $p = 0.13$). At Site 9bS, germination was greater on south aspects (12%) and lowest on north aspects (3%), but there was no significant difference between aspects ($F = 1.51$, $df = 11$, $p = 0.28$). Percentage success was greatest on north aspects at Site 4 (18%), however, the difference among aspects was only close to significant (4-7 %; $F = 2.37$, $df = 11$, $p = 0.15$). Percentage success at Site 9bS was greatest on south aspects (10%) and least on north aspects (1%), and differences between all aspects were not significant ($F = 2.16$, $df = 11$, $p = 0.17$). Comparing both sites using an ANOVA (12 plots seeded on December 1992), indicated no significant difference in mean percentage germination among sites or aspects, but a significant interaction between site and aspect (Table 6). Percentage reproductive success was significantly different between sites, but there was a significant interaction between site and aspect (Table 6).

In 1994, germination of seeds dispersed by sand gilia in 1993 was very low (Site 4S: 35 sand gilias in 15 plots, Site 9bS: 28 individuals in 36 plots). During this year of low rainfall, sand gilia germinated only in plots with a north or east aspect at Site 9bS. At Site 4S, sand gilia germinated in plots of all aspects.

Microtopography was not quantified or manipulated in this study, but it was noted that sand gilia in plots with a south aspect survived only near dead vegetative debris or in openings between sprawling vegetation such as Abronia umbellata.

Associated vegetation: There was no significant difference in basal diameter, percentage germination, or success of sand gilia growing in plots with different associated vegetation cover. On 26 March 1993, the mean basal diameter in plots with 0-25% cover was slightly greater ($\bar{x}$ = 5.5 cm ± 0.73 S.E.) than plots with 25-50% cover ($\bar{x}$ = 5.1 cm ± 0.28 S.E.), but results were not significant ($t = 0.50$, $df = 15$, $p = 0.31$; Fig. 14). There was no significant effect of aspect, percentage cover, or any interaction effect on percentage germination (Table 7). The effect of aspect on percentage success was close to significant ($p = 0.057$).

Slope: A regression analysis indicated no significant effect of slope at Site 9bS on percentage germination ($r^2 = 0.09$, $n = 36$, $p = 0.64$) or success ($r^2 = 0.004$, $n = 36$, $p = 0.98$). At Site 4S, slope also had a non-significant effect on germination ($r^2 = 0.12$, $n = 15$, $p = 0.68$) and success ($r^2 = 0.23$, $n = 15$, $p = 0.42$).

Steep slopes did cause water runoff that apparently washed seeds out of the plot. When there was no naturally occurring sand gilia within 50 m, and water rivulets provided clear evidence of a washout, sand gilia less than one meter out-of-plot was recorded as in-plot sand gilia.

Nursery germination experiments

During nursery trials, there were variable effects of seed storage methods and year of seed collection on germination. Seed burial enhanced germination, and two different sand gilia populations varied significantly in viability of seed. Viability of seed from a population of Gilia tenuiflora ssp. tenuiflora (Fort Ord) varied significantly from that of Gilia tenuiflora ssp. arenaria.

During germination trials, storage methods and year of seed collection varied in the same treatment tray, so results were not analyzed statistically (Table 8). Seedbank and room temperature seed (collected 21 May 1992) had the greatest percentage germination and fewest number of days to germination. Cold-stored seed was the slowest to germinate (15 days). Germination was highly variable for seed collected on different days within the same year. There was no loss in viability of three-year-old seed.

Seed that was slightly buried had significantly greater germination (47%) than non-buried seed (8 %); ($t = 7.19$, $df = 57$, $p < 0.001$; Table 8). Days to germination for this treatment were not statistically analyzed, because non-buried seed germinated in only five cells. When seed was buried, there was no significant difference in percentage germination between seed stored in the cold (46%) or at room-temperature (47%; $t = 0.20$, $df = 56$, $p = 0.42$).

Seeds from Site 4 (Sand City) and Site 9 (Salinas River State Beach) were significantly different in rate and percentage germination. Site 4 had significantly higher germination (71%) than Site 9 (39 %; $t = 4.71$, $df = 78$, $p < 0.001$], but took significantly longer to germinate (Site 4 = 14.3 days, Site 9 = 12.9 days ; $t = 2.56$, $df = 48$, $p < 0.01$; Table 9). Viability of Gilia tenuiflora ssp. tenuiflora (GTT) seed from Fort Ord was significantly different from Gilia tenuiflora ssp. arenaria (GTA) seed (Site 4 and 9 combined). Percentage germination (GTT = 45%, GTA = 60%; $t = 2.18$, $df = 78$, $p < 0.05$) and days to germination (GTT = 9 days, GTA = 13 days; $t = 6.68$, $df = 61$, $p < 0.001$) varied significantly between the two subspecies.

Transplantation

Transplantation was successful at both sites. Eighty-one of 108 (75%) transplanted sand gilia survived to produce seed at Site 4S. Mortality was caused by desiccation (48%), herbivory (37%), and unknown (15%). Final basal diameter of all transplanted sand gilia at Site 4S averaged 19.4 cm ± 1.14 (S.E). Estimated seed production from plants of medium size (15-24 cm) was ~ 1000 seeds (Table 3). Thus, transplanted sand gilia at Site 4 may have dispersed ~81,000 seeds. After the dry winter of 1993-1994 (December-March = 204 mm) only 41 plants germinated from seed dispersed by the transplants in 1993.

At Site 9b, 51 of 66 (77%) transplanted sand gilia survived to produce seed. Final basal diameter of the transplants was not measured at this site. Greatest mortality was from desiccation (66%), followed by herbivory (33%). In 1994, only 17 sand gilia germinated from seed produced by plants transplanted in 1993. Unseparated seedlings (as many as five plants) produced more seed than separated seedlings. Damage to roots during separation appeared more detrimental to growth and survival than competition among the seedlings growing together.

DISCUSSION

Distribution

The ten known populations of sand gilia numbered approximately 100,000 individuals in the Monterey Bay dunes in 1993. Four sand gilia populations are permanently protected (Sites 1, 2, 3, 9), while four other populations lie entirely on private lands where the possibility for preservation is unknown (Sites 5, 7, 8, 10). Two populations are partially protected in conservation easements (Sites 4b, 6a), while part of the population is at risk of development (4a, 6b; Table 2).

Much of the variability in sand gilia numbers from year to year (Table 1) is probably related to rainfall and weather patterns, and secondarily, herbivory and seed burial. Human disturbance may be responsible for degradation of potential habitat, but no "take" of sand gilia has occurred since 1986, when the Spanish Bay population was partially extirpated by development. Habitat loss is likely as dunes are built upon or monopolized by non-native plants. Sand blowouts and iceplant encroachment may be responsible for the severe decline in sand gilia abundance at Marina State Beach from 1985 to the present. Different census-takers also may be responsible for variation in estimates of sand gilia numbers. For instance, sand gilia occurs in separate areas at Salinas River State Beach and could easily be overlooked.

Timing is critical for accurate surveys; they must be conducted at peak reproductive stage (late April-May), when the bright purple flowers are in full bloom. Optimal survey time may vary depending on rainfall, and often lasts only one to two weeks. If location of the population is known, sand gilia beyond peak bloom can be censused, but counts are less accurate. New locations are seldom found without the purple flowers as indicators, because small seeding plants have a diminished basal rosette and are difficult to see. Past surveys for the Natural Diversity Database may be inaccurate because it is difficult to estimate time of peak flowering unless biweekly visits are made to the sites. In 1994, low rainfall apparently precipitated early flowering (April) in several populations around the Monterey Bay (pers. obs.). It is possible, though unlikely, that surveys north of Elkhorn Slough in May 1994 occurred after the flowering period, and existing sand gilia were missed. Surveys did not differentiate between plant size and estimated seed production may vary considerably (275 to 4500 seeds). Size should be recorded, particularly in the smaller populations, to accurately assess biological status.

The size of separate populations is an important concern relative to possible extinction. Small populations may have less genetic variation, reducing the ability to adapt to changing environments and increasing susceptibility to pests and diseases (Barrett and Kohn, 1991). Despite this theoretical relationship between genetic diversity and species persistence, there is no empirical evidence that directly links genetic composition of plant populations to their growth rate or survival (Schemske et al., 1994).

The precipitous decline in numbers at Marina State Beach suggest that this population may be on the verge of extinction (Table 1). Because of unpredictable factors such as precipitation, wind, and temperature in the dunes, sand gilia populations nearing 100 individuals should be closely monitored, and all possible enhancement efforts attempted. These efforts might include weeding of exotic (and possibly native) species, and sand stabilization in blowout areas. In areas with large rabbit populations, caging of plants may be necessary. Watering may be useful, but care must be taken to control any species that may respond to the additional water and overgrow the sand gilia. Light disturbance by feet or tires near existing populations may stimulate a buried seedbank to germinate.

Natural History

The life cycle of sand gilia seems well adapted to the average precipitation patterns in the Monterey Bay dunes. Winter rains usually begin in November and an average of 51 mm is received each month through March (Marina Coast Water District, 1970-1994). The plant usually germinates in January, increases in size February through March, and reaches adult stage by April when rainfall has lessened or ceased. The absence of germination in summer or fall (in nursery trials providing adequate moisture) indicates that the seed may have dormancy requirements that are met after the seed has weathered in the sand, or experienced cold weather.

Sand gilia occurs on stabilized sands, where associated vegetation may provide protection from wind, desiccation, and herbivory. A decumbent to semi-decumbent growth habit may facilitate survival during periods of strong winds. The presence of sand gilia in old tracks and along roads suggests that previous disturbance to the sand may expose buried seed and reduce associated vegetation permitting sand gilia to germinate and grow without undue competition.

Sand gilia occurs in areas where associated vegetation cover is less than 50%, suggesting that it cannot tolerate shade from other plants, or that it can colonize marginal environments other plants cannot. Closest neighbors are usually annual species such as Cryptantha leiocarpa and Chorizanthe spp. that have similar growth rates, so competition for light, nutrients, and moisture probably increase gradually among them all. It is also possible that these factors are not limiting when the plants are actively growing. Aggressive native species and invasive exotics seem to affect sand gilia through desiccation and shading.

Small variations in topography, such as depressions, may provide favorable microsites for sand gilia, perhaps because of increased nutrients and/or shelter from wind and sun. Vegetative litter is often blown or washed into these slight depressions (pers. obs.). Barbour et al. (1985) suggested that litter fall from dune species (several of which are nodulated with nitrogen-fixing bacteria) may provide a slight increase in organic nitrogen in stabilized dunes, relative to more exposed areas. Depressions also may catch insect remains and animal manure, providing an extra source of fertilizer. Alternatively, it is possible that sand gilia seed is blown or washed by rain into these depressions, and then germinates in dense clusters.

All sizes of sand gilia produce seed, so even small plants have a chance to leave progeny. This feature, combined with seed viability of at least three years, facilitates continued survival in an unpredictable environment. The ability of the flower to close in stormy weather may conserve effort by protecting reproductive organs. Self-pollination may have been selected after periods of adverse weather kept flowers closed, with stamens and stigma in close proximity.

Plitmann and Levin (1990) stated that autogamy is frequent in Gilia species. All sand gilia flowers observed in the coastal dunes have a juxtaposition of anthers and stigma, characteristic of self-pollinating species (Rollins, 1963; Schoen, 1981). Despite long hours in the dunes at all times of the day, I never observed pollination by insects. Conditions were often windy or foggy, which may have prevented pollinator flight. Self-pollination allows copious production of seed, even if pollinators are scarce in the coastal strand habitat.

A beefly was observed visiting the closely related subspecies, Gilia tenuiflora ssp. tenuiflora at Fort Ord. This subspecies has slightly larger flowers than Gilia tenuiflora ssp. arenaria, with a stigma exserted 1 to 2 mm. beyond the anthers (A. Day, in Hickman, 1993). Several authors have shown outcrossing rate to be positively correlated

with increased stigma exsertion (Breese, 1959; Rick et al., 1977). Grant and Grant (1965) documented the ability of Gilia tenuiflora ssp. tenuiflora to self-pollinate as well as cross-pollinate. A beefly was observed visiting sand gilia flowers in the nursery, indicating that corolla size may be acceptable for insect pollination. Because the first flowers produced are larger (pers. obs.) they may be more likely to be pollinated by insects than later, smaller flowers. Future studies should include continued vigilance for pollinators.
It seems unlikely that sand gilia persistence is related to lack of pollinators, because the plant appears so successful at self-fertilization.

The primary vectors of seed dispersal for sand gilia appear to be wind and rain. Wind dispersed plants are relatively common in dry habitats, and seeds without modifications for dispersal may be regularly scattered in rainwash (Howe and Smallwood, 1982). The distribution of sand gilia in the Monterey dunes indicates that wind dispersal is important. Populations are now separated in clusters along the coast, suggesting that the plant may have once occurred more extensively in open, hind-dune areas, and currently has a smaller distribution due to human disturbance, invasive vegetation, and loss of habitat. It is also possible that sand gilia has always been rare, scattered in pockets throughout the dunes. Sand gilia can probably colonize any open, sandy area where the seed falls, as long as it is not too deeply buried, receives sufficient moisture, and escapes herbivory. The presence of sand gilia in undeveloped areas, several kilometers inland at Fort Ord, suggests that colonization occurred landward of the coastal dunes in the past. Perhaps farming and grazing eliminated habitat and increased monopolization by annual weeds, preventing sand gilia germination.

Sand gilia survival appears to depend on adequate and consistent rainfall. When rainfall averaged 60 to 80 mm per month, December through February 1992/1993, plants germinated and grew sufficient roots to survive sporadic and lesser rainfall during March and April. I observed that a lack of rainfall in March and April reduced the overall size of sand gilia, resulting in fewer capsules and less seed, but rarely caused death before reproductive maturity.

Low rainfall in January 1992 (32 mm), followed by late field seeding in February 1992, was associated with very low germination of sand gilia in 1992. In contrast, high rainfall in January 1993 (183 mm) was associated with greater germination in seeded plots and record numbers of sand gilia in surveys. A 38-day period without rain from December 1993 to January 1994 may have been responsible for a severe reduction in sand gilia abundance relative to 1993 levels in three separate populations (Table 1, Fig. 8). Variability in rainfall from year to year is expected, and variability in sand gilia abundance, size of plants, and reproductive potential appears closely related to fluctuating precipitation levels.

Field Growth of Naturally Occurring Sand Gilia

Possible reasons for larger sand gilia at Site 4 might include environmental differences (e.g. increased precipitation, soil moisture, or nutrients), genetic differences, or a lower density of sand gilia compared to Site 9. The preliminary soil samples indicated little difference in nutrients between sites, although samples were not replicated. Microtopography may be different between the sites. It is also possible that the shifting sands at Site 4 are beneficial to sand gilia, exposing buried seed, or burying seed lightly for optimal germination. Slight sand burial may stimulate the plants to produce more biomass, however, the disadvantage of sand burial > 1cm (probably common in winter months) was clearly noted in this study.

The high success (77% produced seed) of naturally occurring sand gilia at Site 9bS in 1991 is encouraging for an endangered species. Even a small sand gilia may produce

200 seeds (Table 3), adding to the potential for large fluctuations in population size from year to year. The ability to survive and produce abundant seed indicates that seed production is not a limiting factor to survival. Mortality, caused primarily by herbivory, seemed to be evenly distributed throughout the life cycle. However, plants were not measured until well into juvenile stage (rosette), producing a biased estimate of survivorship.

Low soil moisture, herbivory, and possible nutrient deficiency were the primary factors that affected growth, survivorship, and reproduction in the field. When rainfall was abundant and consistent, herbivory and nutrient deficiency were not observed until sand gilia was well into adult stage. In a year of low rainfall (1993/1994), desiccation magnified the effects of herbivory and nutrient deficiency.

Daytime summer drought has been reported as limiting to growth and survival of seedlings (Davidson et al., 1977; Selter et al., 1986). In this study, sand gilia increased in size while temperatures in the dunes were cool to moderate. Flowering and seed set occurred as temperature increased, when root growth appeared sufficient to support the plant, even if drought occurred. The highest temperatures on the dunes occurred as sand gilia naturally senesced.

Herbivory was a primary cause of mortality for sand gilia. Grazing of basal leaves limits the amount of photosynthate available for growth and reproduction; therefore, the timing of basal leaf growth is important when compared with the timing of vegetative growth and reproduction of the surrounding community (Fiedler, 1987). Proximity of other annual species appeared to reduce grazing on sand gilia in plots, although this was not quantified. In 1994, when rainfall was low and associated annual vegetation was sparse, sand gilia were severely reduced by grazing (pers. obs.).

The primary grazers of Gilia are probably Peromyscus maniculatus (deer mouse), Microtus californicus (California vole), and Sylvilagus bachmani (brush rabbit). Future studies should include trapping to verify the identity of the herbivores. Peromyscus maniculatus was caught in small mammal traps placed in the Fort Ord dunes (U.S. Army Corps of Engineers, 1992). Pitts and Barbour (1979) caught only Peromyscus maniculatus in the dunes at Point Reyes National Seashore in California. Stomach analyses revealed that the mice ate coleopterans, seeds, and green herbage from the dune plants. It is not known if the deer mouse diet is the same in the Monterey dunes. The small seed of sand gilia may be like "popcorn" to mice (W. Pitts, pers. comm.), but food preference trials are needed to explore this possibility. Empty snail shells were seen in the dunes but no evidence of snail grazing was observed, suggesting that the snails are eaten before they can graze the sand gilia. It is also possible, though never observed, that ants may prey upon the tiny sand gilia seed.

Grazing appeared to stimulate sand gilia growth and late flowering when part of the plant remained. Increased seed production might be possible if sufficient moisture were available late in the season (March, April) for continued growth. Fiedler (1987) found that the effects of grazing on the leaves of Calochortus spp. varied greatly among years and populations. It is equally likely that the effects of grazing on sand gilia vary between years and populations. Regrowth of the plant probably depends on soil moisture, nutrient availability, and the incidence of repeat grazing.

A preliminary soil test confirmed that nutrients were substantially lower at Sites 4 and 9b than in a typically fertile soil. Studies documenting the low level of nutrients (particularly N, P, K) in the dunes have suggested these levels may impose major restrictions on coastal plant productivity (Morris et al., 1974; Pavlik, 1982). Atkinson (1973) concluded that most species at two sites in the English dunes were phosphorus deficient. He found that fertilizer supplementation increased plant weight to twice that of controls, and plants were green instead of red. Nutrient deficient sand gilias in this study were red or pale in color, small in size, and often occurred in areas where other vegetation was sparse. It is possible that red or pale plants were also water stressed, or struggling to grow in compacted soil. In nursery germination trials, sand gilia responded vigorously to low levels of fertilizer with increased growth, deep green color, thick stems, and leaves that continued to photosynthize through flowering. Thus, sand gilia seemed adapted to low soil fertility in the dunes, but clearly benefited from addition of nutrients.

Seed Counts

Seed counts provided a measure of reproductive potential and variability among plants and populations. Abundant seed production may offset the high mortality associated with marginal or fluctuating environments (Harper, 1977). During this study, sand gilia produced abundant seed that survived the unpredictability of wind dispersal and sand burial, and germinated despite fluctuating temperatures and rainfall on the dunes.

Variability in capsule size may depend on water availability and plant resources. In this study, the first capsules borne on the primary stem were noticeably larger than later, secondary stem capsules that often produced immature seed. To compensate for this variability in size, the seed number of large and small capsules was averaged. Future studies should test viability of seed from primary versus secondary capsules. A difference in germination ability may help explain the variability in germination recorded in nursery trials, and may indicate that only primary capsules should be collected for optimal germination.

Unopened, ripe capsules should be dissected with the aid of a microscope to accurately determine seed number. The requirement of fully ripened seed for germination trials necessitated gathering fruits that were just dehiscing, which may have slightly biased estimates of seed number.

Field seeding

Seeding is an uncertain method of establishing sand gilia in the field because establishment depends on factors that are unpredictable. The seed must occupy an appropriate microsite, be covered with some sand, and receive consistent moisture, possibly rainfall once per week of ~17 mm, December through March. This suggested rainfall level is estimated from average monthly rainfall in Marina (Marina Coast Water District, 1970-1994), noting that poor germination of sand gilia was associated with rainfall less than 67 mm during at least one month in the winter rainy season. In addition, poor germination was noted in some months when total rainfall exceeded 67 mm but more that one week elapsed between rains. To survive after seeding, grazing on sand gilia must be minimal or nonexistent, and associated vegetation must not outgrow the sand gilia, causing excessive shade or competition.

Germination results in 1993 emphasized the importance of seeding long before germination begins in January and February. Germination failed in 1992, most likely due to late seeding and/or lack of seed burial. It is possible that roots develop much earlier than emergence of the hypocotyl, suggesting that moisture in November and December is critical for imbibition of the seed and subsequent root growth. Sand gilia in plots seeded for twelve months was significantly larger than sand gilia in plots seeded for only three months. Sand gilia's natural cycle of dispersing seed in May and June probably allows the seed to "weather" during the six months before germination, perhaps satisfying an after-ripening requirement. Perhaps the seed needs time and wind to settle in to a "safe site" (Harper, 1977). For sand gilia, a safe site seems to be between sand grains or organic debris where soil moisture and nutrients are sufficient for germination when the rains begin. Light sand burial (< 1cm) may prevent desiccation and/or herbivory of the seed. Higher germination (15%) in Sand City (Site 4S) than at Salinas River State Beach (7%, Site 9bS) may be due to the same factors that resulted in large naturally occurring sand gilia at Site 4. Genetic differences may result in more vigorous seed at Site 4S, or germinating seedlings may have responded to a difference in nutrients, soil moisture or microtopography. Site 4S may have more variable soil texture that catches seeds in pockets of moisture, or more vegetative debris to provide shelter and low levels of nutrients. Herbivory of the seed may have reduced germination at Site 9bS, and grazing of the cotyledons may have occurred in between monitoring visits.

The number of sand gilia producing seed in seeded plots was at least 48% at both sites. Success was greater (75%) for naturally occurring plants at Site 9b in 1991. Variation in herbivory between the two years may have caused the differential success, but it was also observed that naturally occurring plants in 1993 were larger and reached reproductive maturity earlier than seeded sand gilia. Perhaps the naturally occurring seed settled into a microsite and established roots earlier than introduced seed. Field seeding early in the fall might increase germination and reproductive success.

Survivorship curves for sand gilia in seeded plots indicated that the timing of mortality is variable, affecting early and late juveniles, as well as adults (Fig. 13). Grazing may not be related to a specific stage of sand gilia development, but rather to characteristics of the herbivores, such as timing of reproduction. Pitts and Barbour (1979) reported that Peromyscus maniculatus traveled an average of 32 m, and one tagged mouse traveled 260 m, suggesting that herbivore movement from other areas is also likely.

Dune aspect had surprisingly little effect on germination and reproductive success. Germination and success were slightly higher (not significant) on northern aspects at Site 4S in 1993, whereas southern aspects had a slight advantage (not significant) at Site 9bS. Plots with the same aspect may have differed in hours of sun received and soil temperature, perhaps due to shading from tall shrubs or dune forms. Germination and success were affected by an significant interaction between site and aspect, suggesting that (unknown) differences between the sites may be important. Aspect may have greater influence in years of low rainfall, when the effects of solar irradiation are more severe.

Associated vegetation cover at Site 9bS had no significant effect on sand gilia size, germination, or reproductive success in 1993. The apparent lack of competition from associated vegetation was unexpected, because sand gilia has been described as a plant occupying open areas (Natural Diversity Database, 1990), suggesting that competition might affect survival. Perhaps sand gilia requires open areas for germination, but roots later grow deep and most competing dune vegetation is not a concern. It is also possible that associated plant cover may have more effect in years with less precipitation.

Nursery Germination Experiments

Exploring differences in germination as a result of varied storage methods was confounded by the variable seed collection dates within treatments. Germination of seed collected in three different years was more variable within years than among years (Table 8). Seed collections made only six days apart had a 33% difference in percentage germination (cold-stored treatment). Other seed collections 21 days apart, revealed a 46% difference in viability (room temperature treatment). This suggested that sand gilia may produce seed that varies considerably in viability, perhaps related to size and vigor of the plant, or time when the seed is produced (early or late season). This seed variability may be more important than storage method, at least for seed up to three years of age. Cold-stored seed germinated more slowly than seed stored in other ways, possibly because of improper humidity in storage.

Sand gilia seed can survive at least three years with no reduction in viability. Long term viability of the seed is an important advantage when rainfall is insufficient for germination, or blowing sand buries seed too deeply, because there is still germination potential in the following years. Further studies detailing seed longevity are critical. If seed is long-lived with little loss of viability, then the size of the seedbank is important, and the possibility of environmental fluctuations causing extinction is much reduced.

Germination trials illustrated the significant advantage of seed burial over non-burial. This finding agrees with Harper and Benton's (1966) conclusion that burial at shallow depths prevents atmospheric desiccation and maintains a humid environment around the seed, thereby allowing more successful germination. Maun & Riach (1981) suggested that substantial changes in microtopography occur by wind or splashing of raindrops on sandy soils, making it unlikely that a seed will remain unburied on the surface. The small size of sand gilia seed probably facilitates movement with sand grains, which may permit wind dispersal and burial of the seed (sometimes too deeply). Future researchers should vary depth of sand burial to determine optimal coverage of the seed.

Differences in germination between separate sand gilia populations, and between Gilia tenuiflora ssp. arenaria and Gilia tenuiflora ssp. tenuiflora, may be due to genetic variability, or simply the result of not culling immature seed before planting. Seed should be sorted with the aid of a microscope, and shrunken or translucent embryos discarded, for more accurate tests of germination.

Nursery trials can only suggest sand gilia response in the field under more extreme and unpredictable conditions. Correlating optimal germination in the laboratory with soil temperatures and seedling emergence in the field is difficult because relevant data on the microenvironment around the seed is usually not gathered (Barbour et al., 1985). In this study, the difference in germination between nursery trials (34-80%) and field seeding (8-15%) was large, suggesting that sand gilia seeds in the field encounter few sites with adequate moisture, nutrients, and protection to germinate.

The increased vigor of nursery stock indicated that sand gilia may sometimes be moisture or nutrient-limited in the dunes. However, the plant seems adapted to poor soils, and often produces large plants despite possible low nutrient levels.

Transplantation

Transplantation of seedlings from containers was more successful than field seeding. Nursery propagation decreased the uncertainty of germination (8-15% in seeded plots, 34-80% in containers) and eliminated variables that lead to establishment failure. Seedlings were grown beyond the stage most vulnerable to desiccation in the field, the seedling and juvenile stage. Because of the unique design of the supercells, seedlings grew substantial roots that were not disturbed by planting. Container plants were usually larger and produced more seed than naturally occurring sand gilia, due to fertilization and ample water. Grazing may be less severe for transpanted sand gilia than field seeded plants because transplants usually have more leaves left after partial grazing. The percentage of sand gilia producing seed was higher after transplantation (75%) than after seeding (50%), a possible result of fertilizer enhancement, or greater survival after herbivory.

In this study, sand gilia was grown in crowded supercells and produced abundant seed even when seedlings were planted together in one clump. This apparent ability to tolerate competition may be the reason that slow-growing native vegetation appears to have little negative impact on the plant.

As in seeded plots, there was little germination in 1994 from seed dispersed by transplants in 1993, although estimated seed production was considerable at Site 4S (81,000 seeds). Low germination may be due to rainfall that was less than normal in December (44 mm, average = 54 mm) and January (65 mm, average = 70 mm). Three other naturally occurring populations were also much reduced in 1994, suggesting that soil moisture was inadequate for sand gilia germination. It also is possible that seed from transplants was less viable in the field, or contained a higher proportion of shriveled or damaged embryos. Casual observations during nursery trials, however, have indicated no such weakness in second generation seed.

Transplantation should be done early in the rainy season (December) for maximum precipitation. Death of transplanted sand gilia due to desiccation may have been prevented with routine irrigation. Although irrigation may be an unnatural event, the survival of transplants insures prolific seed dispersal.

There is current debate over the value of genetic versus demographic information in the management of rare and endangered species. Schemske et al. (1994) emphasized the need for demographic information on population dynamics of rare species, as well as information on the roll of extinction and colonization in metapopulations (a population of populations). While demographic information is certainly a first step in assessing the status of a species, genetic information also may be invaluable. The amount of genetic variability in a population is often of great interest, particularly in small populations. Schoen (1981) compared selfing and outcrossing species of Gilia achilleifolia from the central coast ranges of California and found less genetic variation in individual selfing populations than in individual outcrossing populations. He also found greater heterozygote frequencies than expected in the selfing populations based on knowledge of outcrossing rates. Genetic differences between Gilia tenuiflora ssp. arenaria and the related subspecies, Gilia tenuiflora ssp. tenuiflora might be determined through electrophoretic analysis. It would be interesting to know if Gilia tenuiflora ssp. arenaria has less genetic variation than its inland relative.

The natural variability of annual plant populations indicates caution in extrapolating habitat characteristics from populations studied at Sand City and Salinas River State Beach to other sand gilia populations along the Monterey coast. These larger populations may have greater genetic diversity and a better ability to handle enviromental perturbations. Management recommendations should be thoroughly tested for efficacy in small and large populations.

Establishment of endangered species in new habitats for mitigation projects in California has not always been successful (Fiedler, 1991). Poor success seems related to lack of knowledge regarding the biology and habitat requirements of the species, or to poorly executed mitigation plans. It is often difficult to match conditions critical for establishment such as microtopography, soil moisture, and nutrient levels, to that of the original population. This study defined habitat characteristics and determined that sand gilia can germinate successfully and reproduce prolifically when conditions are suitable. The plant can tolerate (and perhaps requires) disturbance, suggesting that sand gilia is more limited by lack of suitable habitat than by poor germination or reproductive success. The unpredictability of precipitation, temperature, and wind make survival for any dune plant uncertain. The survival of sand gilia populations through recent drought years, indicates that the seedbank remains viable through periods of extreme conditions.

Sand gilia is endangered because there are only ten known populations, and the number of individuals within populations fluctuates considerably from year to year, depending on rainfall and herbivory. Potential and existing habitat is threatened by human disturbance and invasive non-native species (Natural Diversity Database, 1990), but it is possible that sand gilia has always been "rare" along the Monterey coast. The discovery of sand gilia at Fort Ord doubled the abundance of this subspecies (U.S. Army Corps of Engineers, 1992), suggesting that sand gilia is less rare than previously thought. Recovery of the subspecies from the threat of extinction seems possible.

Summary

Gilia tenuiflora ssp. arenaria is an endangered annual plant with approximately 100,000 individuals spread over ten known populations in the Monterey Bay dunes as of May, 1993. In 1993, 45,590 sand gilia were recorded at Fort Ord (U.S Army Corp of Engineers, 1994), doubling the number of individuals and increasing the range of this endangered species. Only one population at Marina State Beach has declined since 1985, possibly because of unstable sands (blowouts) and iceplant encroachment. Other populations contained 500 to 25,000 individuals in May 1993, and fluctuated considerably in other years. Surveys of three populations in 1994 indicated 80-95% fewer plants than in 1993, presumably due to sporadic and reduced rainfall compared to the high rainfall of 1993.

The factor most limiting to sand gilia germination and establishment seems to be the quantity and timing of winter rainfall. Records suggest that consistent December and January rains are critical for seed to imbibe and germinate. Another important factor is the presence of herbivory. Survivorship curves indicated sand gilia was susceptible to desiccation and herbivory throughout it's life cycle. Herbivory may be very patchy and unpredictable, and is probably more severe in years of reduced rainfall, when associated vegetation is also reduced. Winds may cause debilitating sand burial and desiccation, although this was seen only one year of three in the Sand City population.

Seeding experiments produced relatively low germination (7-15%) in 1993 when rainfall was above average. This suggests that viability of seed is variable, and that sites with sufficient moisture, nutrients, and protection from herbivory are critical for establishment. Sand burial of at least one cm is probably also important for germination of the seed. Prior disturbance along old trails or vehicle tracks, appeared to facilitate sand gilia germination in some areas. The slope and aspect of seeded plots had no significant effect on germination and reproductive success in 1993. Microtopography may play a more important role in survival, or slope and aspect may be less important when rainfall is high. Additional field studies quantifying microtopography in existing sand gilia habitat and manipulating topograpy in seeded plots are recommended.

Nursery germination trials indicated that buried seed germinated better than non-buried seed. There was no advantage to cold-stored seed over seed stored at room temperature, and the year of seed collection (up to three years) had no effect on germination. Seed from different populations of sand gilia and a population of Gilia tenuiflora ssp. tenuiflora varied in rate and percentage germination, suggesting variability among sand gilia populations and between subspecies. Germination results may be more indicative of seed variability among plants than of viability under different conditions.

Transplantation of seedlings from containers was more successful than seeding. Not only was germination greater under optimal nursery conditions than in seeded plots, but 75% of the transplanted sand gilia produced seed compared to 50% of the plants in seeded plots. Transplanted seedlings that are damaged by herbivores can often recover because of their large size. Because sand gilia is endangered, seed should be used efficiently. Thus, transplantation is recommended over field seeding, at least until the effects of microtopography and disturbance on establishment are determined.

Reproductive success of naturally occurring and established plants is high, indicating that germination may be more limiting to sand gilia persistence than survival to reproductive maturity. Seed production is considerable. Longevity of the seed is known to be at least three years, with no reduction in viability.

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Table 1. Number of <u>Gilia</u> <u>tenuiflora</u> ssp. <u>arenaria</u> from limited surveys 1985-1994. Sources: Arnold, 1991; Dorfman, 1990; Julin et al.,1993; Natural Diversity Database [(NDD, Day, Ferreira), 1990]; Thomas Reid Associates [(TRA), 1990]. If no source listed, data from pers obs.

Popul #	Site	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
3a	Navy School Dunes (same population cluster)	700 (NDD)						1043 (Ferreira)	1950	5000-10,000	
3b	Del Monte Dunes							455 (Ferreira)	650	3500	
4a	"East Dunes", Sand City		10,000 (Day)	5090 (TRA)		34650 (TRA)	<10,000 (Ferreira)	11,743 (Arnold)	>20,000	25,000	<1000
4b	Sand Dollar Shopping Ctr. Habitat area							57 (Arnold)	96 (Julin)	<200	180
6	Marina State Beach	10,000 (Day)	300 (Ferreira)		6 (Ferreira)			8	20	325	61
7	Lonestar Sand Co., Marina			2229 (TRA)						1000	
8a	Monterey Dunes Colony (same population cluster)	both clusters combined	20,000							3000-4000	230
8b	Salinas River State Beach	10,000+ (Ferreira)	(Ferreira)	1665 (Ferreira)		8900 (Dorfman)	6300 (Dorfman)		1150-1200	10,000	181
8c	N. Salinas River State Beach									50	8

Table 2. Distribution of Gilia tenuiflora ssp. arenaria. Population number, location, date observed, ownership of population, protection from development, size (number of individuals in population), status of population, and relevant comments.

Pop. #	Name of site (Monterey County)	date obs.	ownership	protection?	size	status	comments
1a	Spanish Bay (1a, 1b = same population cluster)	May, 1993	Pebble Beach Co. private	yes & no	700-1000	healthy	1993 rains stimulated new occurrences plants are on a horse trail cages used to prevent deer browsing
1b	Spanish Bay near Moss Beach	1985	Pebble Beach Co. private	extirpated		extirpated	seed collected for propagation transplants (1993) produced seed (G. Fryberger, pers. comm.)
2	Asilomar State Park	April, 1993	CA. State Parks	yes	550	healthy	new occurrences in area recently trenched (T. Moss, pers. comm.)
3a	Navy School Dunes (3a, 3b = same population cluster)	May, 1993	Dept. of Defense U.S. Navy	yes, (unofficial)	5000-10000	healthy	Navy restoring dunes, footpath through population weeding has increased available habitat
3b	Del Monte Dunes	May, 1993	private	no	3500	healthy	foot traffic through population
4a	Tioga ave, Sand City "East Dunes" (4a, 4b = same population cluster)	April, 1993	private ~40 owners	no	25,000	healthy	Until discovery of Ft. Ord pop, this was largest Gilia pop. known pop. incl. largest size Gilia known
4b	Sand Dollar Shopping Ctr. Habitat Preserve	May, 1993	cons. easement	yes	<200	healthy	seeding and transplantation experiments in Spring, 1993 seed source was "East dunes", seeding efforts yielded 15% germination, transplantation ~75% sucessful (set seed)
5	Ft Ord, coastal Fritzche Airfield	May, 1993	Dept. of Defense U.S. Army	no	45,590	healthy	first discovered 1993 Inland Fort Ord GTA intergrades to Gilia tenuiflora ssp. tenuiflora

Table 2 continued. Distribution of <u>Gilia</u> <u>tenuiflora</u> ssp. <u>arenaria</u> (GTA).

Pop. #	Name of site (Monterey County)	date obs.	ownership	protection?	size	status	comments
6a	Marina State Beach (6a, 6b = same population cluster)	May, 1993	CA. State Parks	yes	325	declining	decline may be due to sand blowouts or iceplant encroachment
6b	Monterey Sand Co. Marina	May, 1993	Monterey Sand	no	350-400	unknown	
7	Lonestar Sand Co. Marina	May, 1993	RMC Lonestar private	no	1000	healthy	
8	Mulligan Hill, Marina	May, 1993	Scattini & Sons private	no	4000	healthy	counted for first time in 1993, though previously known
9a	Monterey Dunes Colony (9a, 9b, 9c = same population cluster)	May, 1993	Monterey Dunes Colony private	yes/no	3500	healthy	<u>GTA</u> is in restoration area appears to be a conservation easement
9b	Salinas River State Beach (Molera Road)	May, 1993	CA. State Parks	yes	10000	healthy	seeding experiments attempted in Feb. 1992, failed seeding experiments attempted in winter 1993 successful, & Feb.1992 plots germinated too. Seeding -7% germination
9c	N. Salinas River State Beach	May, 1993	CA. State Parks	yes	50	small plants	
10	Watertower Hill, Moss Landing	May, 1993	Petersen Trust private	no	400-600	healthy	late blooming population Discovered 1993, in area of recent vehicle disturbance

Table 3. Characteristics of seed production for three size classes of Gilia tenuiflora ssp. arenaria. a) Seeds per capsule; n = capsules from separate plants, b) number of capsules; n = separate plants, and c) estimated seed production (seeds per capsule x number of capsules).

a) Seeds per capsule

Basal diameter	n	$\bar{x}$	S.E.
1-14 cm.	17	25	1.26
15-24 cm.	19	35	1.88
25-64 cm.	24	41	2.42

b) Number of capsules

Basal diameter	n	$\bar{x}$	S.E.
1-14 cm.	33	11	1.15
15-24 cm.	8	32	3.07
25-64 cm.	9	110	40.00

c) Estimated seed production

Basal diameter	Mean	Minimum	Maximum
1-14 cm.	275	234	319
15-24 cm.	1118	956	1291
25-64 cm.	4564	2735	6586

Table 4. Soil Analysis of Site 4 (East Dunes, Sand City) and Site 9b (Salinas River State Beach) on 14 April 1994. Results expressed in kg/ha, 15 cm deep. From a certified analytical report prepared by Soil Control Labs, Watsonville, CA.

Soil characteristics		location		typical fertile soil
		Site 4	Site 9b	
pH value	units	6	6.1	depends on crop
Organic Matter	%	1	2	2+
Ammonia Nitrogen	N	6	6	56-112
Nitrate Nitrogen	N	6	8	34-56
Total Available Nitrogen	N	11	13	90-168
Phosphorus	P_2O_5	22	34	168+
Potassium	K_2O	56	34	392+
Calcium	Ca	448	336	2242+
Magnesium	Mg	78	62	112+
Sulfate	SO_4	11	8	280+
Chloride	Cl	11	34	<112
Sodium	Na	28	34	<336
Conductivity (1:5)	umhos/cm	34	56	<1121
Total soluble salts	ppm	111	185	<3699

Table 5. Mean percentage (± S.E.) germination, success (produced seed), and mortality in 1992 & 1993 for plots seeded in February and December 1992 at Site 4S (Sand City) and Site 9bS (Salinas River State Beach).

	Site 4S		Site 9bS	
	1 plot Feb-92	14 plots Dec-92	24 plots Feb-92	12 plots Dec-92
germination (by March 1992)	0	----	2 ± 1%	----
success (May 1992)		----	37 ± 13%	----
mortality (March-May 1992)		----	63 ± 13%	----
germination (by March 1993)	14%	15 ± 3%	6 ± 1%	8 ± 2%
success (May 1993)	89%	48 ± 7%	57 ± 7%	51 ± 10%
mortality (March-May 1993)	11%	52 ± 7%	43 ± 7%	49 ± 10%

Table 6. ANOVA's (Model I : fixed factors) of percentage germination and success (seed produced) with site (4S = Sand City, 9bS = Salinas River State Beach) and aspect (north, east, south, west) as factors. Site 4S seeded on 23 December 1992, Site 9bS seeded on 11 December 1992.

Percentage germination Source of variation	SS	d.f.	MS	F	p
site	80.6667	1	80.6667	2.11	0.17
aspect	103	3	34.3333	0.90	0.46
site x aspect	425.6667	3	141.8889	3.71	0.03
error	612.667	16	38.2917		

Percentage success Source of variation	SS	d.f.	MS	F	p
site	504.1667	1	504.1667	5.84	0.03
aspect	291	3	97	1.12	0.37
site x aspect	930.8333	3	310.2778	3.59	0.04
error	1382	16	86.375		

Table 7. ANOVA's of percentage germination and success (seed produced) with aspect (north, east, south, west) and percent cover of associated vegetation (0-25%, 25-50%) as factors. Twenty-four plots were seeded on 11 December 1992 at Site 9bS (Salinas River State Beach).

Percent germination Source of variation	SS	d.f.	MS	F	p
aspect	0.00866	3	0.002886	1.76	0.18
% cover	0.0009	1	0.000903	0.55	0.47
aspect & cover	0.000834	3	0.000278	0.17	0.92
error	0.03933	24	0.00164		

Percent success Source of variation	SS	d.f.	MS	F	p
aspect	0.739153	3	0.246384	2.87	0.057
% cover	0.034971	1	0.034971	0.41	0.53
aspect & cover	0.083445	3	0.027815	0.32	0.81
error	2.0606	24	0.08586		

Table 8. Nursery germination of Gilia tenuiflora ssp. arenaria in 1993. Seed storage methods were: Seedbank -20°C, room temperature 16-20°C (R. temp.), and cold-stored for 100 days at 4° C. Seed treatments were: buried to depth of 0.5 cm, or not buried. n = # of supercells each containing 5 seeds.

Seed Storage/ treatment	Seed collection date	% germination n	% germination $\bar{x} \pm 1$ S.E.	Days to germination n	Days to germination $\bar{x} \pm 1$ S.E.
Seedbank/ buried	6/1/90	14	74 ± 6.4	14	12 ± 0.7
R. temp./ buried	5/1/90	12	67 ± 7.9	12	15 ± 0
	4/30/92	13	34 ± 10.7	13	13 ± 0.9
	5/21/92	11	80 ± 6.0	11	12 ± 0.8
Cold-stored/ buried	5/5/91	31	46 ± 6.3	23	13 ± 0.4
	5/16/91	9	38 ± 8.5	13	15 ± 0
	5/22/91	13	71 ± 8.7	13	15 ± 0.6
R.temp./buried	5/21/92	38	47 ± 4.5	34	13 ± 0.2
R.temp./not buried	5/21/92	21	8 ± 3.2	5	13 ± 0.4

Table 9. Nursery germination in 1993 of Gilia tenuiflora ssp. arenaria (GTA) and Gilia tenuiflora ssp. tenuiflora (GTT) using seed collected from three separate locations. Site 4) East Dunes, Sand City (GTA), Site 9) Salinas River State Beach (GTA), and Fort Ord - Picnic Canyon Road (GTT). Seeds were buried to a depth of 0.5 cm. n = # of supercells each containing 5 seeds.

	Percentage Germination		Days to Germination	
Location	n	$\bar{x}$ ± 1 S.E.	n	$\bar{x}$ ± 1 S.E.
Site 4 (GTA)	40	71 ± 5.0	36	14.3 ± 0.5
Site 9 (GTA)	40	39 ± 4.6	36	12.9 ± 0.2
Fort Ord (GTT)	40	45 ± 4.6	36	9.0 ± 0.5

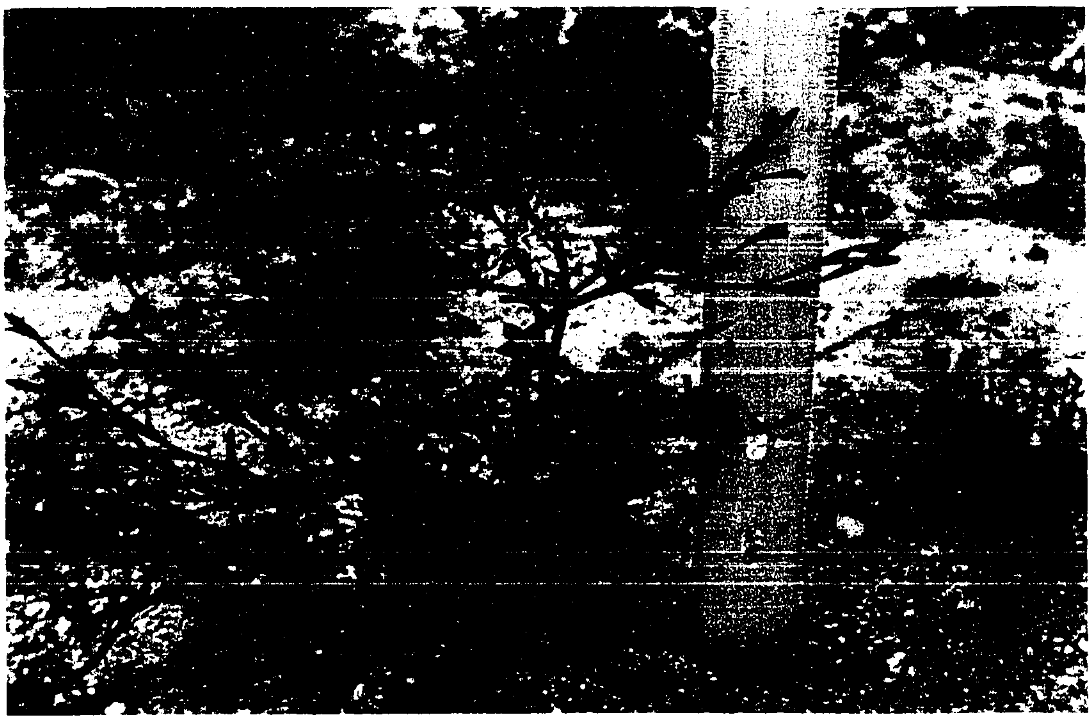


Figure 1. Gilia tenuiflora ssp. arenaria in adult flowering stage.

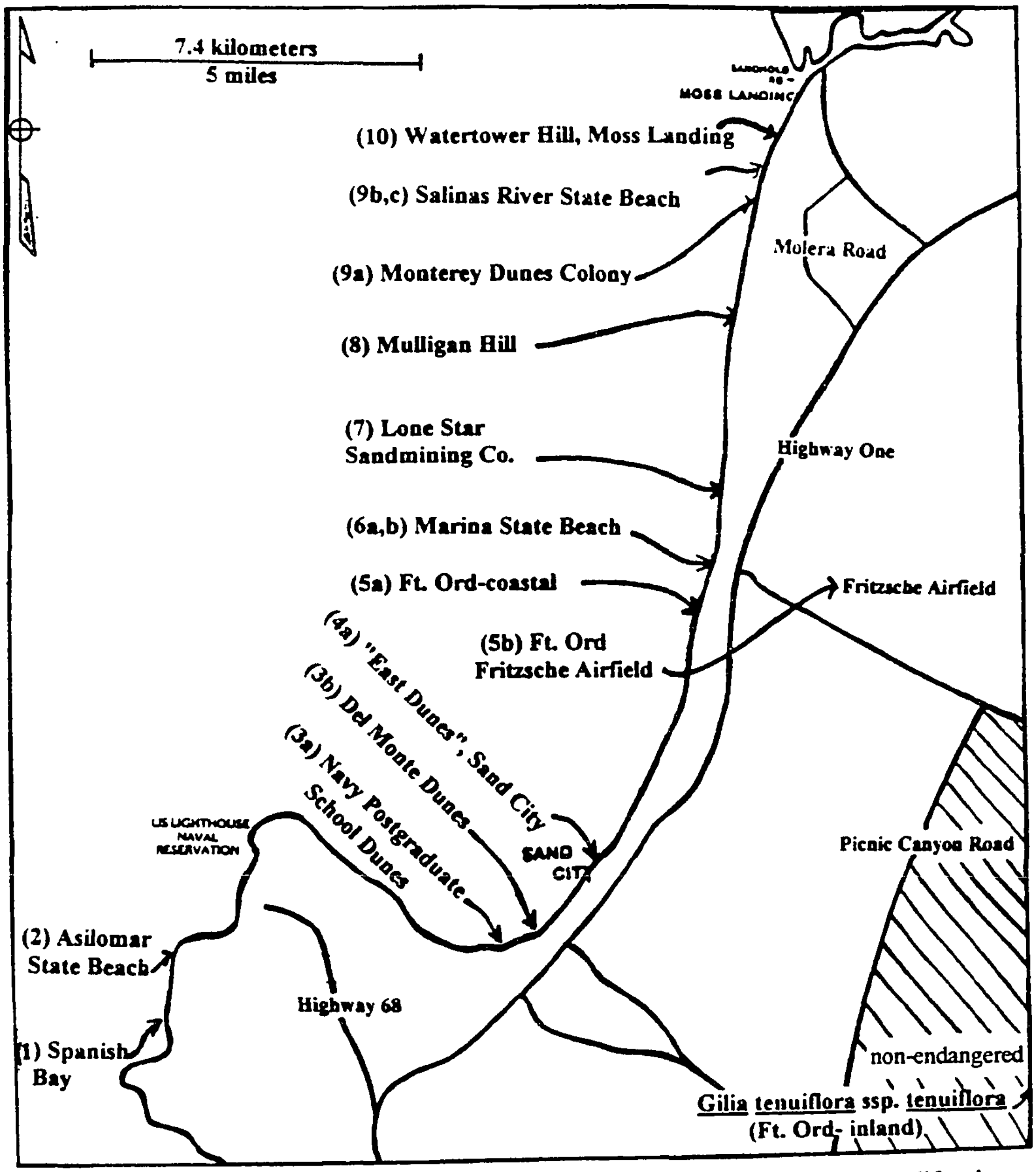
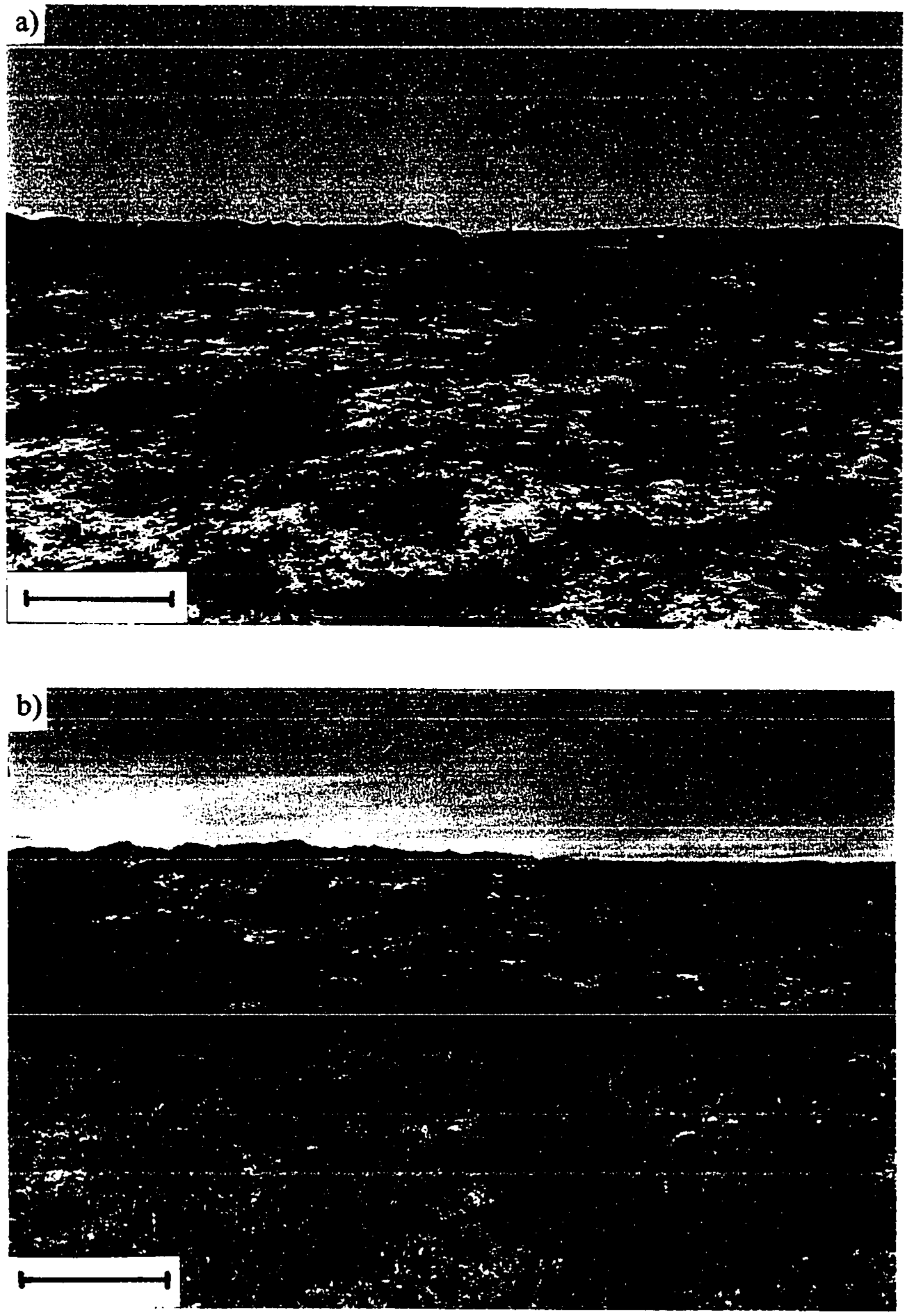


Figure 2. Distribution of Gilia tenuiflora ssp. arenaria around Monterey Bay, California in May 1993. ( ), population numbers used in text.

a)



b)

Figure 3. Characteristic habitat near naturally occurring sand gilia.
a) Site 4 - East Dunes, Sand City and b) Site 9b - Salinas River State Beach (plots located along top of ridge). Scale = 1 m.

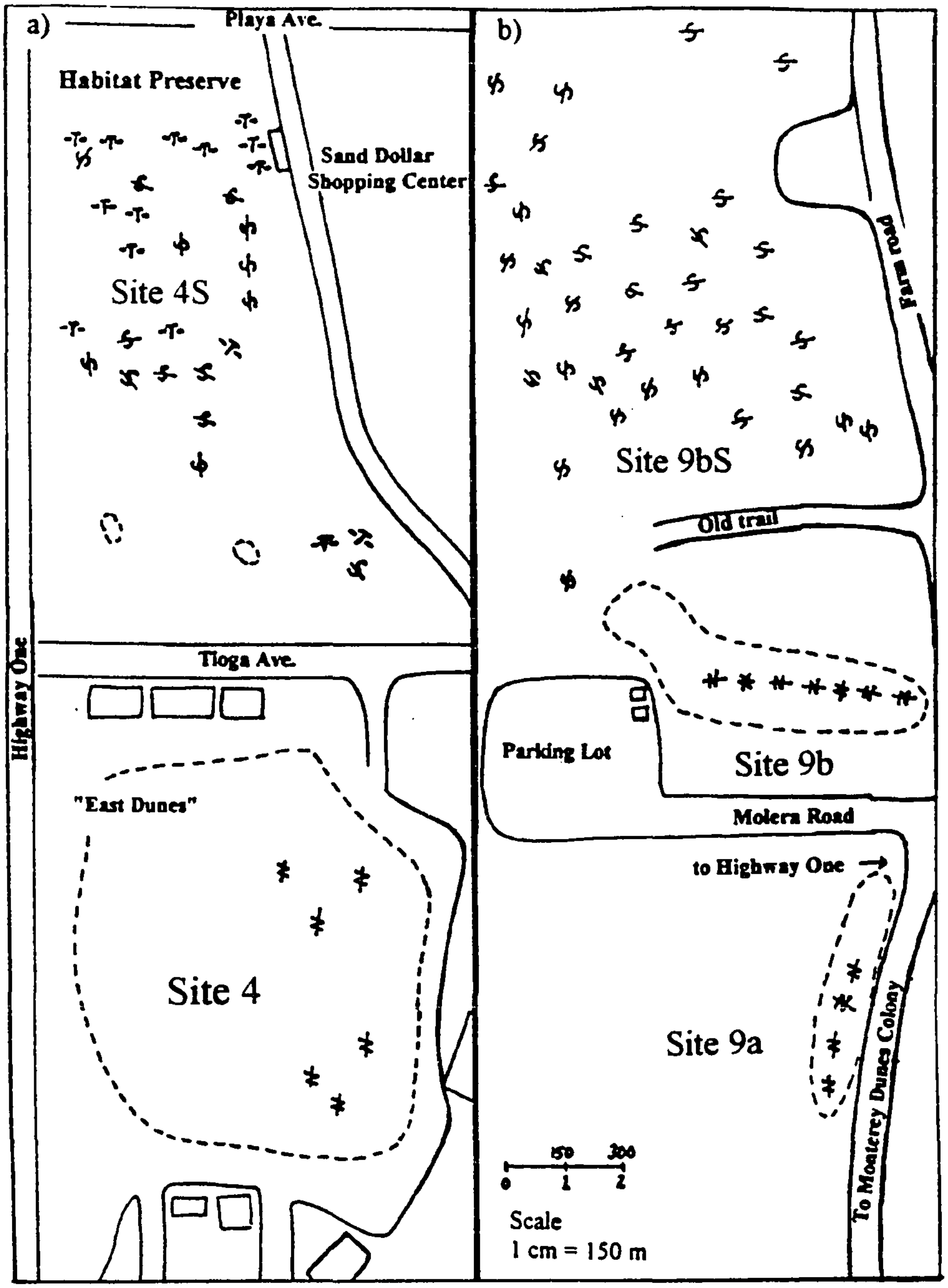


Figure 4. Location of naturally occurring Gilia tenuiflora ssp. arenaria, seeded plots and transplanted areas. Naturally occurring Gilia (⁘); field growth plots (−N−); seeded plots (−S−); transplanted individuals (−T−). a) Site 4S: Habitat Preserve at Sand Dollar Shopping Center (top), and Site 4: East Dunes, Sand City (bottom); b) Site 9bS: Salinas River State Beach (top), and Site 9a&b: Salinas River State Beach and Monterey Dunes Colony (bottom). Top and bottom locations are continuous.

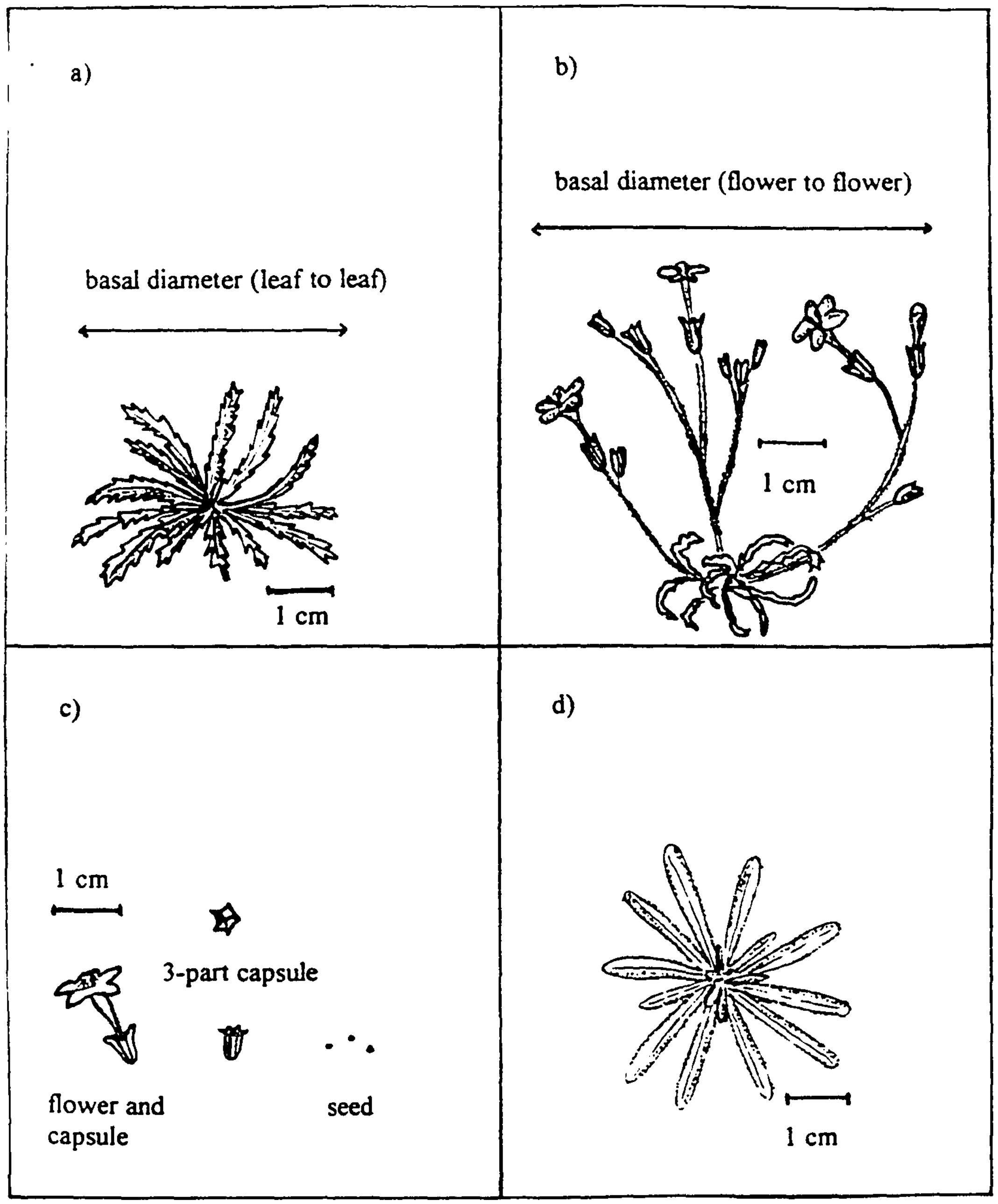


Figure 5. Life stages of Gilia tenuiflora ssp. arenaria and basal rosette of Cryptantha leiocarpa (similar to Gilia in juvenile stage). a) Basal rosette-juvenile stage (diameter measured from leaf tip to leaf tip) b) Budding and flowering adult (diameter measured from flower to flower) c) Flower, capsule, and seed d) Popcorn flower (Cryptantha leiocarpa).

Figure 6. Seeded plot at Salinas River State Beach (Site 9bS) with 25-50% associated vegetation cover. Ruler = 35 cm long.

Figure 7. Germination of Gilia tenuiflora ssp. arenaria in a tray of supercells®. Scale = 7.5 cm.

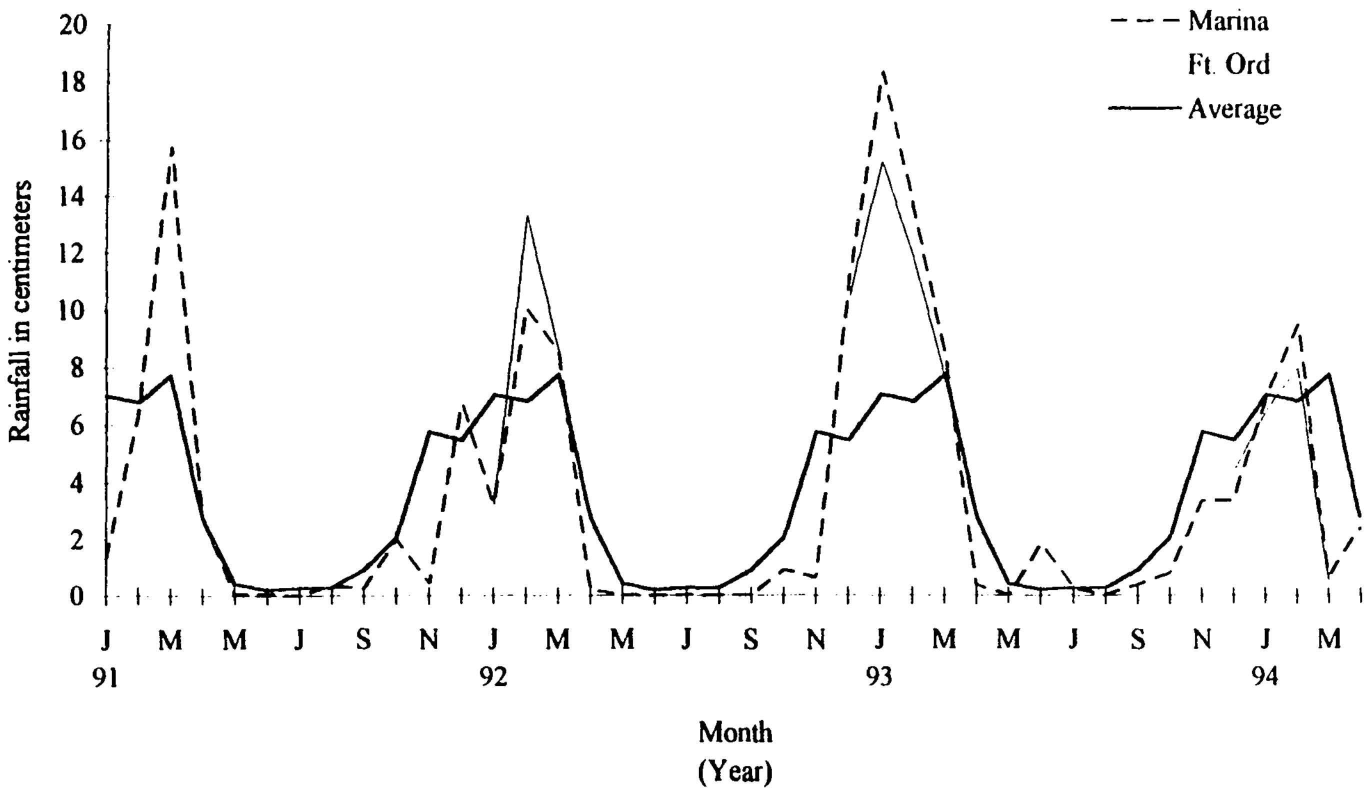


Figure 8. Rainfall (cm) at Marina (Reservation Road, Station 2B) and Fort Ord (Fort Ord Station 36° 42' N, 121° 45.6' W) compared to 24 year average (Reservation Road, Station 2B). Source: Marina Coast Water District (1970-1994) and Naval Postgraduate School, Dept. of Meteorology (1991-1994).

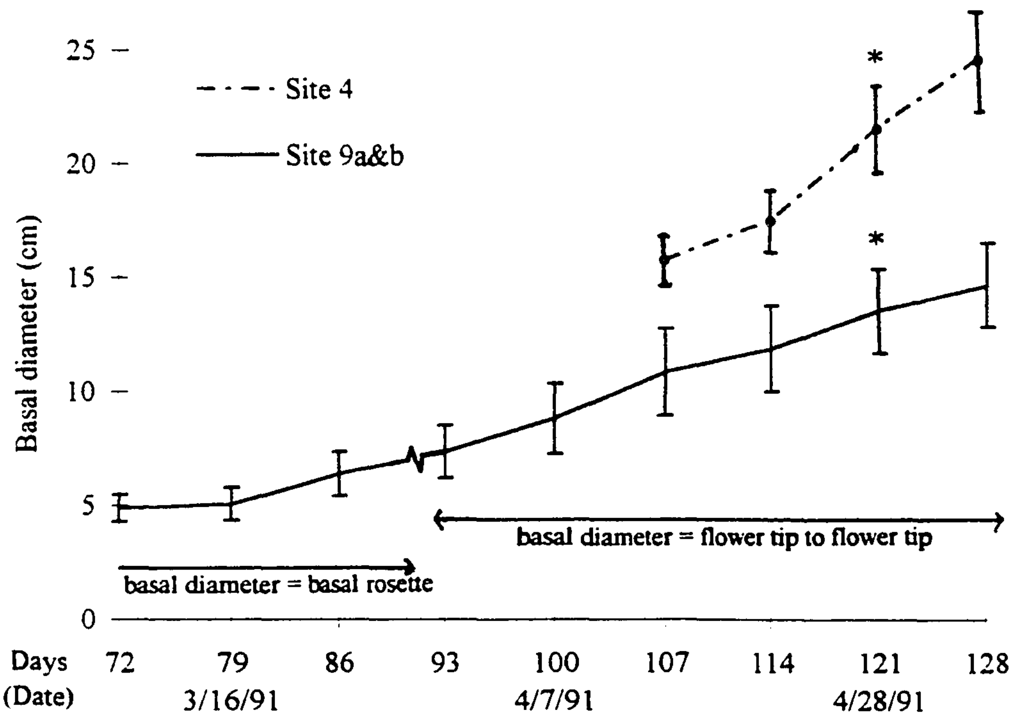


Figure 9. Weekly mean basal diameter (cm) of naturally occuring Gilia tenuiflora ssp. arenaria at Site 4 (n = 6 plots) and Site 9a&b (n =11 plots). Original plots at Site 4 were buried by sand and new plots were started on 14 April 1991. S.E. indicated by vertical lines and calculated from plot means. *, time used for statistical comparisons. Days estimated from life stage of plant.

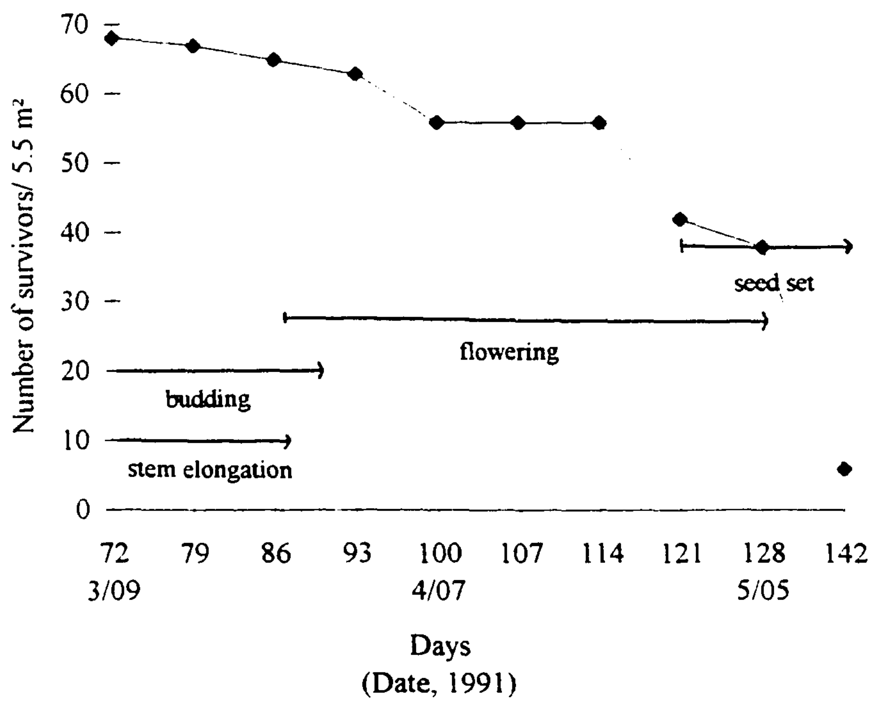


Figure 10. Survivorship of naturally occurring Gilia tenuiflora ssp. arenaria at Site 9a&b (11 plots) beginning 3/09/91. Days estimated from life stage of plant. Early mortality not recorded due to late starting date.

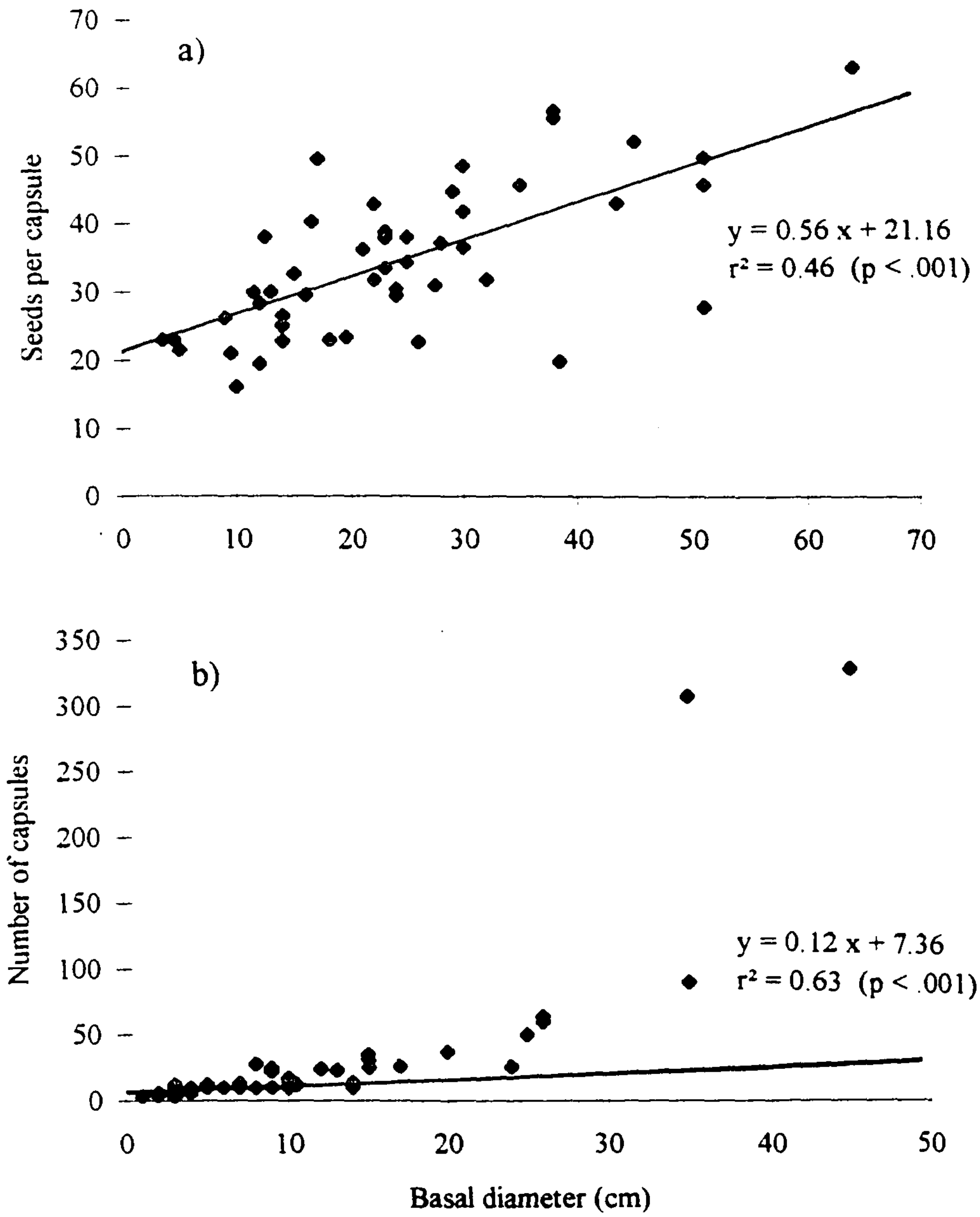


Figure 11. a) Number of seeds per capsule versus plant size (basal diameter in cm) of Gilia tenuiflora ssp. arenaria. b) Number of capsules versus plant size (basal diameter in cm).

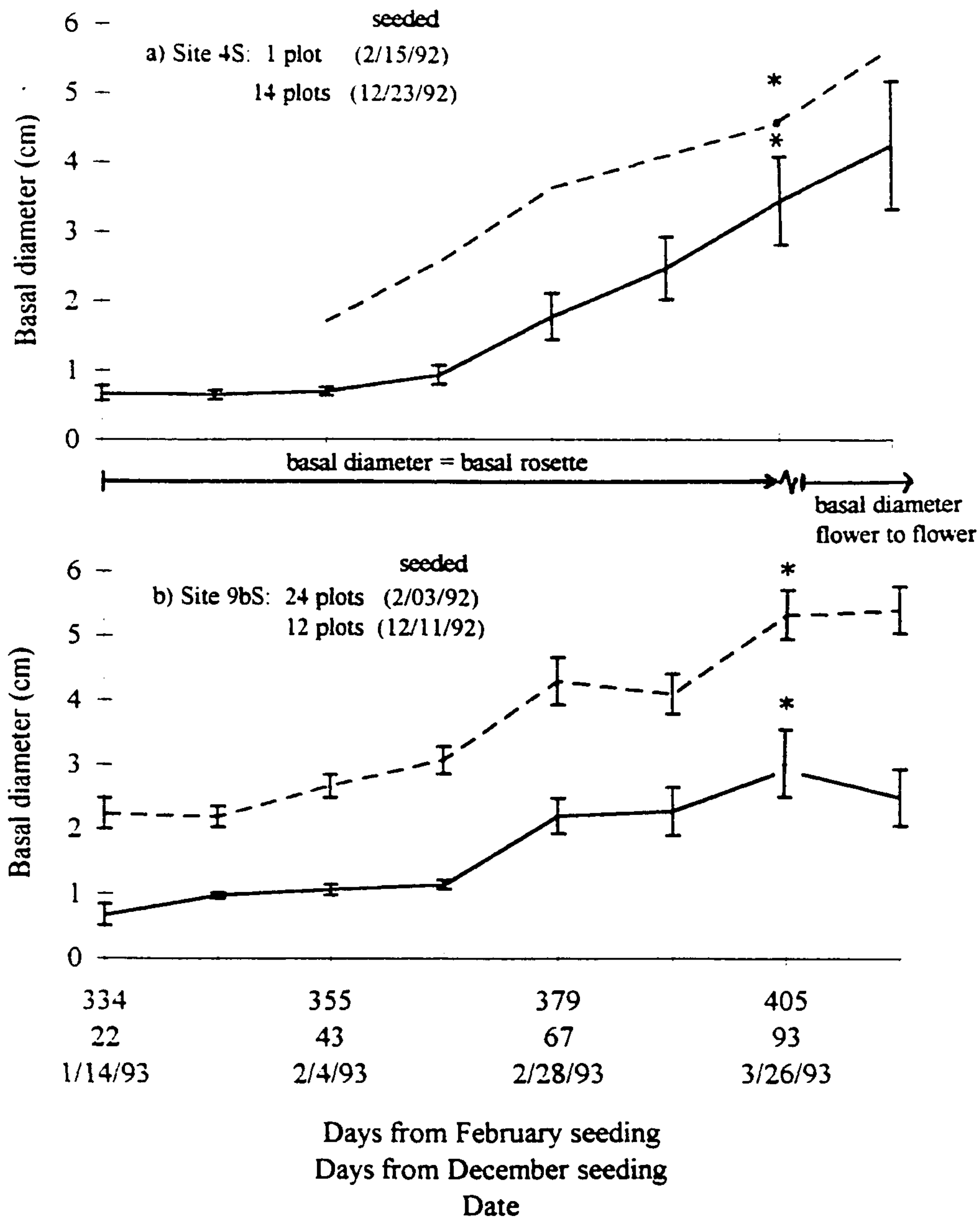


Figure 12. Growth of plants in seeded plots: a) Mean basal diameter (cm) in 15 plots at Site 4S. Single plot seeded on 2/15/92 not found until 2/4/93. b) Mean basal diameter (cm) in 36 plots at Site 9bS. S.E. calculated from plot means and indicated by vertical lines. *, time used for statistical comparisons.

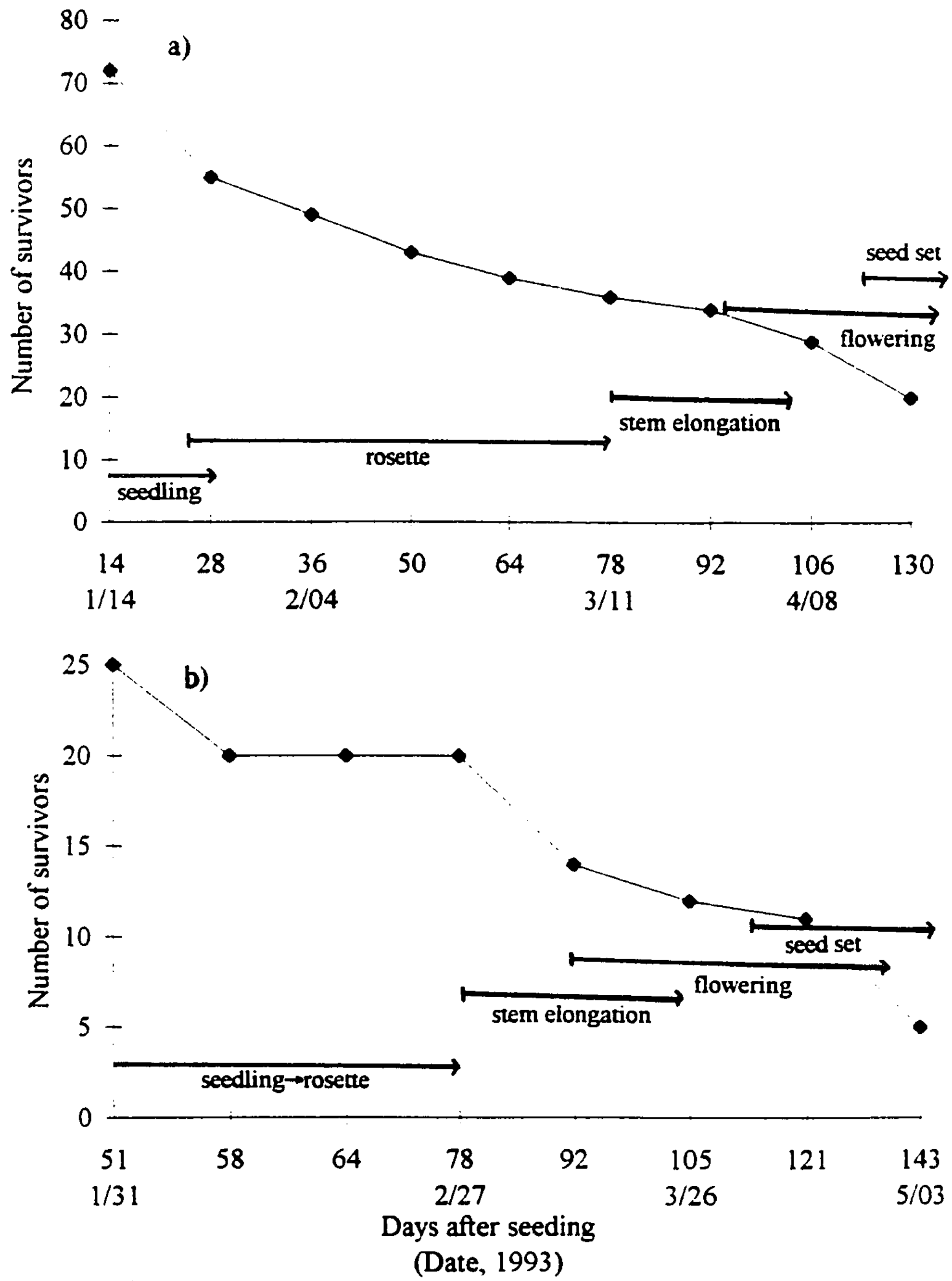


Figure 13. a) Survivorship of Gilia tenuiflora ssp. arenaria.
a) Fourteen plots seeded 12/23/92 at Site 4S ($7m^2$).
b) Twelve plots seeded 12/11/92 at Site 9bS ($6m^2$).

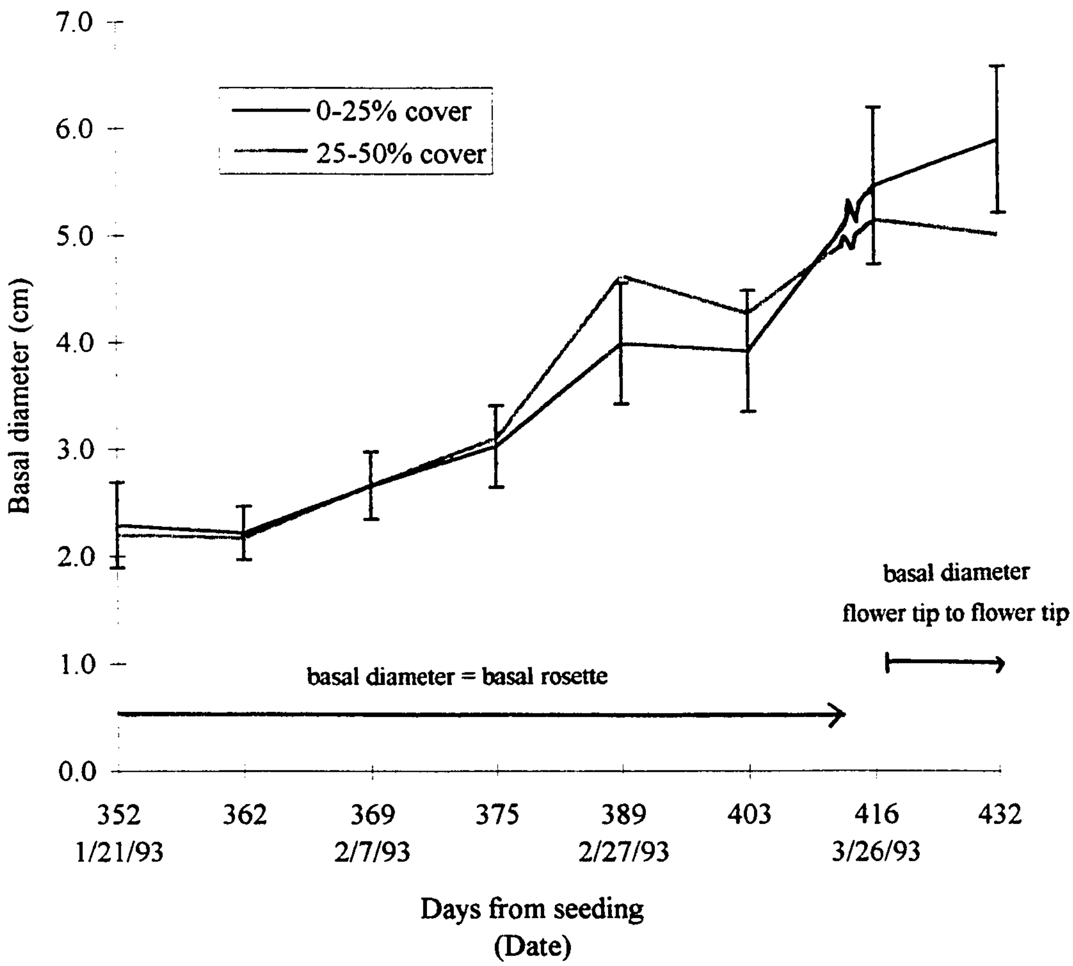


Figure 14. Relationship of percent cover of associated vegetation to basal diameter (cm) of Gilia tenuiflora ssp. arenaria for 24 plots at Site 9bS. S.E. calculated from mean of plot means and indicated by vertical lines. *, time used for statistical comparisons.