# Distribution, Growth Analysis and Reproductive Biology of Cape Ivy (*Delairea odorata* Lem. syn *Senecio mikanioides* Walp.) in California

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# ACKNOWLEDGEMENTS

My intention with this research was to bring some clarity to the management of an invasive species, in hopes of better protecting California's native plant heritage. I had no way of knowing at the outset how many people would help me along the way. The first inspirations for choosing Cape ivy as a research subject were members of the California Invasive Plant Council (Cal-IPC), with their reports of the relentless march of Cape ivy across California and their heroic efforts to hand-pull it all out by the roots. John Randall also encouraged my interest in studying invasive species by helping me make the connection between their control and the conservation of natives. When I decided to go to graduate school and found out that no one was studying Cape ivy, I was fortunate to be welcomed into Joe DiTomaso's office. He enthusiastically agreed when I suggested a study of Cape ivy and provided the unwavering support I needed during the difficult spots in the project.

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## **Abstract**

The distribution, growth and reproductive biology of Cape ivy (*Delairea odorata* Lem. syn. *Senecio mikanioides* Walpers) was the focus of this research. Cape ivy, a vine native to South Africa, is an invasive weed expanding its range in coastal California. A distribution map of California Cape ivy was created, and locations of stipulate or non-stipulate morphological types were compiled. We found Cape ivy occurring in seven plant community types, and predicted that it should occur in five more, refuting the assumption that Cape ivy is an exclusively riparian weed. GIS analysis indicated that in California Cape ivy occurs at elevations between 0 and 891 m, at annual mean temperatures between 10.5 and 17.7°C and in areas with annual precipitation between 232 and 2270 mm. CLIMEX and GARP computer models predicted Cape ivy's potential expansion into moist areas of the San Joaquin Valley and Sierra Nevada foothills. A growth analysis study of four Cape ivy populations grown at varying shade levels gave insight into its genetic structure and growth requirements. Results indicated that there was phenotypic plasticity in growth response to light levels, and that genetic variation was present among and within populations. The growth experiments showed that Cape ivy could survive in shaded areas of inland California that receive sufficient summer moisture. The third research area was Cape ivy reproductive dynamics and seed biology. Cape ivy was shown to be self-incompatible and able to produce viable seed throughout California. Over a three year period, seed from a wide geographic range of populations was sampled and 66% of 104 locations produced viable seed. Seeds weighed between 0.02 and 0.39 mg, and the highest percentage of germination occurred in seeds above 0.20 mg.  Optimal germination occurred between 17 and 25ºC and seeds germinated in light or dark.  Seeds germinated when planted on the soil surface or when buried 1 cm, but did not emerge from deeper burial. Similarly, stem fragments on the soil surface or buried 2 cm emerged, but those buried deeper did not.  The final chapter concludes with a discussion of the management implications of viable, wind-dispersed seed production.

# CHAPTER 1

## Introduction to the Taxonomy, Distribution and Biology of Cape Ivy

### INTRODUCTION

Invasive species are recognized as a serious threat to biological diversity, second only to direct habitat loss and fragmentation (Baker 1986, Mooney and Drake 1989, Bossard et al. 2000, Committee on the Scientific Basis for Predicting the Invasive Potential of Nonindigenous Plants and Plant Pests in the United States 2002). Impacts of invasive plants on wildlands include alteration of ecosystem processes, displacement of native species through competition or alteration of habitat structure, support of nonnative animals, and alteration of gene pools through hybridization (Barrett and Richardson 1986, Bazzaz 1986, Newsome and Noble 1986, Heywood 1989, Noble 1989). Throughout the last century large numbers of extremely damaging plants have been introduced into and allowed to become established in the United States (Mooney et al. 1986, Cox 1999, Mullin et al. 2000).

One example of an invasive species causing considerable impacts to native plants is Cape ivy (*Delairea odorata* Lem.; syn. *Senecio mikanioides* Walpers), a vine native to South Africa that is expanding its range in coastal California and Oregon. The California Invasive Plant Council (Cal-IPC) lists the species on its High List: Species with severe ecological impacts on ecosystems, plant and animal communities, and vegetational structure (Cal-IPC 2005). In a recent study, Cape ivy was found to be associated with significant reductions in vascular plant species richness (Alvarez and Cushman 1997). As another example of its threat to natural communities, a Cape ivy population of 3.5 ha expanded 87% between 1987 and 1997 in the Golden Gate National Recreation Area (GGNRA) in Marin County, California (Alvarez 1997). Based on the current exponential rate of spread, it was estimated that within the next decade more than 400 ha will be infested if no action is taken (Alvarez and Cushman 1997).

## CAPE IVY PLANT DESCRIPTION

Cape ivy is a perennial vine with a glabrous, waxy surface and alternate leaves. The leaf blades are three to eight centimeters long and petioles are often the same length. Leaves are round with five to nine sharp palmate lobes, with hastate or cordate lobes at the base. There are two morphological types, one with and one without rounded stipules (called auricles in South African literature). The eight to twelve flowers per discoid head have a bright yellow, funnel-shaped, tubular corolla, with five ovate revolute lobes. There are eight to nine free phyllaries, three to four millimeters long, with blackish-purple tips, surrounded by one to three small bractioles. The anthers are ecaudate (not tailed), the filaments standing off a little to form a cone. The style is filiform with a bifid stigma, distinctly flaring upward from below, with tips truncate and fimbriate. The pappus is coroniform and uniseriate with bristles flaring out and covered with very thin short stiff hairs. Twenty or more discoid flower heads are produced terminally or axillarily in a corymbose inflorescence. The fruit is oblong, cylindrical, and hairy on the striations (Lemaire 1844, Harvey 1894, Hickman 1993).

Lawrence (1985) studied floral biology of *Senecio*, including Cape ivy. She stated that inflorescence development is determinate with central or apical capitula maturing first, but the sequence of anthesis within capitula (flower heads) is indeterminate as marginal florets mature first. Bisexual florets, such as those in Cape ivy, are protandrous. Anthers dehisce while the florets are still closed, but self-pollination at this stage appears unlikely as the style branches are closely appressed and held together by the narrow corolla. This is called a gynostegium, where the style replaces the filament as the anther-presenting organ (Richards 1997). Pollination only occurs after the style branches have extended beyond the collar of anthers, at which point the branches spread apart and expose the receptive stigmatic surface. In *Senecio*, presentation of pollen appears to depend on dehydration of the anthers (see Figure 1.1).

Lawrence (1980) listed the chromosome number of Cape ivy as 2n = 20 from material collected in Australia. She reasoned that the effective base chromosome number of the genus on a world scale is n = 10. If that is the case, then Africa appears to be the center of origin of the tribe. Africa contains 16 of 33 species studied with n = 10. All but one of the 14 African genera within the Senecioneae have base chromosome numbers equal to 5 or 10. Cape ivy in Australia also has the ancestral African number of chromosomes. The chromosome number is also listed as n = 10 by Ornduff et al. (1963) and Jeffrey (1992). In Barkley (1978) the chromosome number is listed as n = 20 and this may be the origin of the 2n = 40 reference listed in *The Jepson Manual* (Hickman 1993).

## CAPE IVY TAXONOMY

Cape ivy has a confusing taxonomic lineage, perhaps due to the almost simultaneous publication of two distinct names in two languages. The first scientific description of the genus *Delairea* Lem. was published in 1844 (Lemaire 1844). The author described the genus as “distinct without close relatives, somewhat near *Cacaliae* and *Senecioni*. From the *Senecioni* it differs in the uniseriate pappus, strictly homogamous capitula, etc., and by a dual habit.” In 1845 Walpers published a description of a plant he called *Senecio mikanioides* Otto (Walpers 1845). According to the article, the plant was already widely cultivated in Germany and had been mentioned, but not formally described, by Otto in a previous publication. Therefore, the correct citation for the plant is either *Senecio mikanioides* Otto ex Walpers or *Senecio mikanioides* Walpers, which appears in the current Jepson Manual (Hickman 1993). In a later publication by Harvey (1894), the plant was included in *Senecio* and was again called *Senecio mikanioides* Otto, hence the commonly cited name *Senecio mikanioides* Otto ex Harv.

In 1986 and again in 1992, Jeffrey published a revision of the *Senecio* genus re-assigning Cape ivy to *Delairea odorata* Lem. based on the campanulate corolla limb and other morphological characteristics. He believed the species was more closely allied with *Mikaniopsis*, *Cissampelopsis*, and *Austrosynotis* than *Senecio* (Jeffery 1986, 1992). Vincent and Getliffe (1992) studied South African *Senecio* species using the concept of “uniform criteria” proposed by Jeffrey (1977) and retained Cape ivy in *Senecio* (Jeffery 1977, Vincent and Getliffe 1992). They refer to it as *S. mikanioides* [Otto ex] Harvey (=*Delairea odorata* Lem., *fide* Jeffrey, 1986:933). More recently, Bremer (1994), in a summary work on the cladistics and classification of the entire Asteraceae, listed Cape ivy as *Delairea odorata* Lem. Finally, Barkley (1999), in a synoptical key and annotated catalog of the genera for inclusion in the Flora of North America North of Mexico, also included the species as *Delairea* Lem. after referring to it in earlier publications as

*Senecio mikanioides* (Barkley 1978, 1999). In the on-line version of the Jepson Manual (http://ucjeps.berkeley.edu), Barkley (1978) is listed as the authority for an update of the name in the next version of the *Flora of California*. It appears that taxonomists are converging on the name *Delairea odorata* Lem., though many regional floras in California and throughout the world still use the name *Senecio mikanioides* under various authors. Therefore, it would seem advisable to publish using both names until *Delairea* is more widely recognized.

## NATIVE DISTRIBUTION

In both the original descriptions of Cape ivy (Lemaire 1844, Walpers 1845), the specimens examined were wrongly identified as originating in Mexico. It is now known that Cape ivy is native to South Africa. In the *Flora Capensis*, Harvey lists it as occurring in the forests of Uitenhage, Albany and Caffraria as well as being cultivated in Cape and European gardens (Harvey 1894).

Hilliard (1977) includes Cape ivy in his work *The Compositae of Natal*. On its native distribution he writes:

> Widespread, but not much collected, from the Cape peninsula through the southern and eastern Cape to Natal as far north as Nkandia, Nhlazatsche Mt. and the Biggarsberg north of Ladysmith; also recorded from Mohaleshoek in Lesotho. Grows on forest margins or in the forest, in Natal between c. 800 and 1900 m above sea level.

Grobbelaar et al. (1999) conducted research into the current distribution of Cape ivy in South Africa between 1996 and 1999. They visited five major herbaria in South Africa and compiled a list of 81collection locations, ranging in collection date from 1862 to 1975. The non-specific herbarium specimen locations in Figure 1.2 refer to specimens without precise location information that were given approximate map locations. In 1998, Cape ivy locations were mapped in conjunction with surveys to collect potential biological control insects (Figure 1.2). During the surveys, 41 locations were visited and the known native range of the species was increased with a record in the Mpumalanga province 250 km north of previously collected locations.

## INVASIVE DISTRIBUTION

Outside its native range, Cape ivy is known to occur in Europe, Australia, New Zealand, Hawaii, and South America, as well as western North America (Parodi 1959, Abrams and Ferris 1960, Palhinha 1974, Zangheri 1976, Pignatti 1982, Haselwood and Motter 1983, Hirano 1983, Webb et al. 1988, Fagg 1989, Jacobi and Warshauer 1992, Scott and Delfosse 1992, Hickman 1993, de la Torre 1998, Gallo 2000). A comprehensive map of the worldwide distribution compiled from the literature is presented in Figure 1.3. Figure 1.3 also includes actual location data for California and South Africa.

Regarding Cape ivy’s invasive distribution, Hilliard (1977) writes:

> Cultivated as a window plant in Europe, it has escaped in parts of the Low Countries and on the south coast of England; it does not flower there in the open, but does so in the warmer Scilly Isles. Also on St. Helena, where it is probably introduced. It is also established around Buenos Aires, Argentina, and in South Australia and Victoria.

The *Flora Europaea* lists Cape ivy as occurring in the Azores, Britain, Corsica, France, Spain, Italy and Portugal (Chater and Walters 1976). Interestingly, it is not reported to be naturalized in Germany, even though Walpers (1845) reports it as “spread to a great number of gardens and also cultivated quite often indoors.” Cape ivy was also reported to be naturalizing in Croatia (Gallo 2000). In Spain, the plant is an ornamental escape in waste places, abandoned gardens and along paths (Perez 2002). It is known from Spanish provinces on both the Atlantic and Mediterranean coasts: Galicia, Asturias, Cantabria, País Vasco, Andalucia, Barcelona, Terragona, Castellón, Alicante, Almeria, and the Balearic Islands (see Figure 1.4). In September 2001, I visited northern Spain and Portugal and collected Cape ivy distribution data. The locations mapped during that survey are also included in Figure 1.4.

In Australia, Cape ivy is found in all regions except the Northern Territories (Blood 2003) and it is extensively cultivated and naturalized in Victoria, Tasmania, South Australia and New South Wales (Everist 1974). New Zealand, where it was first introduced in 1870, now bans the entry of Cape ivy (Owen 1996, Blood 2003). It grows on forest margins in coastal areas on the North and South islands as well as Stewart Island.

Cape ivy was first collected on the big island of Hawaii in 1910 (Wagner et al. 1990). It is now naturalized in relatively dry areas primarily in the North and South Kona districts of Hawaii, but also sparingly on Maui (Haselwood and Motter 1983, Wagner et al. 1990, Jacobi and Warshauer 1992). The Hawaiian Ecosystems at Risk Project reports it as occurring on Hawaii and Maui with an unconfirmed report on Oahu (University of Hawaii 1996). They also consider it as potentially occurring on all the other islands.

In South America, Cape ivy occurs in Argentina around Buenos Aires (Parodi 1959, Hilliard 1977) and in dune vegetation and coastal scrub in the Mediterranean climate zone of Chile (Montenego et al. 1991).

## CALIFORNIA AND OREGON DISTRIBUTION

In North America, Cape ivy is known to occur in California and Oregon, with one herbarium specimen reported from Richland County, Montana (http://invader.dbs.umt.edu/risk/results.asp). Cape ivy is listed in all the modern floras of California as well as in the regional floras of coastal areas (Jepson 1951, Abrams and Ferris 1960, Thomas 1961, Hoover 1970, Howell 1970, Munz 1974, Smith 1976, Beauchamp 1986, Smith and Wheeler 1992, Hickman 1993, Junak et al. 1995, Best et al. 1996, Matthews 1997). It is assumed to have been introduced into North America through the horticultural trade (Alvarez 1995). Listed in older cultivated plant manuals (Bailey 1949), it was widely available as a nursery plant as recently as the 1970s (Faust 1973, Kindersley 1979), and in 2004, was being sold in the Emeryville, California, Home Depot (Wall 2004). The earliest documentation of Cape ivy in California is from 1892 in Strawberry Canyon, just east of U.C. Berkeley (Accession ID UC36003).

Table 1.1 was derived from specimens housed at a number of California herbaria (UC Davis, Berkeley, Santa Barbara, Riverside, and Irvine; Santa Barbara Botanic Garden, Rancho Santa Ana Botanic Garden, and California State Universities Chico and Humboldt). Davis, Berkeley, Rancho Santa Ana and Humboldt herbaria were visited, and the rest of the collections were viewed electronically using the University and Jepson Herbaria SMASCH Accession database (http://www.mip.berkeley.edu/www_apps/smasch/smasch_accession.html). Table 1.1 contains the collection date, County, Herbarium, collection and accession numbers, phenology, vegetative type (stipulate or non-stipulate), location and elevation. Figure 1.5

is a graph of the year a specimen was first collected in each California county. One collection was made in San Diego County in 1992, though this was a mis-identified specimen with ray florets. Although Cape ivy is listed in the San Diego flora (Beauchamp 1986), there were no other collections in the herbaria surveyed.

## CONTROL AND MANAGEMENT

Given Cape ivy's established presence in California and its known impacts to native plant communities, efforts have focused on both mechanical and chemical control.

Golden Gate National Recreation Area (GGNRA) began managing its Cape ivy populations in the 1990s following a mapping study that showed an increase from 8.8 to 67.3 acres infested between 1987 and 1996 (Alvarez 1997). Their methods involve mapping and prioritizing existing infestations, and containment or removal based on the sensitivity of habitats infested. Containment is accomplished by cutting 1 to 2 meter wide swaths around infested areas, and containment lines are surveyed at regular intervals to make sure infestations are not spreading. All patch removal is done by hand, with native vegetation cleared to at least 0.5 meter above the ground. A similar, but more comprehensive mechanical control methodology is underway in the Santa Cruz Mountains (Moore 1997). Moore uses what he terms the "scorched earth" method in which he clears all native and non-native vegetation to ground level and then returns to hand pull the re-sprouts.

In 2005, two preliminary studies on control of Cape ivy with flaming were presented at the California Invasive Plant Council (Cal-IPC) Annual Symposium. Bossard et al. (2005) found that after six flaming treatments conducted between

November 2004 and July 2005, only plants in heavily shaded areas were controlled. In partial to full sun locations the Cape ivy density decreased, but the species was not eradicated in one season. Baxter and Bromberg (2005) incorporated a flaming trial into their existing Cape ivy management program. Vegetation was removed from the site in fall 2004 and the ground was raked to expose Cape ivy fragments and roots. Three months later re-sprouting Cape ivy was treated with a pass of a propane flaming “wand” at 0.3 to 0.4 meters above the plant. Trials of one, two and three flaming passes were conducted and cover in the flamed plots was assessed afterward. They also concluded that flaming applications were able to reduce cover of Cape ivy, but not eradicate it.

A few studies have been conducted on Cape ivy control with herbicides. The first was performed in Australia where clopyralid (Lontrel®) was used with either a rope-wick or controlled droplet application (Fagg 1989). Control was obtained within 11 weeks of treatment, but the plots were re-colonized 50 to 70% of the original infestation size after 12 months in the absence of follow-up management. The study also examined the effect of clopyralid on native species. A few species in the Solanaceae, Asteraceae and Urticaceae were damaged but were able to re-sprout; all these are families that are known to be damaged by clopyralid.

In a similar study in 1999, Spanish researchers conducted an experiment using combinations of glyphosate, clopyralid, and tribenuron (de la Torre 1999, de la Torre and Arbesu 1999). The best control was found with a combination of glyphosate and tribenuron. These experiments applied the herbicides initially and then again after 10 weeks. During a site visit in September 2001, all the plots were observed to be covered again with Cape ivy as no follow-up control had been done after the initial herbicide sprays.

A third herbicide and solarization control study was performed in California at the Presidio in San Francisco (Bossard and Benefield 1995, Bossard et al. 2000). Treatments were : (1) triclopyr alone, (2) weed whipped and then followed by triclopyr, (3) triclopyr and glyphosate combination, (4) control, and (5) solarized using clear plastic. After one year, they found a difference between the control plots and treatments (2) or (3), but no difference between control and treatments (1) or (5). Another treatment was applied at one year on the (3) treatment blocks and eradication was achieved in the second year. Forbert (1998) also recommended using a mixture of glyphosate and triclopyr.

## PREVIOUS RESEARCH ON CAPE IVY BIOLOGY

The available information on Cape ivy biology is mostly unpublished. Sources include class projects, newsletter articles, notes and personal communications. These sources describe the average growth rate of a single population, size of stem pieces required for propagation, drought tolerance, potentially toxic alkaloid production, and impacts on native plant and insect species richness in infested areas (Stelljes and Seiber 1990, Bossard and Benefield 1995, Catalano et al. 1996, Alvarez 1997, Fisher 1997). Two theses are also available on Cape ivy biology (Alvarez 1995, Rolando 2000) and these will be discussed in subsequent chapters of this dissertation.

## SUMMARY OF OBJECTIVES FOR EACH CHAPTER

The following chapters in this dissertation provide basic biological information on the distribution, growth and reproductive biology of Cape ivy in California. Chapter 2 presents a distribution map for California and Oregon. In addition to point data, information on the type of vegetation Cape ivy is associated with, as well as the presence or absence of stipules is included. Chapter 3 gives insight into the genetic structure and growth requirements of Cape ivy in California and offers a comparison of the growth rate of four populations at varying shade levels. The fourth chapter focuses on the reproductive dynamics and seed biology of the species. Cape ivy is shown to produce viable seed throughout California and is also shown to be self-incompatible. The results of these studies increase our knowledge of the distribution, growth parameters, and reproductive dynamics of a highly invasive wildland weed species.

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**Table 1.1. Cape Ivy Herbarium Records from Ten California Herbaria[1]**

| Date | County | Herbarium | Collection #/ Accession # | Phenology[2] | ST/NS[3] | Location Where Specimen was Collected | Elevation (ft) |
|---|---|---|---|---|---|---|---|
| 2/8/1892 | Alameda | UC | UC36003 | | | Berkeley | |
| 1/26/1899 | Alameda | DAV | 023795 | flower | ST | Berkeley | |
| 2/?/1900 | Alameda | UC | UC36002 | fruit | | Berkeley | |
| 3/1/1902 | Santa Clara | UC | 318/ UC91455 | fruit | | Foothills near Stanford University | |
| 3/1/1902 | Santa Clara | RSA-POM | 5779 | flower | NS | Foothills near Stanford University | |
| 1/15/1905 | Los Angeles | UC | 1194/ UC166862 | fruit | | Pasadena | |
| 7/10/1906 | Los Angeles | RSA-POM | 94677 | vegetative | ST | Rustic Canyon, Santa Monica Mtns., western Los Angeles County | |
| 1/10/1928 | Sacramento | DAV | 2080 | flower | NS | Sacramento, Junior College grounds | |
| 12/31/1930 | Monterey | RSA-POM | | flower | ST | Asilomar State Beach | |
| 1/1/1936 | Marin | UC | 1433/ UC1614418 | | | Bolinas Mesa, 3 miles north of Bolinas | |
| 1/1/1936 | Marin | RSA-POM | 603775<br>29640 | vegetative | ST | Garzoli Ranch, Bolinas Mesa on fence | |
| 1/25/1942 | Humboldt | UC | 17054/ UC1223154 | | | Near Ferndale along Russ Creek | |
| 1/25/1942 | Humboldt | RSA-POM | 167401 | flower | ST | Near Ferndale along Russ Creek, climbing among willows and alders | |
| 1/5/1946 | Ventura | RSA-POM | 40236 | flower | ST | Ventura River between Foster Park and Ventura | |
| 2/28/1948 | Monterey | RSA-POM | 49717 | flower | ST | Carmel Highland above Highlands Inn | |
| 2/28/1948 | Monterey | UCR | 7852/ UCR64444 | flower | ST | Carmel Highland above Highlands Inn | |
| 8/25/1957 | Monterey | RSA-POM | | vegetative | ST | F St. along gulch at 10th and Junipero Streets | |
| 2/3/1957 | San Francisco | RSA-POM | | flower | NS | Presidio, gully above Baker's Beach, below Lincoln Blvd. | |
| 1/19/1958 | San Francisco | UC | 58000/ UC1106152 | | | Russian Hill, north slope | |
| 1/19/1958 | San Francisco | RSA-POM | 118941 | flower | | Russian Hill, north slope | |

**Table 1.1. Cape Ivy Herbarium Records from Ten California Herbaria[1]**

| Date | County | Herbarium | Collection #/ Accession # | Phenology[2] | ST/NS[3] | Location Where Specimen was Collected | Elevation (ft) |
|---|---|---|---|---|---|---|---|
| 1/28/1958 | San Luis Obispo | RSA-POM | 125882 | flower | ST | South end of Cambria on banks of Santa Rosa Creek, closed cone pine forest community | |
| 2/13/1958 | San Luis Obispo | JEPS | 2813/ JEPS99096 | flower | | Santa Rosa Creek, Cambria | |
| 12/18/1958 | San Mateo | JEPS | 7509/ JEPS23534 | flower | | Along Skyline Blvd., just west of San Bruno along roadside | |
| 12/18/1958 | San Mateo | RSA-POM | | flower | NS | Along skyline west of San Bruno | |
| 12/27/1959 | Marin | JEPS | 14736/ JPES30399 | flower | | Inverness | |
| 12/27/1959 | Marin | RSA-POM | 145213 | | | Unknown location | |
| 12/13/1959 | Santa Clara | JEPS | 8517/ JEPS30903 | | | San Francisquito Creek between University Ave. and Bayshore Freeway, Palo Alto | |
| 12/31/1959 | Santa Clara | UC | 8522/ UC1252075 | flower | NS | Along Moody Rd. near Pink Horse Ranch 2 mi. southwest of Los Altos | |
| 12/13/1959 | Santa Clara | RSA-POM | | flower | NS | Along San Francisquito Ck. Between University Ave. and Bayshore Freeway | |
| 12/31/1959 | Santa Clara | RSA-POM | | flower | NS | Along Moody Rd. near Pink Horse Ranch 2 mi. southwest of Los Altos | |
| 12/31/1959 | Santa Clara | DAV | 29675 | Flower/fr | NS | Along Moody Rd. near Pink Horse Ranch 2 mi. southwest of Los Altos | |
| 2/2/1960 | Alameda | JEPS | 4180/ JEPS24453 | fruit | | Sausal Creek near El Cerrito Ave. crossing over Dimond Canyon, Dimond Park, Oakland | 225 |
| 2/2/1960 | Alameda | DAV | 31725 | fruit | ST | Banks of Sausal Creek, near El Cerrito Ave. crossing over Dimond Canyon, Dimond Park, Oakland | |
| 12/17/1961 | Santa Barbara | UCSB | 1336/ UCSB11667 | | | Romero Creek, 0.5 mi. above bridge, in the Santa Ynez Mtns | 1050 |
| 1/5/1962 | Santa Barbara | RSA-POM | 167025 | flower | ST | In bed of Arroyo Burro Creek near Las Positas Rd. | |
| 2/22/1966 | Santa Cruz | RSA-POM | 187202 | flower | ST | Davenport landing in ravine | |
| 2/22/1966 | Santa Cruz | RSA-POM | 187203 | flower | ST | Along HWY 1 about 3 miles southeast of Davenport, 1 mile north of Sand Hill Bluff | |
| 2/19/1967 | Marin | RSA-POM | 195557 | vegetative | NS | In ravine behind Dillon Beach | |

| Table 1.1. Cape Ivy Herbarium Records from Ten California Herbaria[1] | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Date** | **County** | **Herbarium** | **Collection #/ Accession #** | **Phenology[2]** | **ST/NS[3]** | **Location Where Specimen was Collected** | **Elevation (ft)** |
| 2/9/1967 | San Mateo | RSA-POM | 195550 | flower | ST | San Bruno, Skyline Blvd. near intersection of Skyline and Berkshire Dr. | |
| 12/15/1968 | Los Angeles | RSA-POM | 605907 | flower | NS | San Gabriel Mtns., Millard Canyon at National Forest boundary | 4950 |
| 10/27/1968 | Los Angeles | RSA-POM | 605898 | | | San Gabriel Mtns., Millard Canyon at National Forest boundary | 4950 |
| 2/15/1969 | Santa Barbara | UCSB | 445/ UCSB25872 | flower | | Las Llago Creek, Santa Barbara | 15 |
| 11/18/1969 | Santa Barbara | DAV | 104581 | Flower/fr. | ST | West bank of Las Llagas Creek, ca. 15 miles west of Santa Barbara | |
| 11/15/1971 | Humboldt | HSU | | flower | | Next to 101, McKinleyville, north bank road, T6N, R1E, Sec 8 | |
| 1/23/1972 | Santa Barbara | UCSB | 7/ UCSB28086 | flower | | 0.5 mi up Eagle Canyon Creek in Goleta | 40 |
| 12/29/1974 | Los Angeles | RSA-POM | | | | San Gabriel Mtns., Millard Canyon at National Forest boundary | 4950 |
| 12/29/1974 | Los Angeles | UCR | UCR108457 | | | San Gabriel Mtns., Millard Canyon at National Forest boundary | 4950 |
| 1/22/1978 | Orange | UCSB | UCSB56508 | | | Ladd Canyon, Santa Ana Mountains | |
| 5/14/1978 | Santa Barbara | SBBG | SR-211/ SBBG8062 | | | Santa Rosa Island, Vail Ranch behind cookhouse | 50 |
| 10/13/1978 | Orange | RSA-POM | | flower | NS | Santa Ana Mtns., lower Ladd Canyon, reach between west and each forks | |
| 7/13/1979 | Santa Barbara | UCSB | 7900615/ UCSB46122 | | | Base of North bluffs, UC Santa Barbara campus | 10 |
| 11/7/1979 | Humboldt | HSU | | flower | | HSU campus front yard of house across from daycare center | |
| 1/21/1980 | Mendocino | HSU | | flower | | Highway 1 between Elk and Manchester | |
| 3/7/1981 | San Luis Obispo | UCR | 14276/ UCR42873 | | | Along San Luis Creek in southern San Luis Obispo, near intersection of Meisner Road and South Higuera Street | |

**Table 1.1. Cape Ivy Herbarium Records from Ten California Herbaria[1]**

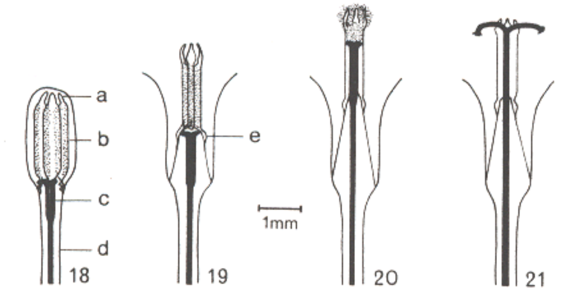
| Date | County | Herbarium | Collection #/ Accession # | Phenology[2] | ST/NS[3] | Location Where Specimen was Collected | Elevation (ft) |
|---|---|---|---|---|---|---|---|
| 11/24/1982 | Orange | UCI | 842/<br>UCSB52429 | flower | | 1.2 km NE, and 1.6 km SW, in the Blue Bird Canyon, at the W-flank of Temple Hill, in Laguna Beach | 623 |
| 11/24/1982 | Orange | UCSB | 842/<br>UCI20329 | flower | | San Clemente Canyon, southern flank of Temple Hill, 2.0km SSE Thurston Sch.; 0.7km NNW Sugarloaf Point | |
| 2/10/1984 | San Luis Obispo | UCR | 1870/<br>UCR42854 | | | Little Morro Creek | |
| 3/3/1985 | San Luis Obispo | UCR | 5395/<br>UCR38143 | | | Oso Flaco Lake, S of Oceano, at end of Oso Flaco Lake Road | 7-10 |
| 12/7/1985 | Alameda | JEPS | 5766/<br>JEPS84957 | | | North side of Albany Hill, near Cerrito Creek, north edge of Albany | |
| 12/7/1985 | Alameda | UC | 5766/<br>UC1561819 | | | North side of Albany Hill, near Cerrito Creek, north edge of Albany | |
| 12/7/1985 | Alameda | RSA-POM | 516340 | flower | NS | Albany Hill near Cerrito Creek, north edge of Albany | |
| 4/25/1989 | Los Angeles | UCR | UCR61054 | | | San Gabriel Mtns., in and near Glendora Wilderness Park, Big Dalton Canyon | 1450 |
| 5/23/1989 | Mendocino | HSU | | vegetative | | Sinkyone wilderness, T24N, R19W, NE ¼ Sec. 26 | 14? |
| 5/23/1989 | Mendocino | DAV | 13028 | vegetative | NS | Bear Harbor, 2.5 air miles SE of Needle Rock ranch house, 4 air miles SE of Four Corners, 15 air miles SW of Garberville | 40 |
| 12/27/1989 | Los Angeles | UCR | 1500/<br>UCR62103 | | | San Gabriel Mtns, Glendora Wilderness Park, N side of Big Dalton Canyon Road, 0.7 mi. E of Glendora Mountain Road. | |
| 6/25/1991 | Los Angeles | RSA-POM | 565746 | vegetative | NS | San Gabriel Mtns., Arroyo Seco Canyon above debris dam and below Oakwilde picnic area along Gabrielino trail | |
| 10/26/1993 | San Luis Obispo | RSA-POM | | flower | NS | Alkaline flat at west edge of Morro Bay | 7 |
| 10/26/1993 | San Luis Obispo | UCR | 8/<br>UCR79504 | flower | NS | Alkaline flat at west edge of Morro Bay | 7 |

**Table 1.1. Cape Ivy Herbarium Records from Ten California Herbaria[1]**

| Date | County | Herbarium | Collection #/ Accession # | Phenology[2] | ST/NS[3] | Location Where Specimen was Collected | Elevation (ft) |
|---|---|---|---|---|---|---|---|
| 2/11/1995 | Los Angeles | RSA-POM | 2537 | flower | NS | North end of San Dimas Rd., directly across road from USFS San Dimas station | |
| 2/11/1995 | Los Angeles | UCR | 2537/ UCR91518 | flower | NS | North end of San Dimas Rd., directly across road from USFS San Dimas station | |
| 11/10/1995 | Los Angeles | RSA-POM | 604525 | flower | NS | Santa Catalina Island, beach at Empire Landing, locally abundant, sandy beach slope | 10 |
| 10/25/1996 | Contra Costa | JEPS | 15358/ JEPS102902 | | | Little Pine Creek, Diablo Foothills Regional Park, dried streambed in partial shade | |
| 12/12/1996 | Yolo | DAV | 139881 | flower | NS | City of Davis, UC Davis campus, flower beds west of Robbins Hall, cultivated | |
| 3/12/1997 | Los Angeles | RSA-POM | 4737 | flower | NS | Zuma Beach area, mouth of Zuma Creek, east end of county beach | |
| 3/12/1997 | Los Angeles | UCR | 4737/ UCR97790 | flower | NS | Zuma Beach area, mouth of Zuma Creek, east end of county beach | |
| 2/20/1999 | Los Angeles | RSA-POM | 630269 | flower | NS | Temescal Canyon, Pacific Palisades, Santa Monica Mountains | 400 |
| 2/15/2000 | Humboldt | CHSC | 79694 | | | McKinleyville School Road, half mile west of Central Ave. | 100 |
| 1/31/2001 | Mendocino | CHSC | 80158 | flower | | Adjacent to Highway 1 at the south edge of Elk | 80 |
| 1/31/2001 | Mendocino | JEPS | 9983/ JEPS102544 | flower | | Adjacent to Highway 1 at the south edge of Elk | 80 |
| 7/17/2003 | Los Angeles | UCR | UCR13239 | | | San Gabriel Mtns., Arroyo Seco, Pasadena, north of Jet Prop. Lab. | 1250 |
| 12/29/2003 | Mendocino | CHSC | 86088 | flower | | North Coast, outer range, about a quarter mile north of Mendocino, at the first ocean side pullout/road | 40 |

1. Herbarium specimens summarized from: UC Davis (DAV), Berkeley (UC and JEPS), Santa Barbara (UCSB), Riverside (UCR), and Irvine (UCI); Santa Barbara Botanic Garden (SBBG), Rancho Santa Ana Botanic Garden (RSA-POM), and California State Universities Chico (CHSC) and Humboldt (HSU).
2. Phenology of herbarium specimen, either vegetative, in flower or in fruit.
3. ST/NS = morphological type, either stipulate (ST) or non-stipulate (NS).

## Figure 1.1. Presentation of Pollen in *Senecio* Species



**Figs 18–21.** Presentation of pollen depends on dehydration of the anthers. **Fig. 18.** Before anthesis the style apex is positioned below the expanded anther collar. **Fig. 19.** Shortly after anthesis the anther collar dehydrates, contracts, and is elevated by the elongating style. **Fig. 20.** The style then passes through the narrow anther collar pushing most of the pollen to the top of the collar. **Fig. 21.** The pollen mass is usually removed by pollen vectors before the style arms spread apart. *a*, Sterile appendage; *b*, anther collar; *c*, style; *d*, corolla; *e*, filament collar.

Source: Lawrence (1985)

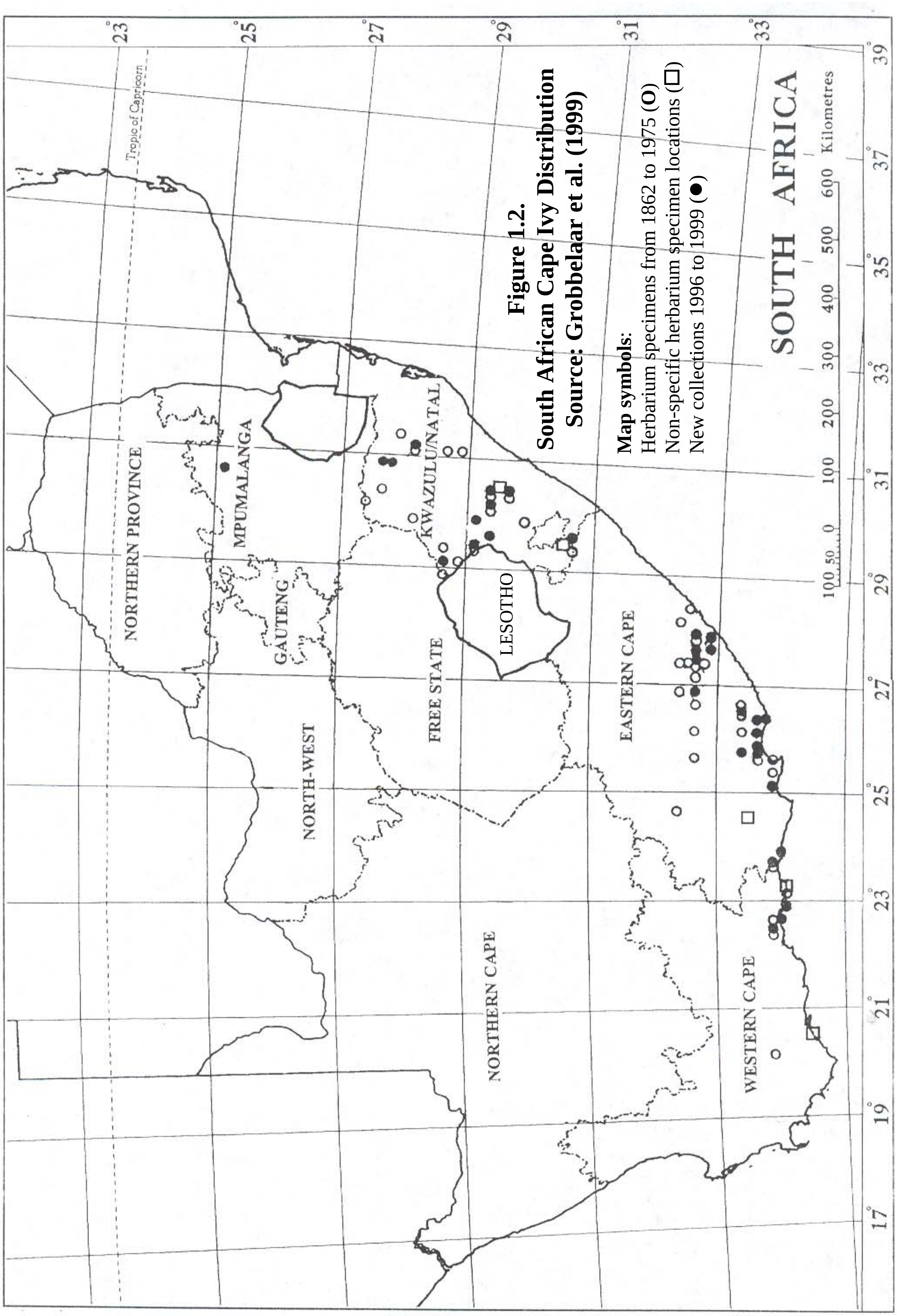
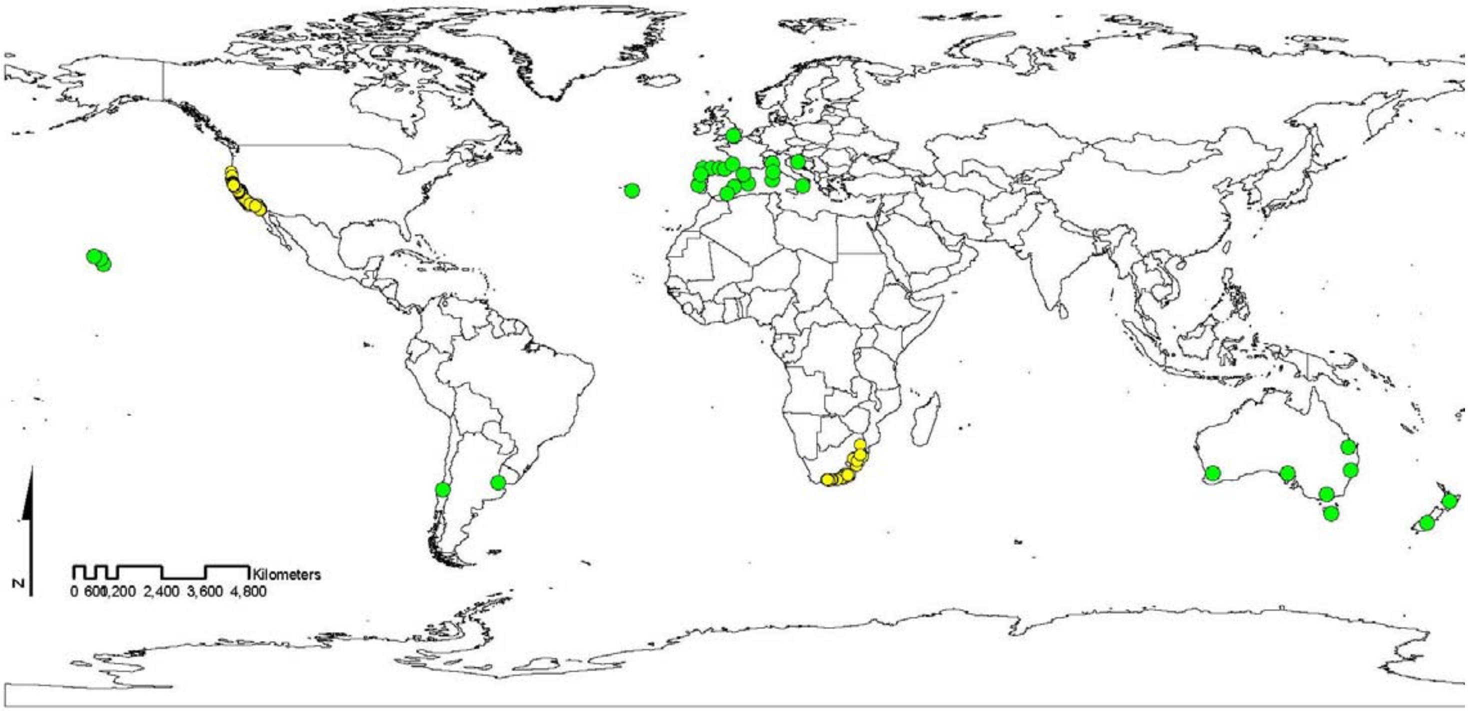


**Figure 1.2.**
**South African Cape Ivy Distribution**
**Source: Grobbelaar et al. (1999)**

**Map symbols**:
Herbarium specimens from 1862 to 1975 (O)
Non-specific herbarium specimen locations (□)
New collections 1996 to 1999 (●)

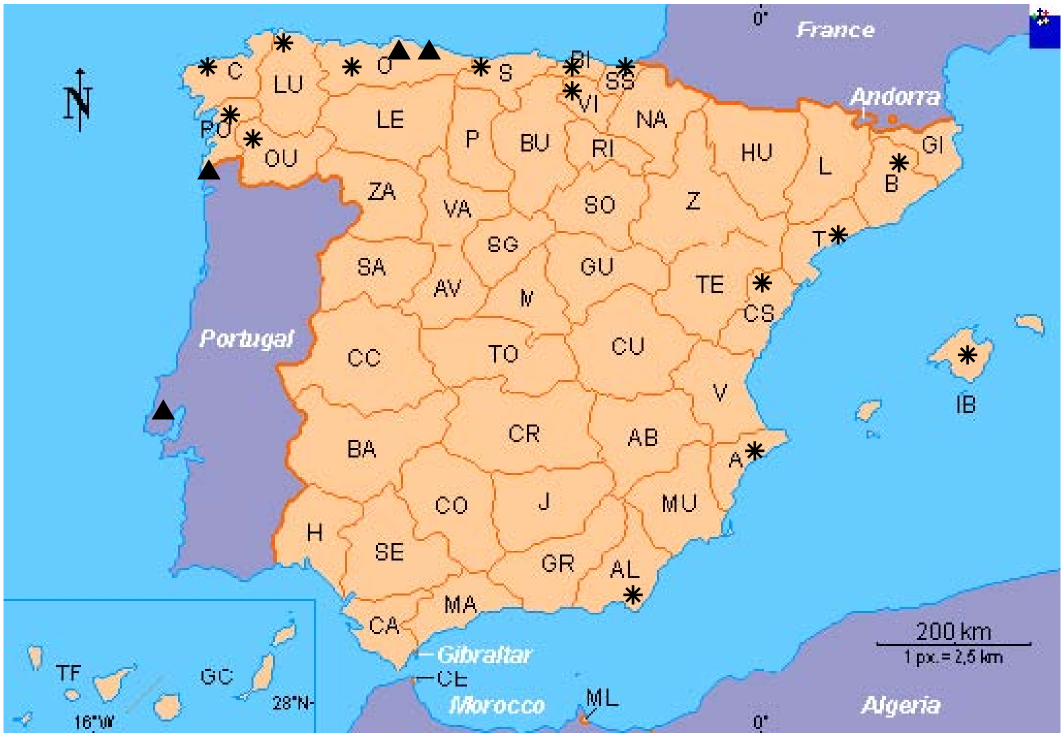
Figure 1.3. Cape Ivy Worldwide Distribution from Literature and Field Observations



🟢 Non-specific location from literature

🟡 Specific location from field observations (California and South Africa)

## Figure 1.4. Locations of Cape Ivy in Spain and Portugal



Base map source: http://www.crwflags.com/fotw/flags/es(prov.html)
Maps and boundary data are copyrighted by http://www.fotw.net/geoindex.html - Flags of the World web site

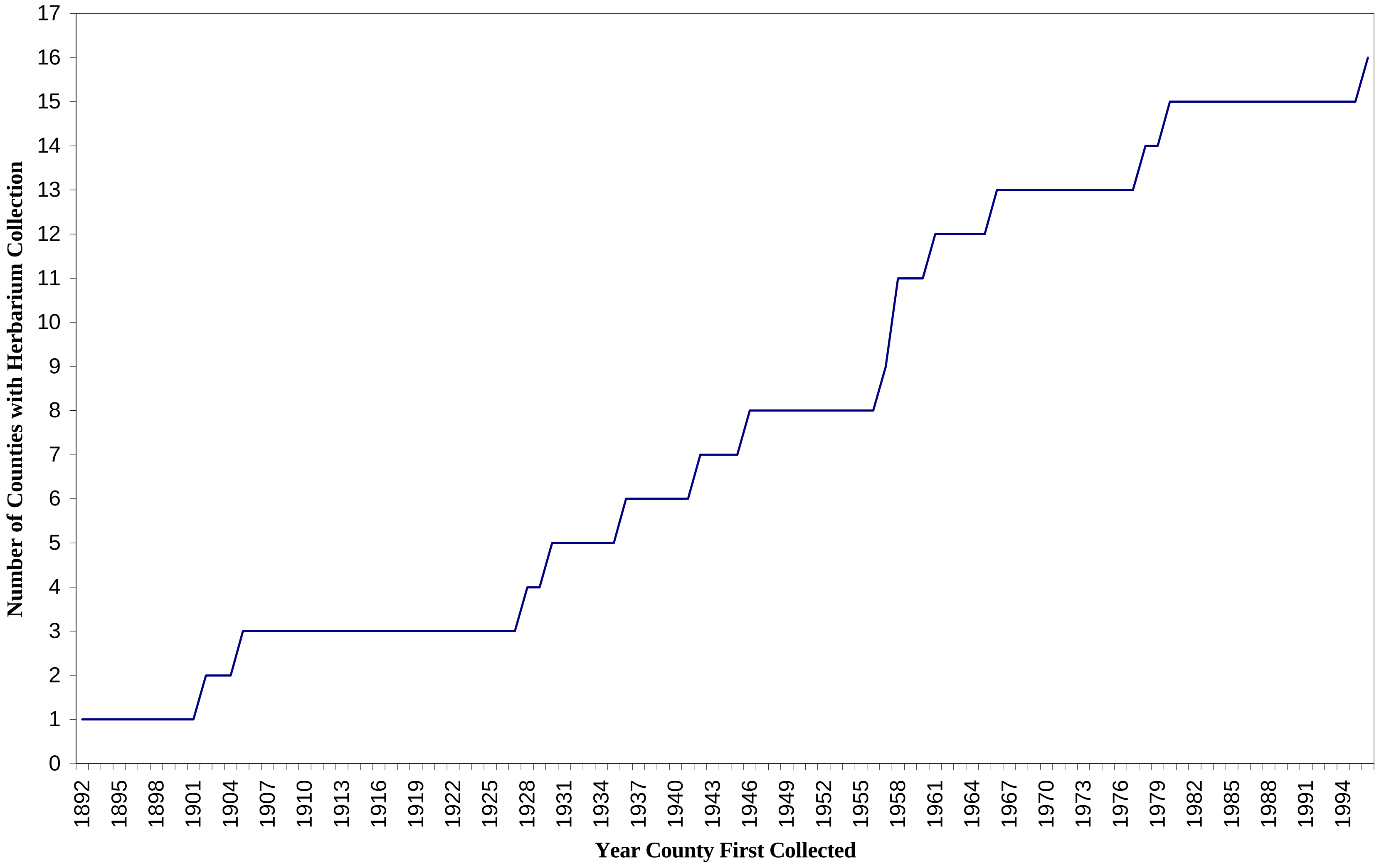
Cape Ivy Location Symbols:

| | |
|---|---|
| ✳ | Perez (2000) Spanish province locations |
| ▲ | Personal observations (2001) |

**Spanish Province Abbreviations**

| Abbreviation | Province |
|---|---|
| C | La Coruña |
| PO | Pontevedra |
| LU | Lugo |
| OU | Ourense |
| O | Austurias |
| S | Cantabria |
| BI | Vizcaya |
| VI | Álava |
| SS | Guipuzcoa |
| B | Barcelona |
| T | Tarragona |
| CS | Castellón |
| IB | Baleares |
| A | Alicante |
| AL | Almeria |

Figure 1.5. Number of California Counties with Cape Ivy Herbarium Record by Year of First Collection



# CHAPTER 2

## Cape Ivy Distribution, Natural Community Associations and Modeling of Potential Distribution in California

### ABSTRACT

Cape ivy was found to occur throughout coastal California and southern Oregon. It was most abundant in urbanized coastal areas such as the San Francisco Bay Area, and Santa Cruz, Monterey, San Luis Obispo, Santa Barbara and Los Angeles counties. We found Cape ivy occurring in seven different broad community types, and predicted that it should occur in five additional community types. These results refute the common assumption that Cape ivy is exclusively a riparian weed. Non-stipulate morphological types occurred more frequently at the northern and southern ends of the distribution, and stipulate types were frequently found in the middle of the distribution, from southern Humboldt County to Los Angeles. Only 21 locations were found that supported both stipulate and non-stipulate plants, and they were most often located in urbanized coastal areas. GIS analysis was used to determine the elevation, temperature and precipitation ranges that Cape ivy occupies in California. The analysis indicated that California Cape ivy occurs at elevations between 0 and 891 meters, at annual mean temperatures between 10.5 and 17.7°C and in areas with annual precipitation ranging between 232 and 2270 mm. GIS analysis was also used to determine which community types Cape ivy would be predicted to occupy and that information was compared with actual observations. The most often predicted and observed community types were urban and agricultural. Field observations were higher for *Eucalyptus* and riparian forest than predicted by CAGAP,

and CAGAP predicted more occurrences in coastal scrub, chaparral, non-native grassland and conifer forest than were observed in the field. Another GIS overlay analysis was run with the California Natural Diversity Database sensitive species location information to determine which species might be threatened by Cape ivy expansion. Lastly, CLIMEX and GARP predictive models were used to estimate the potential range expansion of Cape ivy. The predictions indicated that the San Joaquin Delta and portions of the Sierra Nevada foothills are areas that should be monitored for future range expansion of Cape ivy.

## INTRODUCTION

Cape ivy, which originated in South Africa, is now known to occur in Europe, Australia, New Zealand, Hawaii, and South America, as well as western North America (Parodi 1959, Abrams and Ferris 1960, Palhinha 1974, Zangheri 1976, Pignatti 1982, Haselwood and Motter 1983, Hirano 1983, Webb et al. 1988, Fagg 1989, Jacobi and Warshauer 1992, Scott and Delfosse 1992, Hickman 1993, de la Torre 1998, Gallo 2000). It was first collected in California in 1892 (Accession ID UC36003), and since that time has spread to all coastal counties and many adjacent inland sites (Jepson 1951, Abrams and Ferris 1960, Thomas 1961, Hoover 1970, Howell 1970, Munz 1974, Smith 1976, Beauchamp 1986, Smith and Wheeler 1992, Hickman 1993, Junak et al. 1995, Best et al. 1996, Matthews 1997). Cape ivy’s spread in California is a concern because it invades undisturbed wildland areas, and once established is extremely difficult to eradicate (Alvarez 1997, Bossard et al. 2000). There is no doubt that Cape ivy has firmly established itself along California’s coast, but the question remains as to whether it has occupied the full extent of its potential distribution.

After a non-native species is introduced to a new environment it has three possible fates. The founder can be extirpated, it can naturalize but not become widespread, or it can persist in low numbers, then increase rapidly (Mack 1985, Heywood 1989). The period before rapid increase is often referred to as the lag phase (Moody and Mack 1988), but there is no consensus on how to tell if an introduced species is in the lag phase of an exponential growth trajectory. One hypothesis is that during the lag phase a population undergoes selection in the new environment for locally adapted genotypes, and adapted propagules increase, facilitating the spread of the species (Salisbury 1961, Baker 1974).

Mathematical models have been used to determine which species are in the lag phase and have the potential to shift toward exponential growth (Williamson 1989, Mack 1996). Some models use a comparison of the home range climates of an invader with those in its new location, while others employ logistic regression or genetic algorithms. A summary of the basis of predictive vegetation modeling, including gradient analysis and niche theory, is presented, including a discussion of different types of mathematical and climatic models and how they have been used in predicting invasive species’ ranges.

Predictive vegetation modeling is based on the assumption that vegetation distribution can be predicted from the spatial distribution of environmental variables that correlate with or control plant growth and survival (Franklin 1995, Crossman 2003). The underlying theory is based on the concepts of gradient analysis and ecological niche theory (Franklin 1995). In gradient analysis, it is assumed that vegetation distribution is responsive to changes in environmental, resource and temporal gradients (Whittaker 1973). Gradients can be classified in three ways: indirect, direct or resource (Austin 2002). Indirect gradients do not have a direct effect on a plant's growth and include altitude, slope and aspect. Direct gradients (temperature and soil acidity) influence a plant's growth but are not consumed by the plant, and resource gradients (light, water, nutrients) are used by plants in their growth (Austin 2002, Crossman 2003). The type of gradient used is an important factor in mathematical modeling.

A species' niche is the area it occupies in space and time and can be thought of in two ways. The broader fundamental niche is the area a plant could occupy in the absence of competition, herbivory, and disease, while the narrower realized niche is the smaller resource space occupied when factors such as competition and disease are considered (Austin and Smith 1989). The realized niche is what we observe in nature while the fundamental niche is what we attempt to model with predictive vegetation modeling (Franklin 1995).

Three broad types of predictive models were classified by Franklin (1995): Boolean (discrete) methods, parametric models, and machine learning. Boolean models assign class membership to a location in only one class based on ranges of values of the independent (explanatory) variables (Crossman 2003). Simple Boolean logic or set theory is used to assign classes. BIOCLIM is an example of such a model. Parametric models use statistics to predict the probability of class membership for categorical dependent (response) variables. Examples of this model type include regression or Bayesian statistics. Models applying machine-learning techniques make no underlying assumptions about the input data and mimic a species of biological information processing (Crossman 2003). These models predict probability of class membership for dependent variables based on frequency distributions in the data used to train the model (Franklin 1995). Examples of machine-learning models are classification and regression trees, artificial neural networks and genetic algorithms (including GARP).

There are many studies available that aim to predict the future distribution of invasive plants (Committee on the Scientific Basis for Predicting the Invasive Potential of Nonindigenous Plants and Plant Pests in the United States 2002). A common approach is to use logistic regression models on environmental gradients to determine which gradients explain the observed distribution (Higgins et al. 1999, Collingham et al. 2000). The distribution is then extrapolated to the entire study region. In a study by Higgins (1999) the predicted distribution was overlaid on maps of plant diversity to make predictions about impacts to native plant diversity. This combination of modeling approaches, regression followed by additional analysis, is also becoming more common in predicting invasive species' distributions. For example, Underwood et al. (2004) used logistic regression to select the environmental variables to use in a Genetic Algorithm for Rule-set Production (GARP) analysis used to model the potential range of species groups.

As an alternative to regression, climate matching is widely used as a first step in determining if a plant can survive in a region outside its native range. If a climate is not conducive to growth and survival, then a newly introduced species will not persist (Sutherst et al. 1999, Steinmaus 2002). The assumptions of these types of models are that a species' distribution is determined by climate, and that there is a favorable and unfavorable growth season each year for the species of interest (Sutherst et al. 1999).

One widely used program for climatic matching is called CLIMEX (Sutherst and Maywald 1985). CLIMEX was developed to aid in the prediction of the potential geographical distribution of a species using climatic parameters inferred from an observed distribution (Sutherst et al. 1999). One example of its use for modeling the potential distribution of an invasive plant in California was for velvetleaf (*Abutilon theophrasti*) (Holt and Boose 2000). They found that without irrigation, velvetleaf was not predicted to occur widely in California, and with irrigation it would be able to persist although it has likely occupied its full potential range.

Climate matching methods other than CLIMEX have also been used. Another similar method is the Bioclimate Prediction System (BIOCLIM), which identifies "homoclimes" (areas with similar climates) from mathematical surfaces based on meteorological data (Nix 1986, Panetta and Mitchell 1991). BIOCLIM tallies species' occurrences in categories for each environmental dimension, trims the extreme 5% of the distribution along each ecological dimension, and uses the resulting niche to produce a decision rule (Peterson 2001).

Climate matching can be used to compare native and new ranges, and can also be used to predict areas that could be invaded in the future. For example, *Centaurea maculosa* was predicted to have a broad potential range in Montana based on annual precipitation, length of frost-free period, potential evapotranspiration and mean maximum July temperature for 116 infested sites (Chicoine et al. 1985). In a study that used BIOCLIM as its modeling basis, Panetta and Mitchell (1991) looked at the distribution of three weeds in Australia and used the climatic variables at those sites to predict the distribution in New Zealand. This study was particularly useful because it helped validate or revise the New Zealand quarantine protocols for the weeds under study.

One distribution prediction modeling study, that included Cape ivy, was completed for Hawaii (Jacobi and Warshauer 1992). During the U.S. Fish and Wildlife Service's Hawaii Forest Bird Survey conducted between 1976 and 1981, information was collected on the vegetation present at 7,864 stations along 117 transects on the island of Hawaii. For the modeling study they chose six alien plant species, one of which was Cape ivy. Cape ivy was included because it was considered by Hawaii Volcanoes National Park as a species that could adversely impact native ecosystems. They found Cape ivy primarily on the western flanks of Mauna Kea and Mauna Loa and on the northern and western slopes of Hualalai Volcano (Figure 2.1a). It was found only at stations receiving less than 2500 mm of annual rainfall and between 500 and 2500 m elevation. In order to predict its potential distribution they used the median annual rainfall and the elevations of the observed locations and extrapolated from those to the rest of the stations. The assumptions of the model were that there were no restrictions to the plants' invasion over time (i.e. no physical limits on dispersal, no herbivory, no pathogens, etc.). Cape ivy was predicted to be able to occupy all the sample stations on the western and southwestern side of the island, but it appeared that the high annual rainfall on the eastern side would preclude its spread there (Figure 2.1b**)**.

As part of the development of a baseline for Cape ivy's distribution in California, information was collected on the vegetation community types in which it occurs. There is only one California study that documents the community types Cape ivy occurs in (Alvarez and Cushman 2002). The study compared the invasion of Cape ivy into coastal scrub, willow riparian and alder riparian communities with non-invaded areas and found a 31% decrease in species diversity, an 88% decrease in the abundance of native seedlings, and a 92% decrease in non-native seedlings in plots infested by Cape ivy.

A map of the current distribution and information about the plant communities in which Cape ivy occurs will provide a baseline that can be compared to its distribution at a later date and thus determine the extent of its spread. Two morphological types of Cape ivy are present in California, a stipulate and non-stipulate type. In its native South Africa, Cape ivy is all stipulate, with the exception of one location (Balciunas 1999). Information on Cape ivy locations will also help identify threatened community types or sensitive species which are particularly vulnerable. The native Cape ivy distribution in South Africa can also be used to predict the California locations that may be suitable for Cape ivy invasion in the future.

The questions this research was designed to answer are: (1) Where does Cape ivy occur in California? (2) What plant communities is it most commonly associated with, and do stipulate or non-stipulate types occur in those communities? and (3) What is the potential distribution of the species in California based on its native range and the climates found in California?

# MATERIALS AND METHODS

## Mapping

### California and Oregon Cape Ivy Distribution

The California Exotic Pest Plant Council (now known as the California Invasive Plant Council, Cal-IPC) Cape Ivy Working Group began collecting Cape ivy distribution data in 1995. In May 1995, the distribution of Cape ivy was mapped along streams and hillsides in the coastal region of California, south of Monterey County. Additionally, appropriate habitats such as lakes, campgrounds, and parks along the coast were also surveyed. All populations that were reported by Cal-IPC members, California Native Plant Society (CNPS) members, park rangers, and other concerned citizens were visited and described. The boundaries of the populations were estimated and drawn on maps. The data collected were then digitized as point data on 1:100,000 topographic base maps using MapInfo Professional 5.0.

In 1999, as part of the work for this dissertation, I surveyed additional areas, including coastal counties north of Monterey and the San Francisco Bay Area. In addition to collecting maps from experts, data were collected using a hand-held GPS (Global Positioning System) (Trimble GeoExplorer) with an overall corrected accuracy of 1 to 3 meters. A series of sites originally mapped in 1995 by Cal-IPC were re-surveyed for Cape ivy in 2000 and 95% of locations visited still supported the species.

Several individuals and organizations provided large Cape ivy distribution data sets that were incorporated into the database. Most notable was an extensive set of maps provided by Golden Gate National Recreation Area (GGNRA) employees. These maps included data from Marin, San Francisco and San Mateo counties in the form of ArcView shapefiles.  Electronic data were also provided for Pt. Reyes National Seashore by the National Park Service, Catalina Island by the Catalina Island Conservancy, and Contra Costa County by the Contra Costa Watershed Forum.  The other data collected were on paper maps which were digitized onto 1:100,000 scale topographic maps.  Other mapping points were provided for a number of counties from Del Norte to San Diego.

All the spatial data were brought into a GIS (Geographic Information System).  In 1999, MapInfo Professional 5.0 was used to create maps, store and edit the data.  The GPS data was exported from Pathfinder to a MapInfo format, and ArcView shapefiles were converted to MapInfo format and included in the GIS.  Some of the data provided by GGNRA was polygon or line data and these were converted to point data for the final analysis.

Data collection with the Trimble GeoExplorer GPS continued in 2000, with the addition of data collection for vegetation community type, stipulate or non-stipulate morphological type, and seed production.  From 2001 to 2004, data was collected with a Garmin eTrex Vista GPS with accuracy of 15 meters alone and < 3 meters with the Wide Area Augmentation System (WAAS) enabled.  Waypoints collected with the eTrex Vista were converted to ArcView shapefiles with Waypoint+ version 1.8.03.  After conversion, the data files were edited to contain attribute fields listed in Table 2.1.  The final maps are in the Teale-Albers projection, geographic coordinate system NAD 1927.  Seed viability was tested (see Chapter 4) and where that information was available the viability data were entered into the attribute field.

In order to compare the community types containing Cape ivy infestations in California with the distribution of natural vegetation types, a copy of the California Gap

Analysis Project (CAGAP) data (Davis et al. 1998) was acquired. The CAGAP vegetation cover layer contains vegetation attributes for landscape scale map units, including canopy dominant species, canopy density, presence of regional endemic species, and wetland habitats (Davis et al. 1998). Each polygon is classified using different vegetation classification methods, one of which is the California Natural Diversity Data Base (CNDDB) community type which classifies vegetation using a 5 number land cover code (Holland 1986). The CNDDB community type was chosen for the mapping analysis and field data was collected using the 5 number code.

Populations of Cape ivy were also mapped in Spain and Portugal in 2001. Cape ivy has been reported to be invasive in southern Europe (Catalano et al. 1996, de la Torre 1999). The mapping effort was not extensive, and was designed as a cursory survey to evaluate the community types and the distribution of stipulate or non-stipulate morphological types in the region. The surveys were conducted between September 14 and 21, 2001, and waypoints were collected using the eTrex Vista described above. Waypoints were downloaded into MapSource 3.03 and maps were produced using base data purchased for Spain and Portugal. The survey extended from Oviedo, in the Austurias region of northern Spain, and continued west along the northern coast. A few locations were also mapped in northern Portugal and near Lisbon in the town of Sintra.

## GIS Analysis

### South African Vegetation Types

In 1999, at the beginning of an ongoing Cape ivy biological control investigation in South Africa, researchers collected Cape ivy at 41 locations (Figure 2.2). This information was included in an appendix in Grobbelaar et al. (1999) as a table with latitude and longitude. The latitude and longitude data from that table was used to create an ArcView point shapefile with the collection locations. These locations were then overlain on the South African map such that it was possible to extract information on the communities where they occurred. The base layer for vegetation type used was called “Terrestrial Biomes” and was included in the ArcView 9.0 ESRI Data and Maps CD for the World, Europe, Canada and Mexico. The “Terrestrial Biomes” layer contained a field with vegetation types called ECO_NAME. These polygons were developed by the World Wildlife Fund and others (Olson et al. 2001). The terrestrial biome types proved useful for analysis because a detailed description of each is available on line (http://www.worldwildlife.org/wildworld/profiles/terrestrial_at.html). In the type discussions, a general description of the dominant plant species is provided, as well as climate and elevation of the areas of interest, which are summarized in Table 2.2.

## Cape Ivy Distribution in California and Oregon

### *BIOCLIM Raster Extraction*

GIS analysis was performed with ArcView version 9.0 and the Spatial Analyst extension (version 9.0). Polygon data collected in the distribution mapping phase were converted to points and 1465 Cape ivy point locations were used as the basis for GIS analysis. In order to determine the elevation and climate parameters associated with the distribution data set in California, the point data was joined with BIOCLIM raster datasets. The bioclimatic variables (BIOCLIM) raster layers were derived from WorldClim interpolated climate layers (http://biogeo.berkeley.edu/worldclim/methods.htm). The WorldClim climate layers contain precipitation records for 47,554 locations, mean temperature from 24,542 locations, and minimum and maximum temperature for 14,835 locations (Hijmans et al. 2004). WorldClim altitude was obtained from the Shuttle Radar Topography Mission (SRTM) Digital Elevation Models (http://www2.jpl.nasa.gov/srtm/). Grids used in the analysis were at 30 seconds (1 kilometer). A spatial join of Cape ivy point data and BIOCLIM rasters was accomplished with the ArcView Spatial Analyst "extract values to points" tool. For example, when the BIOCLIM annual precipitation raster data set was spatially joined to the Cape ivy point data a column with annual precipitation was generated in the attribute table. This was repeated for all the raster layers. Excel and JMP IN (version 5.1) were then used to determine the range and mean values for the raster layers.

### *CAGAP*

An overlay analysis was done comparing the Cape ivy point data to the attributes available in the CAGAP data set (landcov.shp file dated 1998). The overlap with vegetation community types was the main focus of this analysis. Prediction of potential range using vegetation type has been called a "surrogate" method because it uses a single environmental variable such as vegetation (Stockwell and Peterson 2002). Experts or field observations determine which vegetation types are favorable for a species and predictions are made based on the mapped distribution of a vegetation type. For this analysis the Cape ivy points were buffered out 500 meters and any overlap in the resulting polygons was dissolved. The resulting layer then was overlain with the CAGAP analysis land cover data and the polygons that overlapped in the CAGAP were highlighted and saved as a separate layer. The predicted polygon attributes then were exported into Excel and JMP IN for analysis.

### *CNDDB Sensitive Species Overlay*

Further overlay analysis was performed with the Cape ivy point data and the California Natural Diversity Database (CNDDB) sensitive species location data. The data are available within an application called RareFind, a Windows based program designed to perform queries and produce reports. RareFind comes with GIS layers, which were used for this analysis (RareFind version 3.0.5 dated September 2, 2005). The CNDDB data consists of locations for sensitive plants, animals and natural communities as well as population data voluntarily submitted by field biologists. Sensitive species are defined as federally and state listed plants and animals, all species that are candidates for listing, all species of special concern and those species that are considered sensitive by government agencies and conservation organizations (http://www.dfg.ca.gov/whdab/pdfs/cnddbfaq.pdf). The data are then reviewed for accuracy and mapped by CNDDB personnel as “occurrences” at various levels of precision, from specific points to non-specific buffered polygons.

For the CNDDB GIS analysis, Cape ivy points were buffered out 100 meters to represent the current extent of their direct or indirect influence on sensitive species locations. The “select by location” feature in ArcView was used to select the sensitive species occurrences, which overlapped with the 100 meter buffered points. The selected polygons from the CNDDB data were then saved into a separate shapefile. Another file was created with Cape ivy points buffered out to 500 meters, representing an estimate of future spread, while another shapefile with sensitive species occurrences was generated for comparison.

## Predictive Vegetation Modeling

Two types of models were chosen to evaluate the potential spread of Cape ivy in California: CLIMEX and GARP. The CLIMEX modeling type is inverse or inferential, while the GARP model uses a reductionist, mechanistic approach (Sutherst 2003). Both models can use point data as inputs, and in the case of CLIMEX, the point data collected in California can be used to verify the predictions made by the model constructed using the native range in South Africa. Both models can also be used starting with the species' native range and projecting it onto the potential range. Cape ivy presence point data was available for modeling, some of it with associated vegetation community type. Some models have difficulty with data sets containing only presence data. The GARP model was chosen because is it is not biased by the lack of absence data (Anderson et al. 2003). To my knowledge, no papers have been published that compare the results of these two models.

### CLIMEX

The CLIMEX program was first introduced by Sutherst and Maywald (1985). It was designed to compare the potential for growth and persistence of organisms in different locations when biological information suitable for a population model is not available. Indices are calculated that describe the potential for a population to grow and persist through stressful climatic periods, and these are combined to form an overall suitability estimate called the Ecoclimatic Index (EI) which is scaled between 1 and 100

(Sutherst and Maywald 1985). The other calculated indices are a Growth Index (GI) and stress indices for Hot, Wet, Dry, and Cold. The Growth Index is composed of sub-indices for temperature (TI), moisture (MI) and light (LI). Each stress index has two parts. A threshold parameter determines the level at which stress is accumulated and a rate parameter models the rate of stress accumulation. The EI is the product of the Growth Index and the stress indices. Most published predictions include a map of the EI for overall suitability of an area for a species. Areas with wet and dry seasons have a maximum achievable EI of 50, and values above 50 are rare outside the tropics (Sutherst 2003). Values greater than 20 can support large populations (Sutherst 2003).

The CLIMEX model can be applied either with the “Compare Locations” or “Match Climates” function. The “Match Climates” algorithm compares meteorological data from different locations. It is often used when no other biological information is available. It generates a Match Index (MI), which is a scaled correlation coefficient (0.6-1.0). Values of MI less than 0.6 are considered a poor match (Sutherst 2003). Compare Locations is used to predict the potential geographical distribution of a species based on its climatic preferences and generates the EI and other indices described above (Sutherst et al. 1999).

Several papers have been published which use CLIMEX to predict the distribution of South African species introduced into Australia (Hughes and Maywald 1990, Pheloung and Scott 1996, Pheloung et al. 1996). Pheloung and Scott (1996) predicted the potential distribution of *Asparagus asparagoides* and *A. declinatus* and compared the results of CLIMEX with the BIOCLIM system developed by Nix (1986). The native distribution of *A. asparagoides* is similar to Cape ivy’s and the model parameters are included in the CLIMEX program. The same authors examined the potential distribution of *Emex australis* and *E. spinosa* in Australia and once again compared the CLIMEX and BIOCLIM models. *Emex australis* is native to South Africa, but its distribution is further west than that of Cape ivy. The potential distribution of Russian wheat aphid, *Diuraphis noxia*, has also been predicted for Australia (Hughes and Maywald 1990) and the parameters are in the CLIMEX program. The Russian wheat aphid native range is throughout South Africa so this was also not used for parameterization. These papers were useful when beginning the process of fitting the CLIMEX model to Cape ivy's native distribution.

In addition to examining papers that used CLIMEX on native South African species, all the biological information available on Cape ivy's climatic tolerances was gathered for use in parameterization. In South Africa, Cape ivy has been observed growing at elevations between 5 and 1800 meters above sea level (Grobbelaar et al. 1999, Rolando 2000). In Hawaii it occurs between 500 and 2500 meters elevation and at annual precipitation levels below 2500 mm (Jacobi and Warshauer 1992). According to the BIOCLIM GIS analysis described above, in California it occurs at elevations between 0 and 891 meters, in areas with mean annual precipitation between 232 and 2270 mm, and the maximum and minimum temperatures it can tolerate are between 1.8 and 31.8°C (Table 2.3). In seed temperature germination experiments described in Chapter 4, seeds germinated at temperatures between 8 and 32°C with an optimum germination temperature of 20.6°C. In growth experiments described in Chapter 3, Cape ivy populations showed a low tolerance for a combination of high light and high temperatures.

In order to find the weather stations in CLIMEX that were closest to the Cape ivy locations collected in 1999, a spatial join was completed in ArcView with the South African climate stations and the Cape ivy points. This spatial join created columns in the Cape ivy point attribute table with the name of the closest station and its distance. Seventeen weather stations were selected and the meteorological graphs for the stations were examined to look for climatic trends. The seventeen weather stations were also used in the “Match Climates” feature in CLIMEX to determine areas of California that match the climates where Cape ivy occurs in South Africa.

After gathering the background data the next step was to fit the model to the native South African distribution. Meteorological data used for fitting the model comes with CLIMEX, but it only includes 14 stations for California. To improve the fit of the model to Cape ivy in California, NOAA weather station data for temperature and moisture was added to a separate *.met file which was used to run the model for California.

CLIMEX modeling started with the Mediterranean template because that predicted a similar fit to the South African and worldwide distribution. The *Asparagus asparagoides* model was also used for reference (Table 2.4). The CLIMEX manual suggests starting with the growth indices and then moving on to change the stress indices as necessary. The stress interactions are changed last, and in the case of the Mediterranean Template, the Hot-Wet stress is included to exclude Mediterranean species from tropical areas (Sutherst et al. 1999). The temperature index was varied first and changed only slightly from the Mediterranean Template. When lower temperature values were chosen (DV0 = 1ºC, 5ºC) the distribution in South Africa was little changed and the distribution in California included more Sierra Nevada foothill locations. However, the worldwide distribution expanded to include the Pacific Northwest. Setting DV0 to 7ºC gave the optimum Pacific Coast distribution while allowing the California distribution to extend as far north as Orick, Humboldt County, California, and did not appreciably change the South African prediction. This temperature index also matched the European and New Zealand distribution well. Next the moisture index, a measure of soil moisture calculated from rainfall and evapotranspiration data, was varied. Using the Mediterranean Template values for the moisture index predicted a larger area in South Africa than Cape ivy naturally occupies, so the values for SM0 to SM3 were raised to represent Cape ivy's occurrence in moister soil microclimates. Diapause and light indices were not changed.

The stress indices were altered last. Cold stress was changed so that stress began accumulating at 5ºC instead of 0ºC; the rate of stress accumulation was set to the *Asparagus asparagoides* level and the other parameters were not changed. This maintained the coastal northern California locations. The heat and dry stress parameters were not altered from the Mediterranean template. The threshold accumulation for wet stress (SMWS) and the wet stress rate were altered so wet stress would start accumulating when soils were wetter than the template levels. Hot-Wet stress was left at the Mediterranean Template level. The final parameters used for the model are listed in Table 2.4. The parameters for the Mediterranean template and *Asparagus asparagoides* are also listed for comparison.

### GARP

The Genetic Algorithm for Rule-Set Prediction (GARP) is a machine-learning model. It generates rules (if-then statements) about the presence or absence of a species in a given location through an iterative, evolutionary approach. The rules used include logistic regression models, environmental envelope models, and categorical models. The resulting set of best models, or rule set, can be projected onto geography to provide predictions of geographic distributions (Stockwell and Peterson 2002).

In the literature on GARP modeling, environmental data coverages used to run the model vary with availability for the study area. Some commonly used coverages are average annual precipitation, average annual temperature, elevation, potential vegetation, and soil or geological features (Godown and Peterson 2000, Anderson et al. 2002, Lim et al. 2002, Peterson et al. 2002, Stockwell and Peterson 2002, Anderson 2003, Drake and Bossenbroek 2004). Using all the BIOCLIM coverages listed in Table 2.3 there appeared to be an over-fit of the models to the input points, while using a few coverages caused an underfit. Median annual rainfall and elevation were used exclusively in the Cape ivy modeling study conducted in Hawaii (Jacobi and Warshauer 1992). Underwood et al. (2004) used Canonical Correspondence Analysis on plot data to select the environmental variables that best predicted non-native species occurrence. They used percent cover of trees, shrubs and herbaceous species as well as slope and elevation in their GARP models. Based on the results of the CLIMEX model runs we also found that temperature and moisture were important predictors of Cape ivy distribution in California, so GARP models were tested using BIOCLIM temperature and precipitation variables.

The optimal number of species presence points suggested for GARP models was shown to be 50 or more (Stockwell and Peterson 2002). The set used for modeling contained 811 Cape ivy points collected between 2001 and 2004. For each modeling session twenty runs were done with a convergence limit of 0.01 and 1,000 maximum iterations. The model was run with 50% of the input points held out for training and with the Best Subset Selection Parameters on Active as suggested by Anderson (2003). The omission error was 10% and the commission threshold was 50%. Figure 2.3 shows an example of the model set-up. Outputs were ASCII grids that were then processed in ArcView with the ASCII to Raster conversion tool. Most of the grids required reclassification, which was done with the spatial analyst tool, and then the best subsets rasters were added using the raster calculator in spatial analyst. Various combinations of the BIOCLIM layers were compared.

## RESULTS and DISCUSSION

### Mapping

#### California and Oregon Cape Ivy Distribution

Figures 2.4a to 2.4m show the distribution of Cape ivy in California and Oregon. The mapping symbols indicate whether the morphology of plants at the location was stipulate, non-stipulate, both or unknown. Starting from the north non-stipulate plants were observed in Curry County, Oregon, in Pistol River along the old Highway 1 alignment (Figure 2.4a). Only a few locations of unknown morphology were reported south of the Oregon locations in Redwood State and National Parks in Del Norte County (Figure 2.4b). An historic location was reported from Crescent City, but it was not located during field surveys. Humboldt County contains a number of Cape ivy locations near Orick, and in Trinidad, McKinleyville and Arcata (Figure 2.4c). It was also observed growing along the Eel River southeast of Ferndale and in several locations in Shelter Cove. Non-stipulate plants were seen in northern Humboldt County, and stipulate plants were seen in Shelter Cove. Cape ivy was widespread in Mendocino County, occurring in all the large urban areas from Ft. Bragg in the north to Gualala in the south and along Highway 1 in between (Figure 2.4d). Cape ivy was also found in most of the major river systems. Mendocino County plants were mostly stipulate, but non-stipulate and mixed populations were also observed. Sonoma County was also heavily infested along the coast, with populations at Sea Ranch, Bodega Bay and at inland locations within Sonoma County near Petaluma and Glen Ellen (Figure 2.4e). Sonoma County plants were stipulate in the northern locations, and non-stipulate in the southern and inland parts of the County.

The San Francisco Bay Area was heavily infested and detailed digital mapping of Pt. Reyes National Seashore, Golden Gate National Recreation Area and Contra Costa County was included in the database. Cape ivy occurred at many locations within the San Francisco Bay Area in Contra Costa, Alameda, San Francisco, Santa Clara, and San Mateo counties (Figure 2.4f). The mapping contains only a small representative sample of locations in the urbanized Bay Area. For instance, in Contra Costa County a systematic survey of creeks found Cape ivy occurring in 22 locations along Kirken, Alhambra, Las Trampas, Pinole, San Pablo and Mt. Diablo creeks. Bay Area populations were stipulate, non-stipulate, or mixed, although many were mapped before we began collecting morphological information. One of the furthest inland sites in Northern California was along Kirken Creek, approximately 60 kilometers from the Pacific Ocean. Coastal San Mateo County was highly invaded by Cape ivy, with infestations found in every coastal creek surveyed (Figure 2.4g). Detailed mapping information was provided for San Pedro Creek in Pacifica and San Francisquito Creek in Palo Alto. Plants in San Mateo County were mostly stipulate, but a few non-stipulate and mixed populations were encountered. Information on the morphology of Santa Clara County Cape ivy was not available.

Moving south from the San Francisco Bay Area, Santa Cruz County was also heavily infested in coastal streams and urbanized areas (Figure 2.4h). One of the worst infestations was observed in Watsonville Slough. Cape ivy in Santa Cruz County was either stipulate or non-stipulate, with one location in Davenport supporting both morphological types. Monterey County had mostly stipulate plants on the coast with a prevalence of non-stipulate types in the Prunedale area (Figure 2.4i). Urbanized areas in Monterey County were not thoroughly mapped and so the number of Cape ivy locations are probably much higher than the maps indicate. Cape ivy infests areas of the Ventana Wilderness (http://www.ventanawild.org/news/se99/capeivy.html), but specific location information was not available to include in this mapping effort. Urbanized areas of San Luis Obispo County also supported thriving populations of Cape ivy. Large populations of stipulate, non-stipulate or mixed morphological types were observed in Cambria, Morro Bay, San Luis Obispo, Avila and Oceano (Figure 2.4j).

In Southern California, Santa Barbara County supported large Cape ivy populations in the urbanized coastal areas, with smaller populations occurring further north in Lompoc and Orcutt (Figure 2.4k). Santa Barbara plants were mostly stipulate or of mixed morphology. Cape ivy is also known to occur on three Channel Islands: Santa Rosa, Santa Cruz and Santa Catalina. Detailed mapping information was provided for

Santa Catalina Island. Other notable locations in Southern California were Los Angeles County, that had a Cape ivy location in San Dimas Canyon located approximately 67 km from the Pacific Ocean. Many Southern California locations were non-stipulate, with mixtures of stipulate and non-stipulate types occurring in coastal areas of Los Angeles County (Figure 2.4l). San Diego County supported non-stipulate Cape ivy, with infestations in coastal urban areas and along streams in the inland towns of Fallbrook and Bonsall (Figure 2.4m).

Cape ivy has been known to occur in California since 1892, yet many of the historic floras only mention it in passing and do not indicate it as a widespread weed (Munz 1974, Smith 1976, Beauchamp 1986, Junak et al. 1995). In the 1970s it was noted as “climbing on trees, mostly willows, along coastal streams,” and “forming dense tangles in shaded canyons or on moist open slopes” (Hoover 1970, Howell 1970). Floras from the 1990s mentioned it as common or invasive in coastal areas (Best et al. 1996, Matthews 1997), but surprisingly as late as 1992 the Mendocino Flora mentions it as “occasional but seldom collected” (Smith and Wheeler 1992).

Cape ivy is still grown horticulturally in California’s Central Valley. Interestingly, in 1928, the plant was collected on the grounds of Sacramento Junior College (DAV 2080, Table 1.1). It has also been observed flowering in a landscape in downtown Sacramento (2002) and is well established in at least three Davis landscapes (personal communication with Rejmanek, M., Shapiro, A. and C. Bossard). As recently as 1998 it was part of the landscape around Robbins Hall on the UC Davis campus where it was growing in deep shade on the west side of the building.

## GIS Analysis

### South African Vegetation Types

There is little information on the vegetation community types where Cape ivy occurs in South Africa. Rolando (2000) noted that it occurred sporadically along *Podocarpus* forest margins in mistbelt vegetation. The GIS analysis of the Cape ivy point locations collected in 1999 placed them into six of the WWF terrestrial biome types (Table 2.2 and Figure 2.2). The summary here serves as an introduction to Cape ivy's associations and environmental tolerances in its native habitat. Starting from the west in the Western Cape Province, six collection locations were contained in the Kynsa-Amatole Montane Forest, an area that receives year-round rainfall with a maximum in early and late summer. The points were in the Kynsa portion of the ecoregion, which is composed of tropical trees and is a fire-adapted vegetation type. Lowland Fynbos and Renosterveld points were located east of the Kynsa Forest and intermixed with the Albany thickets biome. Lowland Fynbos receives winter rain and is a sclerophyllous, evergreen, fire-prone shrubland. In contrast, Albany thickets vegetation receives non-seasonal sporadic rainfall and is a denser, spiny shrubland. Moving further east the KwaZulu-Cape Coastal Forest receives low winter rainfall and is a mixed evergreen and semi-deciduous forest interspersed with thornveld. The most common biome types containing populations of Cape ivy are the Drakensberg Montane Grasslands, Woodlands and Forests, and the Maputaland-Pondoland Brushland and Thickets. The Drakensberg type occurs at higher elevations than Cape ivy was observed at in South Africa. It is located in the medium altitudes of the Drakensberg Mountains and also has the largest temperature variation of the regions, with most areas cold and wet throughout the year.

This region contains the *Podocarpus* forests where Rolando mentioned Cape ivy occurring (Rolando 2000). Maputaland-Pondoland Brushland is located at lower elevations and occurs along rivers flowing out of the Drakensberg Mountains. Most annual precipitation falls in the warm summer months between October and March and the vegetation is predominantly evergreen sclerophyllous plants.

The climates in which the biomes occur do not suggest any discernable climatic patterns for the distribution of Cape ivy in South Africa. It occurs in areas with winter rain, summer rain, or sporadic rain, and in areas with or without frost. The primary trend, however, is that most of the areas where it grows are temperate and not Mediterranean.

### Distribution in California and Oregon

The California climate where Cape ivy grows can be broadly described as Mediterranean. Mediterranean climates are characterized by dry summers and an average of 25 to 100 cm annual rainfall concentrated during the mild winter (Dallman 1998). Snow is infrequent except at higher elevations, and the amount of winter rain is highly variable from year to year.

#### *BIOCLIM Raster Extraction*

Table 2.3 contains the results of the BIOCLIM raster extraction with all Cape ivy points. It indicates that Cape ivy in California occurs at elevations between 0 and 891 meters, at annual mean temperatures between 10.5 and 17.7°C and in areas with annual precipitation ranging between 232 and 2270 mm. Examining the maximum temperature of the warmest month and the minimum temperature of the coldest month, it appears Cape ivy can tolerate temperatures between 1.8 and 31.8°C.

*CAGAP*

Table 2.5 contains the results of the CAGAP overlay analysis and also includes community type data collected in the field. The data set used to create the CAGAP overlay contained all 1485 research points, while the field data set of community types was much smaller, although it was included in the larger set. The numbers in the first column are the CNDDB Holland (1986) community types, the Specific Type column is the name of the type and the General Type column was generated to aid in analysis of broad types and trends. The N columns for CAGAP and Field Data indicate how many polygons or points were contained in that community type.

Several interesting trends are evident in the vegetation types predicted by the CAGAP or observed in the field. A second table (Table 2.6) was prepared summarizing the general types and the number of locations either predicted or observed. It also contains a column with the mapped distribution in square kilometers predicted by the CAGAP analysis. The analysis predicted Cape ivy potentially occurring in 145,234 $km^2$ ($3.5 \times 10^7$ acres) of California, 36% of the total area of California. Although the predicted and observed columns were generated using different data sets, a comparison of types is useful to assess the potential threats to native vegetation communities from Cape ivy infestation. First, the urban or agricultural type is the largest predicted by CAGAP and was one of the most often observed types in the field. This was expected because Cape ivy was introduced as a horticultural plant and many of the surveys have been conducted in easily accessible urban areas. Field observations indicate more Cape ivy locations in non-native *Eucalyptus* forests than predicted by CAGAP. Almost twice as much Coastal Scrub infestation was predicted by the CAGAP than was observed. This community type is one not often considered threatened by Cape ivy so efforts should be made to track Cape ivy populations that occur there.

The CAGAP analysis was useful in that it predicted a few community types where Cape ivy was not observed or only minimal observations were made. These included Chaparral (8 types), Non-native grassland, and Conifer forest (10 types). This finding warrants further study. In only one case, Riparian forest (9 types) were the observations much larger in the field observations than the CAGAP analysis. While the exact numbers in each column are not always comparable, their magnitude is indicative of the level of infestation in those vegetation types.

The final column in Table 2.6 was generated using the total mapped distribution in square kilometers for each community type from the CAGAP report. Cape ivy was predicted to potentially occupy 145,234 km$^2$ (3.5 x 10$^7$ acres), 36% of the total area of California.

### *CNDDB Sensitive Species Overlay*

Table 2.7 contains the CNDDB sensitive species summary table organized by phylogenetic group. The number of polygons overlapped by the 100 m and 500 m Cape ivy buffers is also shown. The “Mean number of occurrence polygons” columns refer to the number of occurrences for each species or community type that overlapped with the Cape ivy polygons at 100 and 500 m buffers. For instance, in the case of vascular plants, at the 100 m buffer level, there were 163 species with overlap predicted and a mean number of 2.2 occurrences per species.

As can be seen in Table 2.7, the number of occurrence overlaps for each species was small, both at the 100 and 500 m buffer sizes. In all cases, except non-vascular plants, the number of overlapped polygons and the mean number of occurrences increased with the 500 m buffer. This raises the question, of whether there are some species with only a few recorded occurrences. If true, a finding of 10 or more Cape ivy overlaps would be sufficient to cover a majority of the known distribution of these species with restricted ranges.

To answer this question, I examined the species with more than 10 occurrence "hits" in the overlap analysis **(**Table 2.8**)**. With the 100 m buffer, only animals overlapped while the 500 m buffer overlapped both animals and plants. By comparing the total number of occurrences contained in the CNDDB with the number of overlapped polygons, a percentage overlap was calculated for each buffer size. Plants tended to have smaller total numbers of populations and in some cases 40% or more were potentially impacted by the expansion of Cape ivy [San Francisco Bay spineflower (*Chorizanthe cuspidata* var. *cuspidata*), Franciscan thistle (*Cirsium andrewsii*), San Francisco gumplant (*Grindelia hirsutula* var. *maritima*), perennial goldfields (*Lasthenia macrantha* ssp. *macrantha*) and marsh microseris (*Microseris paludosa*)].

Another overlap category of note was the overlap with steelhead salmon streams throughout the state. At the 500 m buffer level the percentage of overlap with Cape ivy ranged between 42 and 50% of streams supporting steelhead salmon. No published studies have been completed on the toxicity of Cape ivy to fish, except an unreplicated 10 week class project that indicated die-off of golden shiner (*Notemigonus crysoleucus*) (Bossard unpublished data). Balciunas (2000) also conducted some preliminary toxicity tests on mosquito larvae (*Orthopodomyia signifera*) and mosquito fish (*Gambusia affinis*) with Cape ivy and a native plant, *Petasites frigidus* var. *palmatus*. Results were mixed.

In some cases Cape ivy had no effect or survival in Cape ivy treated water was higher than controls. When *Petasites* was crushed and added to water containing mosquito fish, mortality was almost immediate; crushed Cape ivy leaves caused mortality in two to three days. The concentrations used in the study were higher than those which would be found in nature and the effects on native species are also unknown. In the event that Cape ivy is shown to have toxicity to native fish, its proximity to a large number of steelhead occurrences is worrisome.

The one invertebrate with 10 or more overlapping polygons was the Monarch butterfly (*Danus plexippus*), that overlapped 13 or 25% of the CNDDB occurrences. The potential for Cape ivy alkaloids to effect the Monarch butterfly has been studied indirectly. Cape ivy, like other members of the *Senecio* tribe, is known to contain pyrrolizidine alkaloids (Manske 1936, Adams and Gianturco 1956, Stelljes et al. 1991, Catalano et al. 1996), which can cause liver damage in humans, animals and fish (Hendricks et al. 1981). Monarch butterflies were found to have differences in pyrrolizidine alkaloid concentrations before and after arriving at their over-wintering location that included Cape ivy as a nectar source (Stelljes and Seiber 1990). The butterflies accumulate the pyrrolizidine alkaloids, perhaps as a predator defense. Cape ivy provides food for the butterflies in winter when many native species are dormant.

## Predictive Vegetation Modeling

### CLIMEX

Figure 2.2 depicts the South African locations where Cape ivy was collected in 1999 (Grobbelaar et al. 1999). It also includes the 17 CLIMEX weather stations that were closest to each collection location as determined with an ArcView spatial join. The majority of the 41 collection locations were in the Eastern Cape province, followed by KwaZulu Natal, Western Cape and Mpumalanga. When the “Match Climates” feature of CLIMEX was used to compare the 17 South African weather stations to those in California, only eight California climate stations provided matches. These are listed in Table 2.9 and all but one occur in the Eastern Cape Province. This suggests that the region of origin for the Cape ivy in California , based on the similarity of climates, would be the Eastern Cape Province.

The CLIMEX model results depict the Ecoclimatic Index (EI) for South Africa, the World and California with and without irrigation (Figures 2.5a to d). The larger circles are areas with the highest probability of Cape ivy occurrence.

For South Africa (Figure 2.5a), the model predicts Cape ivy’s distribution further west on the Western Cape than it occurs. After varying all the model parameters it was not possible to eliminate it from that area. The modeled distribution does match the region in the Eastern Cape with climates similar to California and extends north as far as the natural distribution. The worldwide distribution matches all the known Cape ivy locations except Hawaii (Figure 2.5b). The fit is good for Australia and Tasmania, New Zealand, and Europe. The prediction for Europe is large, but it does cover all the locations where it is known to occur: Azores, Britain, Corsica, France, Spain, Italy and Portugal (Chater and Walters 1976). However, the model does over-predict Cape ivy range with predictions that it should occur in Mexico, in the northern part of South America and further north in Africa.

The California Ecoclimatic Index (EI) prediction for California roughly matches the known distribution, but the EI values are relatively low (Figure 2.5c). The EI values for 135 stations ranged between 0.1 and 25.5 with a mean of 6.1 and standard error of 0.5. The only location with an EI above 20 was at Shelter Cove, Humboldt County, a location that does support a vigorous population. The 33 locations with an EI over 10 are mostly coastal sites and have Cape ivy populations. The model predicts 7 locations in the Central Valley and Sierra Nevada foothills. The EI values for these sites are less than 10, except in the case of Paradise that has an EI of 11. EI values greater than 20 can support large populations (Sutherst 2003), lower values indicate that the climatic opportunities for establishment throughout the year are lower. With repeated introductions through horticulture and the addition of supplemental irrigation, Cape ivy may have been able to overcome the climatic stresses it faced in California.

Using the same CLIMEX parameters listed in Table 2.4, an irrigation scenario was added to the model to see how the predicted distribution in California might change in microclimates with higher moisture availability. The addition of 30 mm per week of irrigation in both summer and winter resulted in the prediction in Figure 2.5d. This raised the EI values on the coast significantly. The EI values for 147 stations ranged between 0.1 and 79.3 with a mean of 24.3 and standard error of 2.0. For this model 62 stations had EI values over 20. They were located throughout coastal Northern and Southern California, including Catalina. The furthest inland known points of Mt. Diablo (EI 21.4) in Northern California and Claremont (EI 22.7) in Southern California were also included. Interestingly, the model no longer predicted most of the Sierra foothill locations with the exception of Placerville. Instead, it expanded the prediction to include the San Joaquin Delta, some locations further inland in Southern California, and one outlier in the Mojave Desert at Mitchell Caverns.

CLIMEX modeling indicates that Cape ivy's distribution is most likely to increase in coastal California, but it has the potential to expand into the Sierra Nevada foothills. In areas which receive water throughout the year, such as riparian areas or locations with coastal fog influence, the Ecoclimatic Index for Cape ivy is much higher. With added moisture it also has the chance to survive in the San Joaquin Delta and further inland in Southern California. Models that were run with a lower temperature index (setting DV0 to 1ºC) predicted Cape ivy occurring much farther north into Oregon and Washington and also predicted high elevation Sierra Nevada occurrences, suggesting that Cape ivy's distribution may be limited by low temperatures, as well as available moisture.

I did not encounter any other publications that used the CLIMEX irrigation scenario for a wildland weed. However, Cape ivy is often found in riparian and wetland habitats. Another source of additional moisture would be the frequent summer fogs experienced in coastal California. Fog is an important contributor to the annual water balance in coastal California. In a study conducted in the Eel River Valley, Humboldt County, California, as much as 42.5 cm of fog water were collected beneath the forest crown during the summer fog season (Azevedo and Morgan 1974). They found fog precipitation events yielded as much as 8 cm and could last several days, beginning in the late evening and ending just after sunrise. Another California coastal study, conducted in Pt. Reyes, examined the isotopic composition of fog water as well as tree and soil water in order to determine whether fog water was being used by vegetation (Ingraham and

Matthews 1995). They found a gradient of use of the fog-drip water. Closer to the coast the vegetation appeared to use fog-drip all year, while further inland it was used seasonally and still farther inland vegetation used only ground water which could contain some fog-drip. These studies demonstrate that fog-drip is available to plants in the immediate coastal area of California, but studies conducted with a wide variety of species show that they differ in their ability to absorb water through their leaves (Stone 1957). Cape ivy leaves possess a thick waxy cuticle which may be a barrier to absorption of fog-drip. However, Cape ivy roots are located near the surface, allowing access to the additional soil moisture supplied by fog. Given the amount of water available to coastal plants through fog-drip it seems appropriate to use the CLIMEX irrigation scenario to simulate the additional moisture available to plants in the fog belt.

Two papers have been published that use CLIMEX to predict the distribution of South African weeds introduced into Australia (Pheloung and Scott 1996, Pheloung et al. 1996), and one paper predicts the distribution for a California weed (Holt and Boose 2000). The goal of CLIMEX modeling is to capture the core features of a species' climatic requirements (Sutherst 2003). Analysis in these papers typically starts with an examination of the species' native distribution and an attempt to fit the model to the native range. The matched native distribution then is projected onto the non-native area of interest and comparisons are made between the actual and predicted distribution. In some cases the results of CLIMEX are compared to another modeling method. Two of the Australian studies compare the CLIMEX results to a model called Climate System that is similar to BIOCLIM (Pheloung and Scott 1996, Pheloung et al. 1996).

The two Australian papers are similar in that they use the known non-native distribution of a weed in Australia to compare to the results of the CLIMEX model. In the case of the Australian prediction for *Emex australis*, a weed of disturbed locations, it was found that the predicted distribution matched the current distribution fairly well (Pheloung et al. 1996). The predicted range was larger than the current distribution in several areas so the authors surmise that other factors such as soil type or land management may be limiting its spread. A prediction of *Asparagus asparagoides* range was similar in that it matched the current Australian distribution and predicted a slightly larger area of potential spread (Pheloung and Scott 1996). One isolated population in the predicted area was identified as a threat, but in most cases *A. asparagoides* is assumed to have already reached the limits of its potential distribution in Australia. Pheloung et al. (1996) recommended control of nascent foci in areas identified as suitable for invasion.

For California, a model of velvetleaf (*Abutilon theophrasti*) was prepared to examine the potential distribution of this agricultural weed (Holt and Boose 2000). This study used herbarium records to confirm the results of the CLIMEX model. Because velvetleaf is a weed of irrigated agriculture, they used the “Irrigation” feature of CLIMEX that allows the addition of set amounts of moisture to the meteorological database in either “winter” or “summer.” For their analysis, Holt and Boose (2000) added 70 mm per week of irrigation during the summer (April to October). They found that without irrigation, velvetleaf was not predicted to occur widely in California, and with irrigation it would be able to persist although it has likely occupied its full potential range. The parameters used for the velvetleaf CLIMEX model were compared with data available in the literature. This is an aspect of the Cape ivy model that could be improved. As information becomes available on Cape ivy's response to temperature and moisture, these data could be added to improve the model.

The results of the two Australian papers mentioned above are similar to the Cape ivy model results in that the predicted distribution of Cape ivy in California matches the actual distribution. However, the Cape ivy EI values are quite low when compared to the size and vitality of actual populations. Therefore, the use of the "Irrigation" feature is useful to improve the EI values while still matching the general shape of the distribution. This indicates that areas predicted as potential range expansions could only be occupied if supplemental moisture is available during the dry season.

### GARP

Figures 2.6 a, b and c display GARP modeling results generated with different input parameters. The Best Subsets procedure was used with 20 runs so that half of the 20 were selected by the program and those were summed using the Raster Calculator in ArcView. The legend depicts how many times the raster cells had a value of 1, so the coastal areas with darker colors had a higher probability of Cape ivy occurrence than the lighter inland areas. Figure 2.6a and b are similar; the main difference is the lack of elevation as a parameter in Figure 2.6b. The interesting result is they both predict Cape ivy occurrence in the Sacramento Delta region and northeast into the Sierra foothills. They also weakly predict occurrences in the southeastern part of California in the Mojave and Sonoran deserts. To determine whether the desert predictions were based on the elevation parameter, the elevation layer was run separately (Figure 2.6c). This analysis predicts Cape ivy should occur throughout the entire Central Valley, in the low elevation desert, and in coastal areas. Some of these areas were still predicted as potential range without using elevation, but the predictions for the Central Valley and desert decreased considerably.

The GARP results predict the area that Cape ivy is known to occupy, and they also predict that the Sacramento/San Joaquin Delta regions are potentially suitable for Cape ivy. This area is known to support Cape ivy in horticultural settings.

Two papers are available that use GARP to predict the distribution of non-native plants (Peterson et al. 2003, Underwood et al. 2004). Most of the other GARP papers available focus on predicting the distribution of mammals or birds (Godown and Peterson 2000, Anderson et al. 2002, Burton et al. 2002, Lim et al. 2002, Peterson et al. 2002, Anderson et al. 2003). Peterson et al. (2003) was the first to apply the GARP model to invasive plant species. They examined the potential distributions of garlic mustard (*Alliaria petiolata*), sericea lespedeza (*Lespedeza cuneata*), Russian olive (*Elaeagnus angustifolia*), and hydrilla (*Hydrilla verticillata*) in North America. Their analysis differs from mine in that they used a jackknife procedure on the native distribution to determine which environmental layers contributed negatively to model performance. Although their procedure was more detailed than mine, they also used a best subsets procedure when making their North American predictions. Interestingly, the jackknife procedure eliminated elevation as a variable in the final analysis for garlic mustard and sericea lespedeza. The main difference between their study and mine is the use of the native distribution to model the non-native distribution. Perhaps in the future enough information would be available on Cape ivy's native distribution to apply this methodology.

One study was published using GARP to predict non-native species distributions in Yosemite National Park, California (Underwood et al. 2004). They used logistic regression on plot data instead of a jackknife procedure to select the environmental variables to use in their GARP model. The variables used in the GARP analysis were percent cover of trees, shrubs and herbaceous species, and slope and elevation. Elevation was eliminated as a variable in the Cape ivy analysis; perhaps this reflects the smaller scale of the Yosemite study as compared to the state-wide analysis. In their study, models were run a set number of times and then the best subsets were added at the end to develop the final prediction surface. Their models predicted some widespread, unsampled areas that will be the focus of future monitoring efforts. This study emphasizes the usefulness of collecting plot data from locations of non-native plants to use in fine scale modeling efforts. This approach might be useful for a management area such as Golden Gate National Recreation Area (GGNRA) that has an active Cape ivy removal program. The managers at GGNRA could use predictive modeling based on plot data determine where best to focus their control efforts.

## GARP and CLIMEX Comparison

The CLIMEX and GARP models are similar in most of their predictions of Cape ivy distribution along the California coast, but they differ in predictions for the potential of Cape ivy to spread inland. The most comparable models are Figure 2.5d and 2.6b, because 2.6b does not include elevation and that is not a factor in the CLIMEX model. Both predict the potential for Cape ivy to occupy the Sacramento area and the foothills directly to the east near Auburn and Placerville. The CLIMEX prediction is geographically broader, ranging from the east side of the Great Valley north of Redding at Shasta Dam to east of Fresno. GARP, by comparison, predicts only a slight potential for range expansion into the northern and southern Sierra foothills.

## CONCLUSIONS

The questions originally posed in this portion of the research were successfully addressed and some other interesting information was gained in the process. The first question of where Cape ivy occurs in California was answered through collection of information from experts and field mapping. This information will be made available to local weed management professionals, and when an electronic repository of California weed locations is developed, it will be included in that database.

The second question about what types of plant communities contain populations of stipulate and non-stipulate forms of Cape ivy was also addressed. We found Cape ivy occurring in seven different broad community types and predict that it should occur in five additional community types (Table 2.6). This refutes the common assumption that Cape ivy is an exclusively riparian weed. Some examples of non-riparian types it occupied were coastal scrub, chaparral, oak woodland and conifer forest. Some state-wide trends in distribution of morphological types were observed. Non-stipulate types occurred more frequently at the northern and southern ends of the distribution, while stipulate types were frequently found in the middle of the distribution, from southern Humboldt County to Los Angeles. Only 21 locations were found that supported both stipulate and non-stipulate plants and they were most often found in urbanized coastal areas. More detailed information could be compiled on this topic, with the collection of plot data within Cape ivy populations. A correlation analysis of Cape ivy occurrence with parameters such as soil moisture, soil type, canopy cover, slope, aspect, or specific plant species associates might provide further insight into factors containing the spread of the species. The results of this type of analysis could be useful in parameterizing predictive models such as CLIMEX and GARP.

In addition to the information gained on California Cape ivy, GIS analysis was used to compile information on the South African distribution. Using actual occurrence data, six different ecoregions where Cape ivy occurs were identified (Table 2.2). Occurrence data were also used to determine the nearest weather stations in CLIMEX and then a Match Climates analysis was used to identify matching weather stations in California. This provided useful information because it indicated that California climates most closely match South African weather stations near Cape ivy locations in the Eastern Cape (see Figure 2.2 and Table 2.9). This information could be useful for the ongoing biological control effort because insect collections could be focused in the Eastern Cape Province.

The third question on what might be the potential distribution of the species in California based on its native range and the climates found in California, was addressed using GIS analysis as well as CLIMEX and GARP models. GIS analysis was used to determine the elevation, temperature and precipitation ranges that Cape ivy occupies in California. These environmental determinants of climatic range were used to select parameters for the GARP model, and the CLIMEX model was run based on the climates found in Cape ivy’s native range. Potential range expansions were predicted for the San Joaquin Delta and Sierra Nevada foothills, as well as along riparian areas in the Central

Valley. This information could be used to develop a watch list of areas which could be invaded.

One of the over-arching questions of this dissertation is how can knowledge of Cape ivy biology contribute to its management? The preliminary state-wide mapping now available will be an aid in regional weed planning and can be used by local Weed Management Areas to identify the threat Cape ivy poses in their area. Another practical application of the distribution data and GIS was the CNDDB sensitive species overlay analysis. Although the threat to native species biodiversity was not directly measured, the CNDDB dataset served as a surrogate for native biodiversity. The findings that six plants of limited distribution and 50% of steelhead streams were in the potential expansion range of Cape ivy populations is a significant result for those concerned with management of both plant and animal species in California.

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**Table 2.1. Attributes of Cape Ivy Final Mapping Shapefiles**

| **Field Name** | **Description** |
|---|---|
| SHAPE | All points |
| SITECODE | Map identification point, using county abbreviation and number |
| COUNTY | County |
| GPS | True or False |
| VISITED | Date of GPS |
| SURVEYOR | Surveyor or source of data |
| ENTEREDBY | Person digitized by |
| DATAFILE | Name of rover file for GPS data or original shapefile name |
| SCI_NAME | *Delairea odorata* |
| COMMENT | Source of data, location, directions, etc. |
| GPS CODE | Waypoint code for eTrex Vista data |
| VEGTYPE | Holland (1986) numerical code used by CAGAP (Davis et al. 1998) |
| ST_NS | Either stipulate (ST), non-stipulate (NS) or both (STNS) |
| VIABLE | Viable seeds present, Yes or No |
| LATITUDE | Generated with the “add XY” tool in ArcView 9.0 after conversion to the NAD83 datum. |
| LONGITUDE | Generated with the “add XY” tool in ArcView 9.0 after conversion to the NAD83 datum. |

**Table 2.2. South African Terrestrial Ecoregions Cape Ivy Occurs in, Number of Collections, Observed Elevation and Climate**

| **Terrestrial Ecoregions with Cape Ivy Occurrence** | **South African Province** | **N CI pts[1]** | **Elevations (m)[1]** | **Temperature ºC** | **Precipitation Patterns, Rainfall Averages** |
|---|---|---|---|---|---|
| Knysna-Amatole montane forests | Western Cape<br>Eastern Cape | 6 | 5 to 200 | Mean temperatures 23.8 in February (summer) and 18.2 in August (winter) | Rainfall throughout the year with maxima in early and late summer.<br>Annual rainfall between 525 and 1220 mm |
| Lowland fynbos and renosterveld | Eastern Cape | 3 | 100 to 300 | Little frost and temperatures up to 30 | Winter rain between 250 and 2000 mm annually, most commonly between 300 and 750 mm |
| Albany thickets | Eastern Cape | 3 | 50 to 100 | Average temperature range 10 to 35 | Non-seasonal, sporadic rainfall. Valley mists common towards the coast, provide additional moisture<br>450 to 550 mm annual rainfall |
| KwaZulu-Cape coastal forest mosaic | Eastern Cape | 5 | 50 to 250 | Mean maximum temp 15 to 24, mean min temp 10 to 15 | Northern extent has more rain in summer, south has lower rainfall in the winter. Precipitation range 900 to 1500 mm |
| Drakensberg montane grasslands, woodlands and forests | Eastern Cape<br>KwaZulu-Natal<br>Mpumalanga | 17 | 400 to 1800 | Little snow but severe frost, temps range from –13 to 40, averaging 15 | Annual precipitation range 450 to 1100 mm |
| Maputaland-Pondoland brushland and thickets | Eastern Cape | 2 | 150 to 600 | Temperature range from 12 to 26 with no frost | 75% of annual precipitation falls in warm summer months between October and March. Rainfall per year is below 800 mm. |
| Both Drakensberg and Maputaland | KwaZulu-Natal | 5 | 900 to 1600 | -- | -- |

1. Number of collections in a terrestrial ecoregion and approximate elevations observed by Grobbelaar et al. (1999).

**Table 2.3. Cape Ivy Distribution Attributes Extracted from BIOCLIM[1] Raster Data (N=932 except where noted)**

| BIOCLIM Variable | Mean ± SE | Minimum Value | Maximum Value | Notes |
|---|---|---|---|---|
| Elevation (m) N=1057 | 66.7 | 0 | 891 | Source: USDA |
| **Annual Mean Temperature (ºC)** | **13.3 ± 0.04** | **10.5** | **17.7** | |
| Max Temperature of Warmest Month (ºC) | 23.2 ± 0.08 | 19.5 | 31.8 | |
| Min Temperature of Coldest Month (ºC) | 4.6 ± 0.03 | 1.8 | 7.9 | |
| Temperature Annual Range | 18.6 ± 0.09 | 14.4 | 29 | Max temp warmest month-Min temp coldest month |
| Mean Temperature of Wettest Quarter[2] (ºC) | 10.3 ± 0.04 | 7.8 | 14 | |
| Mean Temperaure of Driest Quarter (ºC) | 16.5 ± 0.06 | 12.4 | 22.9 | |
| Mean Temperature of Warmest Quarter (ºC) | 17 ± 0.06 | 13.4 | 23.5 | |
| Mean Temperature of Coldest Quarter (ºC) | 0.2 ± 0.09 | 0 | 2.4 | |
| Mean Diurnal Range (ºC) | 10.8 ± 0.06 | 8 | 15 | [Mean of monthly (max temp-min temp)] |
| Temperature Seasonality | 28.2 ± 0.2 | 15.4 | 49.8 | Standard deviation |
| **Mean Annual Precipitation (mm)** | **826 ± 11** | **232** | **2270** | |
| Precipitation of Wettest Month (mm) | 140 ± 1.6 | 37 | 328 | |
| Precipitation of Driest Month (mm) | 1.1 ± 0.04 | 0 | 10 | |
| Precipitation of Wettest Quarter (mm) | 369 ± 4.5 | 101 | 950 | |
| Precipitation of Driest Quarter (mm) | 8.2 ± 0.3 | 0 | 72 | |
| Precipitation of Warmest Quarter (mm) | 20.1 ± 0.6 | 2 | 87 | |
| Precipitation of Coldest Quarter (mm) | 8.2 ± 0.3 | 0 | 72 | |
| Precipitation Seasonality | 78.5 ± 0.13 | 63 | 89 | Coefficient of Variation |

1. BIOCLIM link http://biogeo.berkeley.edu/worldclim/bioclim.htm
2. Quarter is three months (1/4 of the year)

**Table 2.4. CLIMEX Parameters Used for Cape Ivy Model with Comparisons to the Mediterranean Template and *Asparagus asparagoides***

| Parameter Group | Parameter | Mediterranean Template | *A. asparagoides*[1] | Cape Ivy |
|---|---|---|---|---|
| Temperature Index | DV0 | 10 | 10 | 7 |
| | DV1 | 16 | 15 | 16 |
| | DV2 | 24 | 18 | 23 |
| | DV3 | 28 | 30 | 30 |
| Moisture Index | SM0 | 0.1 | 0.3 | 0.3 |
| | SM1 | 0.4 | 0.5 | 0.6 |
| | SM2 | 0.7 | 1.2 | 1.1 |
| | SM3 | 1.5 | 1.5 | 2 |
| Cold Stress | TTCS | 0 | 6 | 5 |
| | THCS | 0.005 | 0.001 | 0.001 |
| | DTCS | 15 | 15 | 15 |
| | DHCS | 0.001 | 0.0001 | 0.001 |
| Heat Stress | TTHS | 30 | 30 | 30 |
| | THHS | 0.002 | 0.005 | 0.002 |
| | DTHS | 0 | 0 | 0 |
| | DHHS | 0 | 0 | 0 |
| Dry Stress | SMDS | 0.02 | 0.2 | 0.02 |
| | HDS | 0.05 | 0.005 | 0.05 |
| Wet Stress | SMWS | 1.6 | 2.5 | 2.5 |
| | HWS | 0.0015 | 0.002 | 0.002 |
| Hot-Wet Stress | TTHW | 23 | 20 | 23 |
| | MTHW | 0.5 | 1.2 | 0.5 |
| | PHW | 0.075 | 0.1 | 0.075 |

1. Phelong and Scott, 1996.

**Table 2.5. Cape Ivy Community Types Predicted with CAGAP or Observed**

| CNDDB Community Type Code[1] | General Type | Specific Type | N CAGAP | N Field Data |
|---|---|---|---|---|
| 11100 | Urban or agriculture | Urban or built-up land | 92 | 33 |
| 11200 | Urban or agriculture | Agricultural land | 40 | -- |
| 11201 | Urban or agriculture | Row and field crops | 1 | -- |
| 11210 | Urban or agriculture | Orchards and vineyards | 3 | -- |
| 11300 | Non-native forest | Eucalyptus | 1 | 11 |
| 11510 | Waterways | Streams and canals | 1 | -- |
| 11540 | Waterways | Bays and estuaries | 9 | -- |
| 11720 | Beaches and Dunes | Beaches and coastal dunes | 4 | -- |
| 11730 | Beaches and Dunes | Sandy areas other than beaches | 2 | -- |
| 21310 | Coastal Scrub | Northern dune scrub | -- | 1 |
| 21320 | Coastal Scrub | Central dune scrub | 2 | -- |
| 31100 | Coastal Scrub | Northern coastal bluff scrub | | 12 |
| 31200 | Coastal Scrub | Southern coastal bluff scrub | 3 | -- |
| 32100 | Coastal Scrub | Northern (Franciscan) coastal scrub | 22 | 12 |
| 32200 | Coastal Scrub | Central (Lucian) coastal scrub | 26 | 5 |
| 32300 | Coastal Scrub | Venturan coastal sage scrub | 9 | 3 |
| 32500 | Coastal Scrub | Diegan coastal sage scrub | 1 | -- |
| 32600 | Coastal Scrub | Diablan sage scrub | 1 | -- |
| 37110 | Chaparral | Northern mixed chaparral | 3 | -- |
| 37200 | Chaparral | Chamise chaparral | 5 | -- |
| 37810 | Chaparral | Buck brush chaparral | 3 | -- |
| 37820 | Chaparral | Blue brush chaparral | 5 | -- |
| 37830 | Chaparral | Hoary-leaved chaparral | 3 | -- |
| 37840 | Chaparral | Big pod chaparral | 11 | -- |
| 37C20 | Chaparral | Central maritime chaparral | 1 | -- |
| 37G00 | Chaparral | Coastal sage-chaparral scrub | 4 | -- |
| 41000 | Prairie | Coastal prairie | 26 | -- |
| 42200 | Non-native grassland | Non-native grassland | 51 | -- |
| 52110 | Salt marsh | Northern coastal salt marsh | 1 | -- |
| 52120 | Salt marsh | Southern coastal salt marsh | 1 | 1 |
| 52410 | Freshwater marsh | Coastal and valley freshwater marsh | 1 | -- |
| 61110 | Riparian forest | Northern coast black cottonwood riparian forest | -- | 1 |
| 61130 | Riparian forest | Red alder riparian forest | -- | 23 |
| 61210 | Riparian forest | Central coast cottonwood-sycamore riparian forest | -- | 2 |
| 61220 | Riparian forest | Central coast live oak riparian forest | -- | 1 |
| 61230 | Riparian forest | Central coast arroyo willow riparian forest | 2 | 28 |
| 61310 | Riparian forest | Southern coast live oak riparian forest | -- | 2 |
| 61320 | Riparian forest | Southern arroyo willow riparian forest | -- | 6 |

| Table 2.5. Cape Ivy Community Types Predicted with CAGAP or Observed | | | | |
|---|---|---|---|---|
| **CNDDB Community Type Code[1]** | **General Type** | **Specific Type** | **N CAGAP** | **N Field Data** |
| 62100 | Riparian forest | Sycamore alluvial woodland | -- | 1 |
| 62400 | Riparian forest | Southern sycamore-alder riparian woodland | -- | 4 |
| 63100 | Riparian forest | Northern coast riparian scrub | -- | 21 |
| 63310 | Riparian scrub | Mule fat scrub | 1 | -- |
| 63320 | Riparian scrub | Southern willow scrub | -- | 1 |
| 71160 | Oak woodland | Coast live oak woodland | 4 | 13 |
| 81100 | Conifer forest | Mixed evergreen forest | 20 | -- |
| 81310 | Oak woodland | Coast live oak forest | 9 | -- |
| 82100 | Conifer forest | Sitka spruce-grand fir forest | 4 | -- |
| 82310 | Conifer forest | Alluvial redwood forest | 1 | -- |
| 82320 | Conifer forest | Upland redwood forest | 38 | 1 |
| 82420 | Conifer forest | Upland Douglas fir forest | 1 | -- |
| 83120 | Conifer forest | Bishop pine forest | 6 | 1 |
| 83130 | Conifer forest | Monterey pine forest | 7 | -- |
| 83161 | Conifer forest | Mendocino pygmy cypress forest | 1 | -- |
| 84110 | Conifer forest | Coast range mixed conifer forest | 1 | -- |
| 84130 | Conifer forest | Coast range ponderosa pine forest | 1 | -- |
| 84180 | Conifer forest | Ultramafic mixed coniferous forest | 1 | -- |
| 1. Community codes from Holland (1986). | | | | |

**Table 2.6. Summary of Cape Ivy Community Types Predicted with CAGAP or Observed and Their Area of California Based on CAGAP Statewide Totals**

| **General Type** | **Predicted N CAGAP** | **Observed N Field Data** | **Total Mapped Area in California (km$^2$)** |
|---|---|---|---|
| Urban and Agriculture | 100 | 33 | 70,778 |
| Non-native forest (*Eucalyptus*) | 1 | 11 | 35 |
| Beaches and Dunes | 6 | 0 | 73 |
| Coastal Scrub | 64 | 33 | 5,857 |
| Chaparral | 35 | 0 | 14,543 |
| Coastal Prairie | 26 | 0 | 880 |
| Non-native grassland | 51 | 0 | 27,483 |
| Coastal salt marsh | 2 | 1 | 11 |
| Freshwater marsh | 1 | 0 | 501 |
| Riparian forest | 3 | 82 | 374 |
| Oak woodland | 13 | 13 | 3,366 |
| Conifer forest | 81 | 2 | 21,333 |
| **Total** | **383** | **175** | **145,234** |

| Table 2.7. CNDDB Sensitive Species Overlap with Cape Ivy Summarized by Group Classification | | | | |
|---|---|---|---|---|
| **Group Classification** | **N polygons 100/m** | **Mean # polygons 100/m ± SE** | **N polygons 500/m** | **Mean # polygons 500/m ± SE** |
| Natural Community | 24 | 2.1 ± 0.3 | 35 | 2.4 ± 0.4 |
| Non-Vascular Plant | 8 | 1 | 8 | 1.5 ± 0.3 |
| Vascular Plant | 163 | 2.2 ± 0.1 | 211 | 2.8 ± 0.2 |
| Invertebrate | 32 | 3.5 ± 1.3 | 37 | 5.1 ± 2.2 |
| Fish | 7 | 9.3 ± 4.6 | 9 | 10 ± 5.0 |
| Reptile | 7 | 3.4 ± 1.1 | 9 | 4.8 ± 1.5 |
| Amphibian | 4 | 4.8 ± 2.8 | 8 | 6.9 ± 4.6 |
| Bird | 20 | 2.6 ± 0.6 | 28 | 3.3 ± 0.8 |
| Mammal | 13 | 2.2 ± 0.5 | 18 | 2.8 ± 0.6 |

**Table 2.8. CNDDB Sensitive Species Polygons Overlapped by Cape Ivy at Two Buffer Sizes**

| Scientific Name | Common Name | Number of occurrences tracked by CNDDB | Occurrence overlap predicted with 100 m buffer | Occurrence overlap predicted with 500 m buffer | Percentage of Total tracked Occurrences 100 m/500 m |
|---|---|---|---|---|---|
| *Rana aurora draytonii* | California red-legged frog | 831 | 13 | 39 | 1.6/4.7 |
| *Charadrius alexandrinus nivosus* | Western snowy plover | 109 | 13 | 22 | 12/20 |
| *Eucyclogobius newberryi* | Tidewater goby | 112 | 28 | 41 | 25/37 |
| *Oncorhynchus mykiss irideus* | Steelhead Central Coast | 28 | 13 | 14 | 46/50 |
| *Oncorhynchus mykiss irideus* | Steelhead South/Central Coast | 27 | 9 | 12 | 33/44 |
| *Oncorhynchus mykiss irideus* | Southern steelhead Southern California | 12 | 4 | 5 | 33/42 |
| *Danaus plexippus* | Monarch butterfly | 335 | 43 | 83 | 13/25 |
| *Arborimus pomo* | Red tree vole | 208 | -- | 10 | --/5 |
| *Emys (=Clemmys) marmorata* | Western pond turtle | 302 | -- | 11 | --/3.6 |
| *Emys (=Clemmys) marmorata pallida* | Southwestern pond turtle | 308 | -- | 13 | --/4.2 |
| *Campanula californica* | Swamp harebell | 100 | -- | 10 | --/10 |
| *Castilleja mendocinensis* | Mendocino coast Indian paintbrush | 42 | -- | 12 | --/29 |
| *Chorizanthe cuspidata* var. *cuspidata* | San Francisco Bay spineflower | 20 | -- | 10 | --/50 |
| *Cirsium andrewsii* | Franciscan thistle | 27 | -- | 11 | --/41 |
| *Grindelia hirsutula* var. *maritima* | San Francisco gumplant | 15 | -- | 11 | --/73 |
| *Lasthenia macrantha* ssp. *macrantha* | Perennial goldfields | 32 | -- | 13 | --/41 |
| *Microseris paludosa* | Marsh microseris | 22 | -- | 10 | --/46 |

| Table 2.9. South African Weather Stations Occuring Closest to Cape Ivy Collections and Climatic Similarities Determined with Match Climates Feature in CLIMEX | | |
|---|---|---|
| **South Africa Weather Stations Nearest Cape Ivy Collections** | **South African Province** | **# California Stations Matched** |
| Addo | Eastern Cape | 10 |
| Bird Island | Eastern Cape | 7 |
| Cape St. Francis | Eastern Cape | 7 |
| Cedara | KwaZulu-Natal | 0 |
| Deepwalls | Western Cape | 0 |
| East London | KwaZulu-Natal | 0 |
| George | Western Cape | 0 |
| Grahamstown | Eastern Cape | 4 |
| Grootspruit | KwaZulu-Natal | 2 |
| Hermitage | Eastern Cape | 9 |
| King Williamtown | Eastern Cape | 3 |
| Kokstad | KwaZulu-Natal | 0 |
| Ladysmith | KwaZulu-Natal | 0 |
| Lovedale | Eastern Cape | 5 |
| Lydenburg | Mpumalanga | 0 |
| Melmoth | KwaZulu-Natal | 0 |
| Nottingham Road | KwaZulu-Natal | 0 |

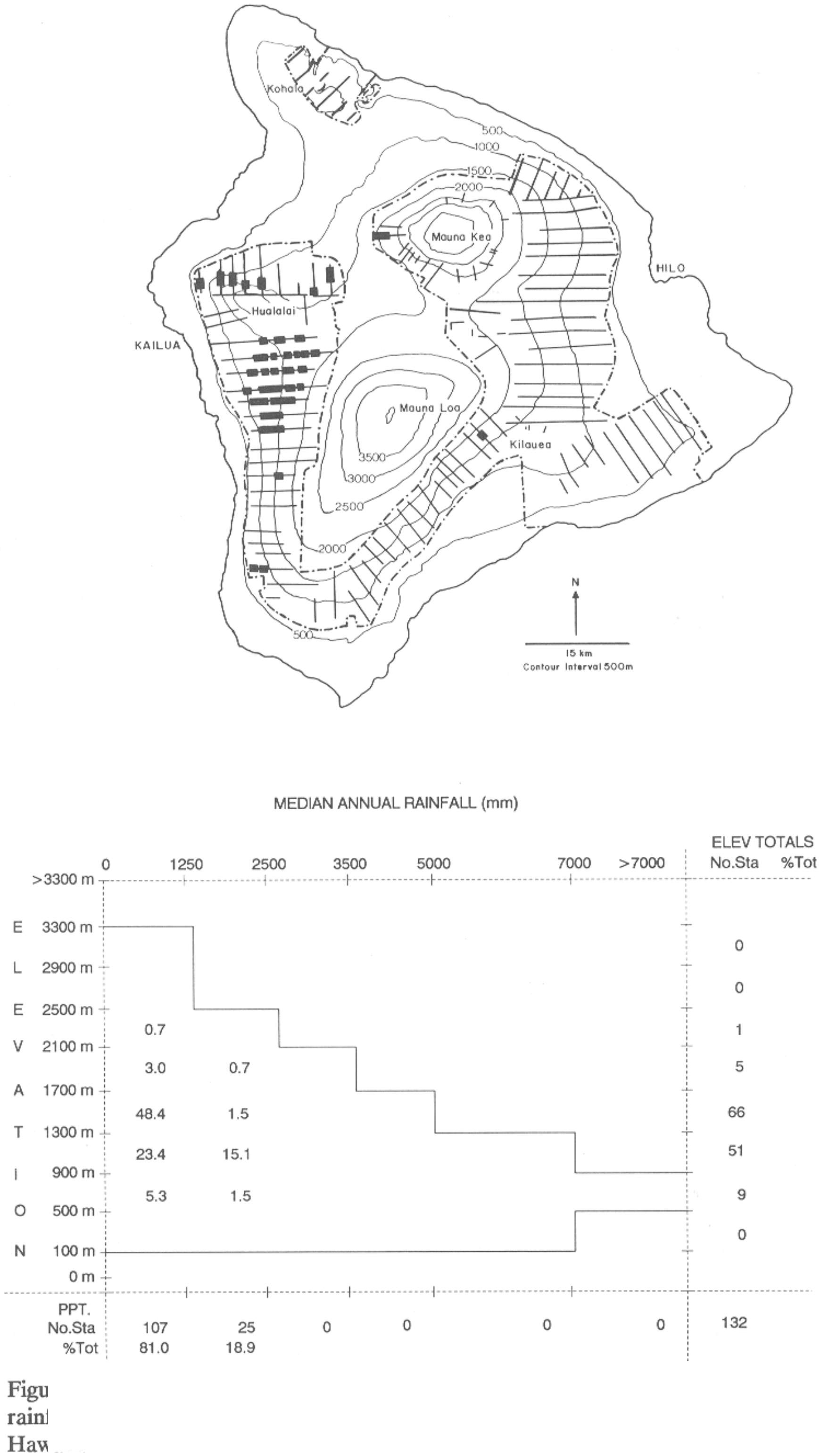


Figure 2.1a. Cape Ivy Occurrence During the Hawai'i Forest Bird Survey on the Island of Hawai'i and Plot of Percent Total Stations Containing Cape Ivy in Elevation and Rainfall Classes. Source Jacobi and Warshauer 1992.

**Figure 2.1b. Predicted Distribution of Cape Ivy Along the Hawai’i Forest Bird Survey Transects on The Island of Hawai’i Based on Median Annual Rainfall and Elevation of Sites Where the Species was Found in 1976-1981. Source Jacobi and Warshauer 1992.**

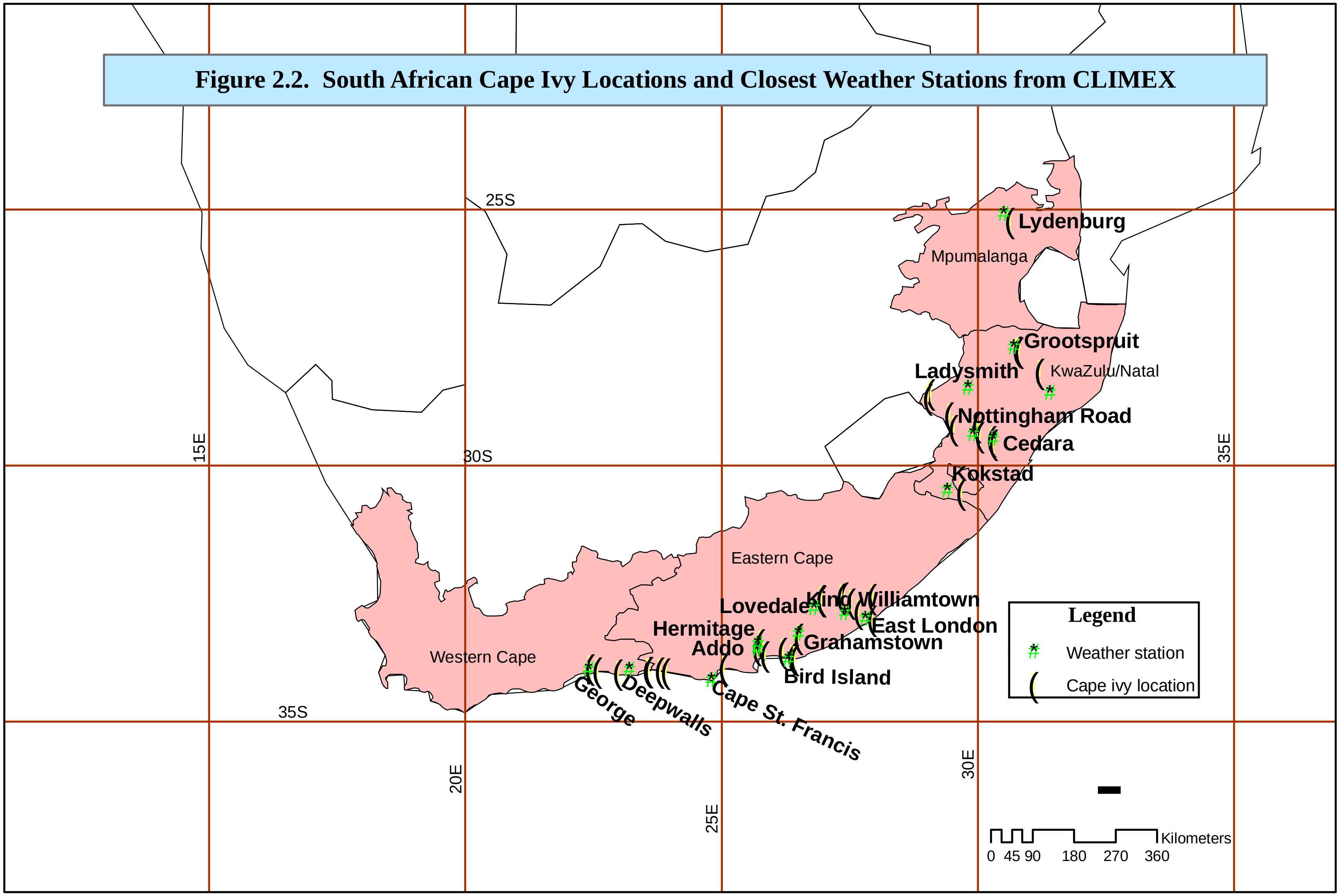
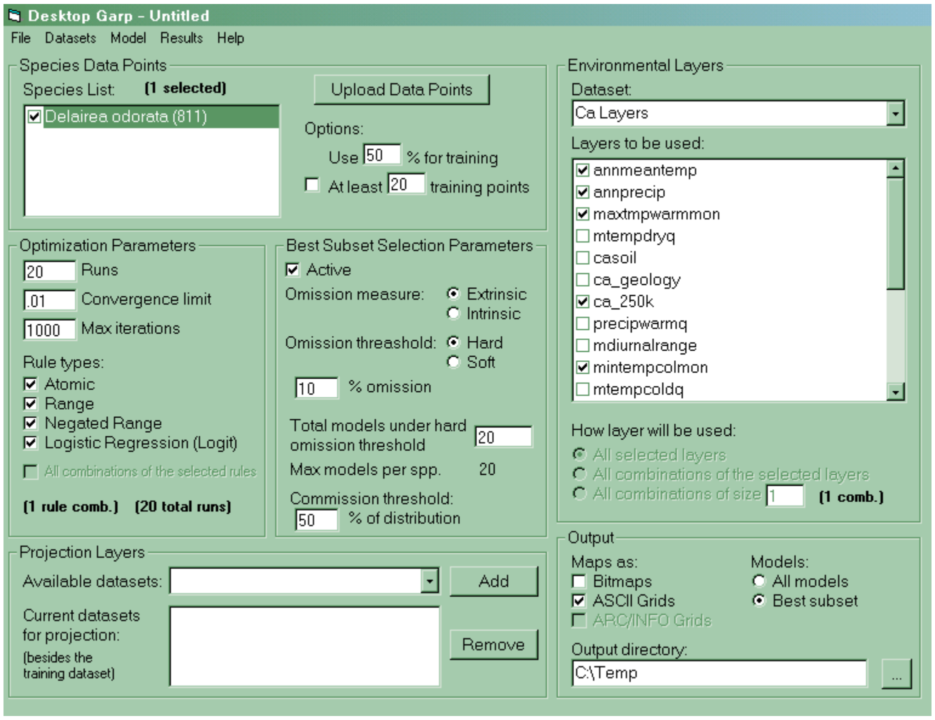


Figure 2.2. South African Cape Ivy Locations and Closest Weather Stations from CLIMEX



Species Data Points

Species List: **(1 selected)**

☑ Delairea odorata (811)

Options:

Use 50 % for training

☐ At least 20 training points

Optimization Parameters

20 Runs

.01 Convergence limit

1000 Max iterations

Rule types:

- ☑ Atomic
- ☑ Range
- ☑ Negated Range
- ☑ Logistic Regression (Logit)
- ☐ All combinations of the selected rules

**(1 rule comb.)** **(20 total runs)**

Best Subset Selection Parameters

☑ Active

Omission measure: ● Extrinsic ○ Intrinsic

Omission threashold: ● Hard ○ Soft

10 % omission

Total models under hard omission threshold 20

Max models per spp. 20

Commission threshold: 50 % of distribution

Projection Layers

Available datasets:

Current datasets for projection: (besides the training dataset)

Environmental Layers

Dataset: Ca Layers

Layers to be used:

- ☑ annmeantemp
- ☑ annprecip
- ☑ maxtmpwarmmon
- ☐ mtempdryq
- ☐ casoil
- ☐ ca_geology
- ☑ ca_250k
- ☐ precipwarmq
- ☐ mdiurnalrange
- ☑ mintempcolmon
- ☐ mtempcoldq

How layer will be used:

- ● All selected layers
- ○ All combinations of the selected layers
- ○ All combinations of size 1 **(1 comb.)**

Output

Maps as:

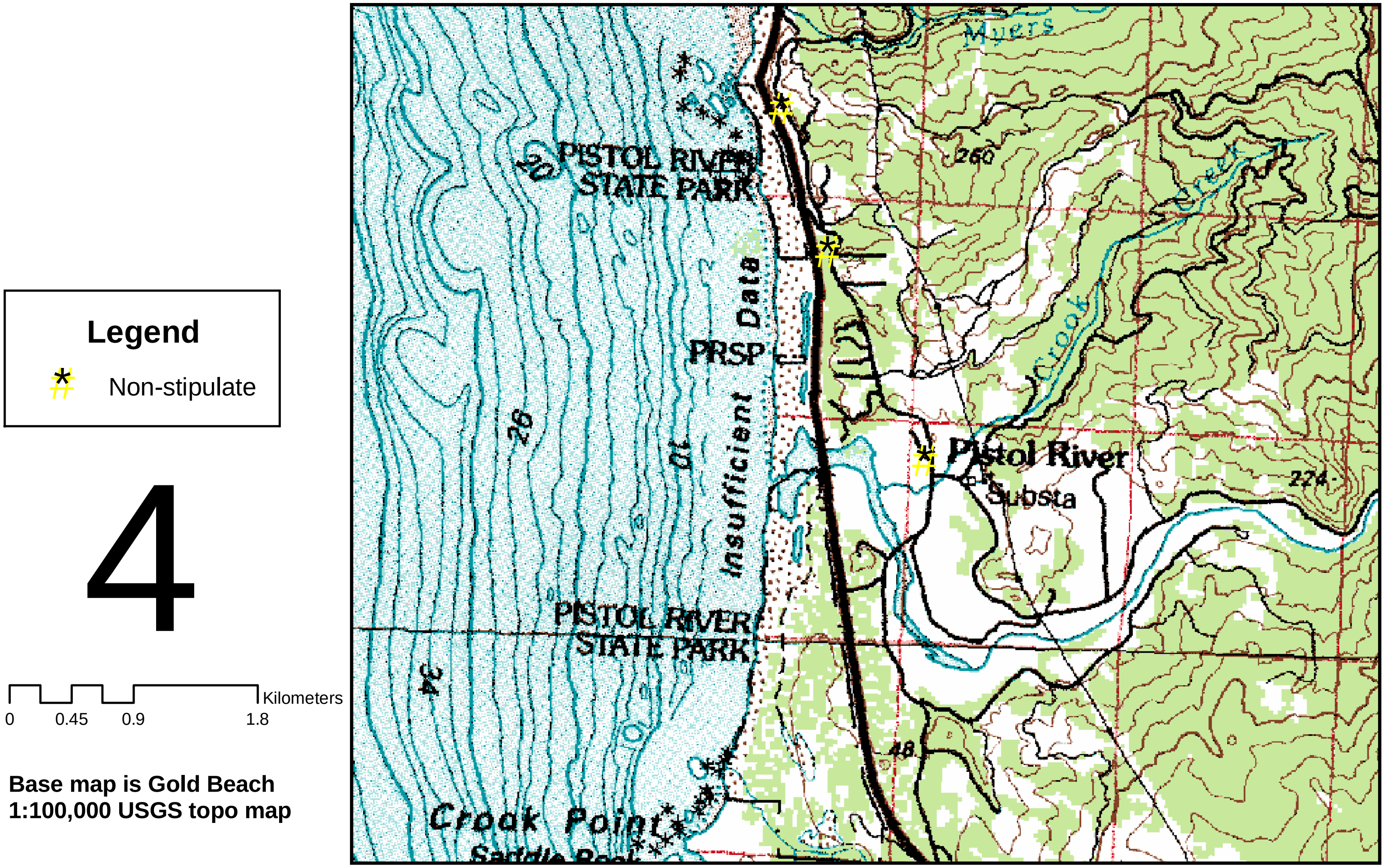
- ☐ Bitmaps
- ☑ ASCII Grids
- ☐ ARC/INFO Grids

Models:

- ○ All models
- ● Best subset

Output directory: C:\Temp

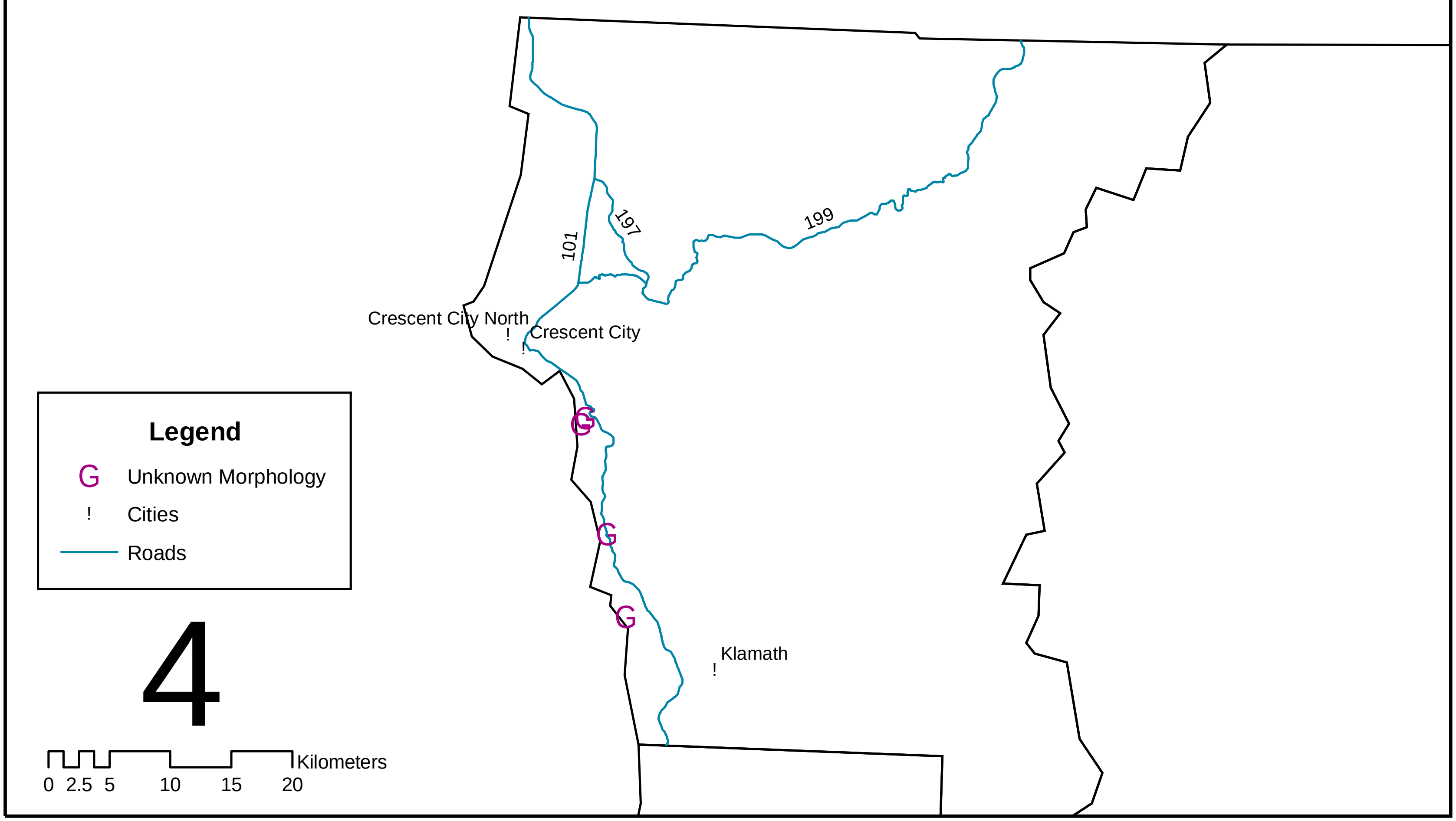
**Figure 2.3. GARP Model Set-Up Example**



Base map is Gold Beach
1:100,000 USGS topo map

Figure 2.4a. Curry County, Oregon, Cape Ivy Locations

**Figure 2.4b. Del Norte County Cape Ivy Locations**



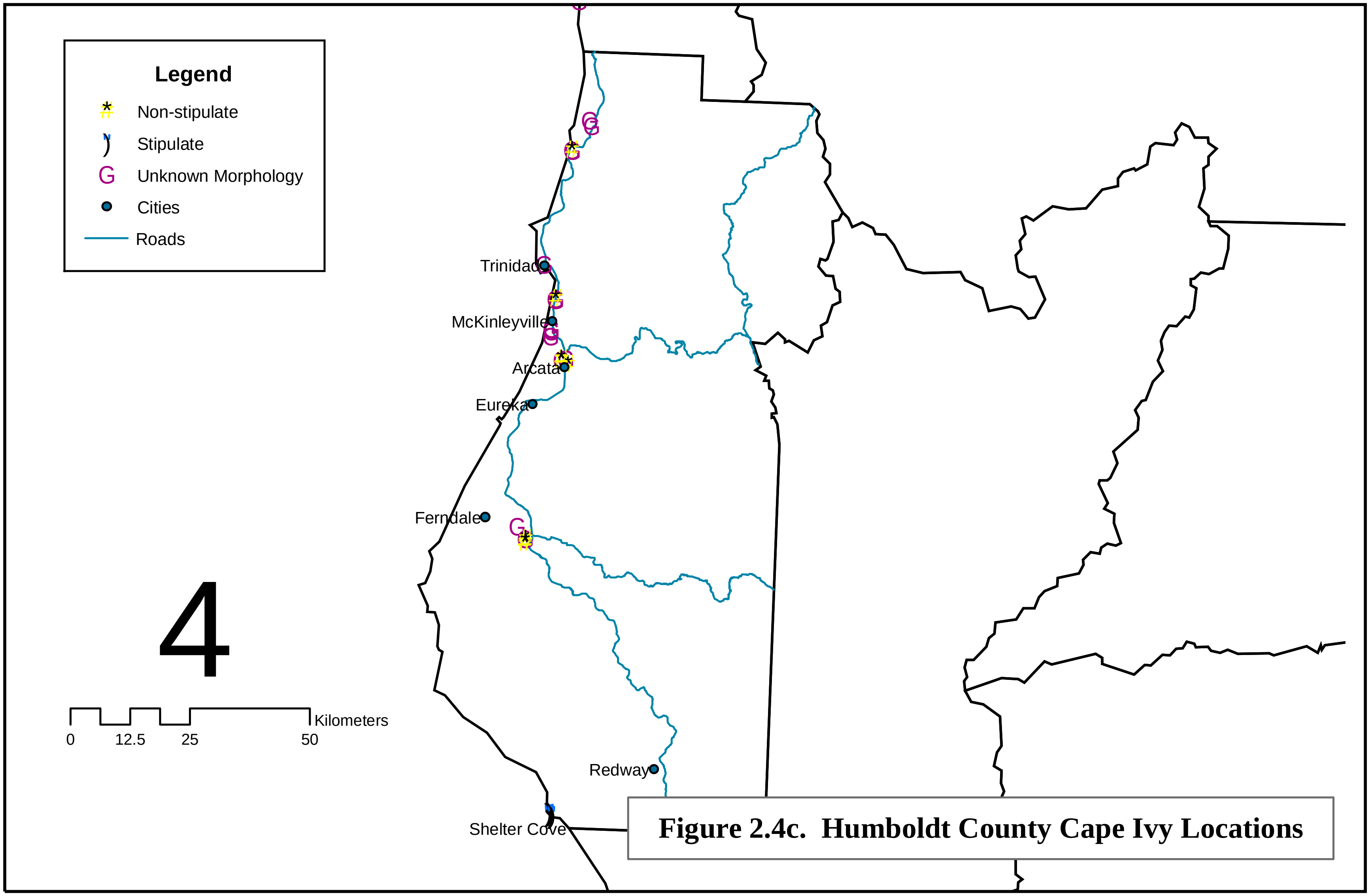


Figure 2.4c. Humboldt County Cape Ivy Locations

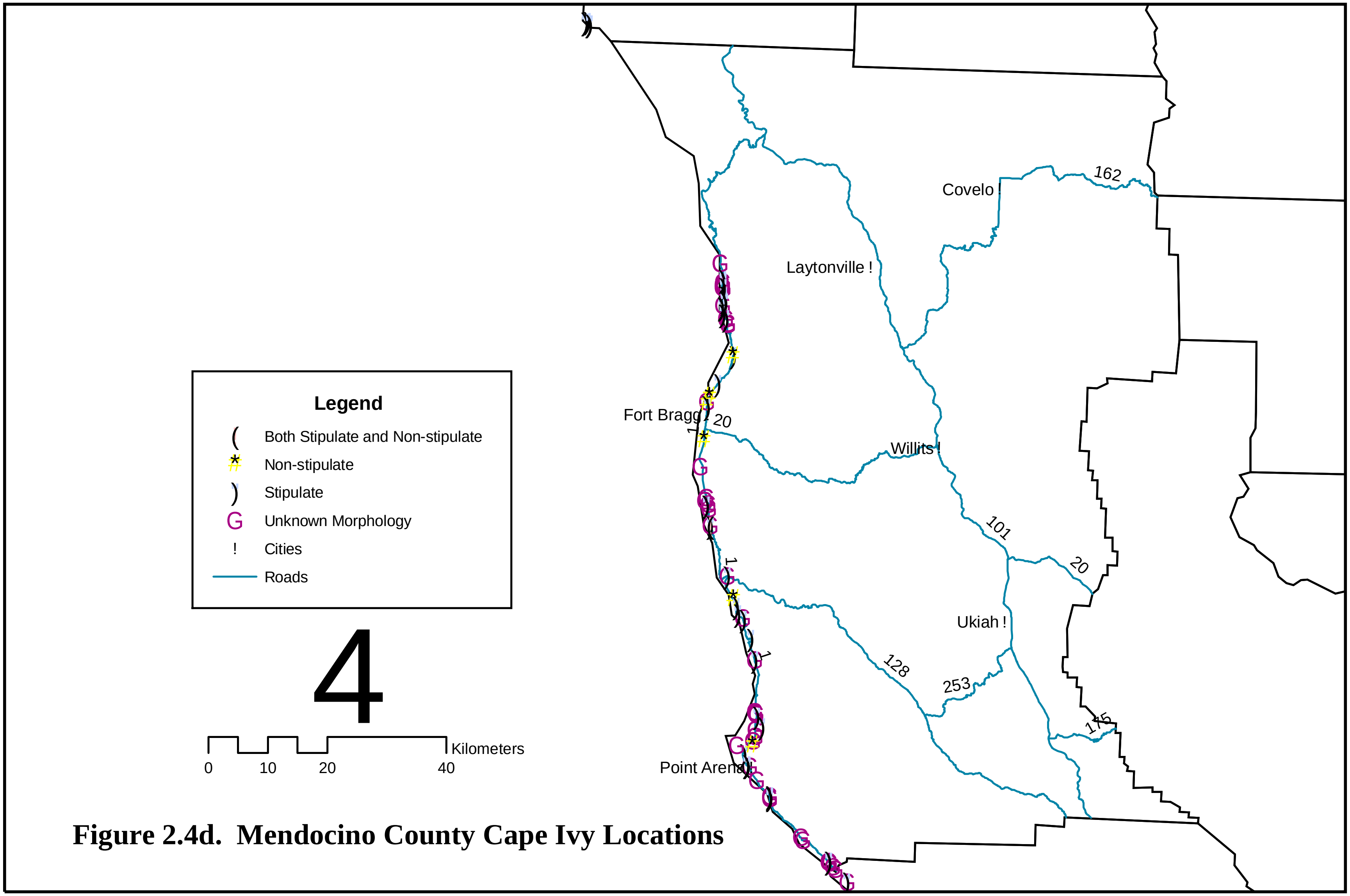


**Figure 2.4d. Mendocino County Cape Ivy Locations**

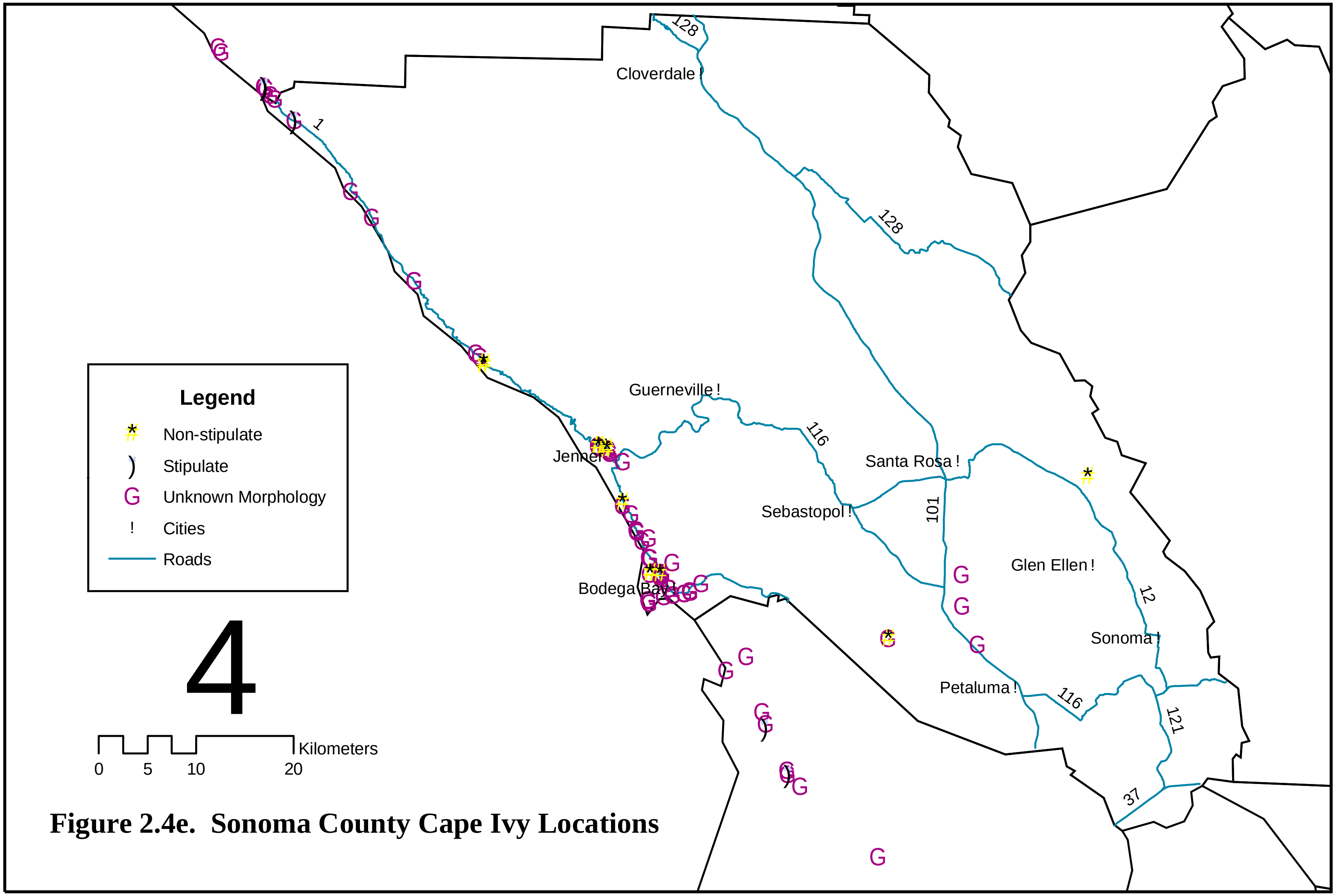


**Figure 2.4e. Sonoma County Cape Ivy Locations**

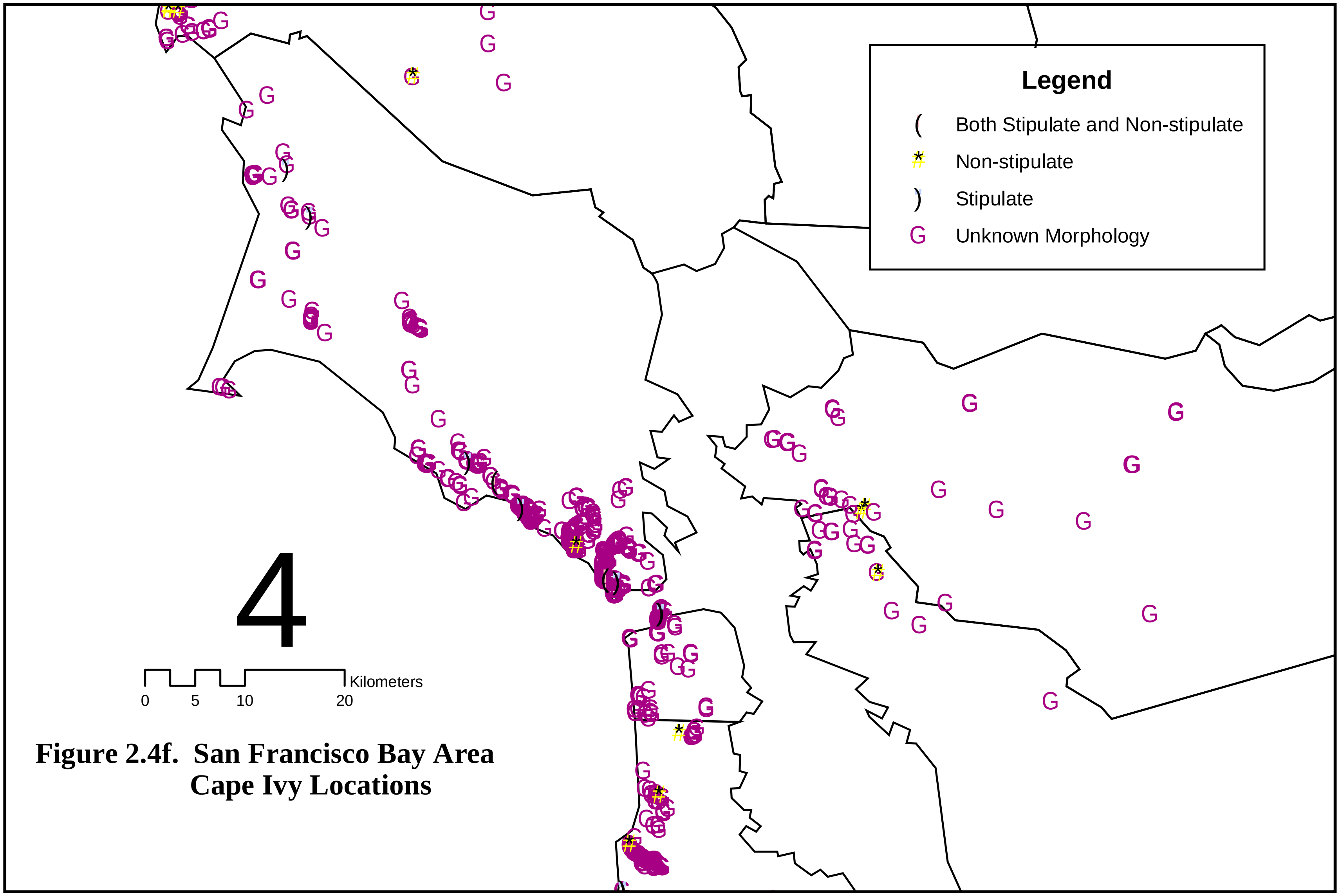


**Figure 2.4f. San Francisco Bay Area Cape Ivy Locations**

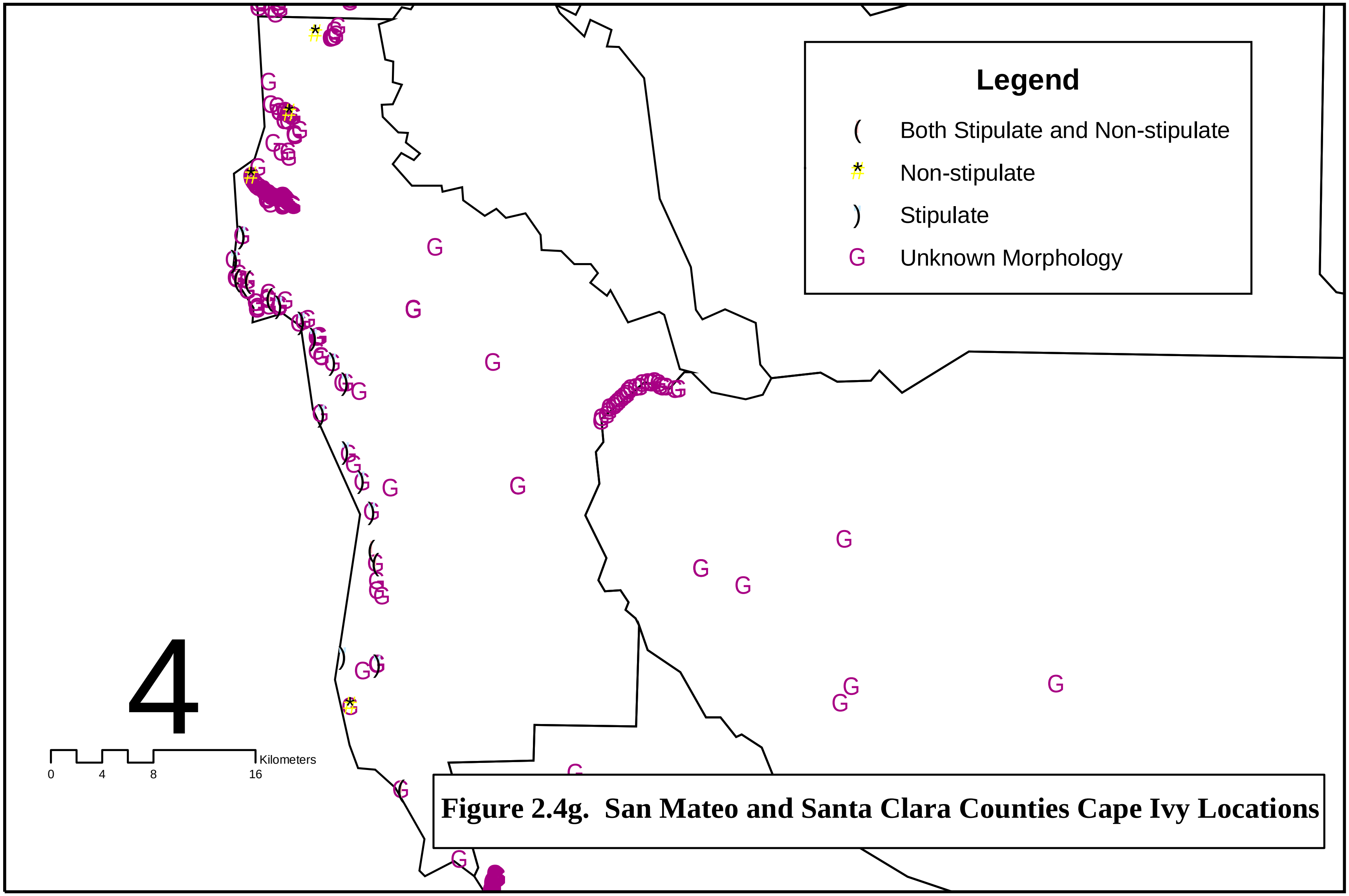


Figure 2.4g. San Mateo and Santa Clara Counties Cape Ivy Locations

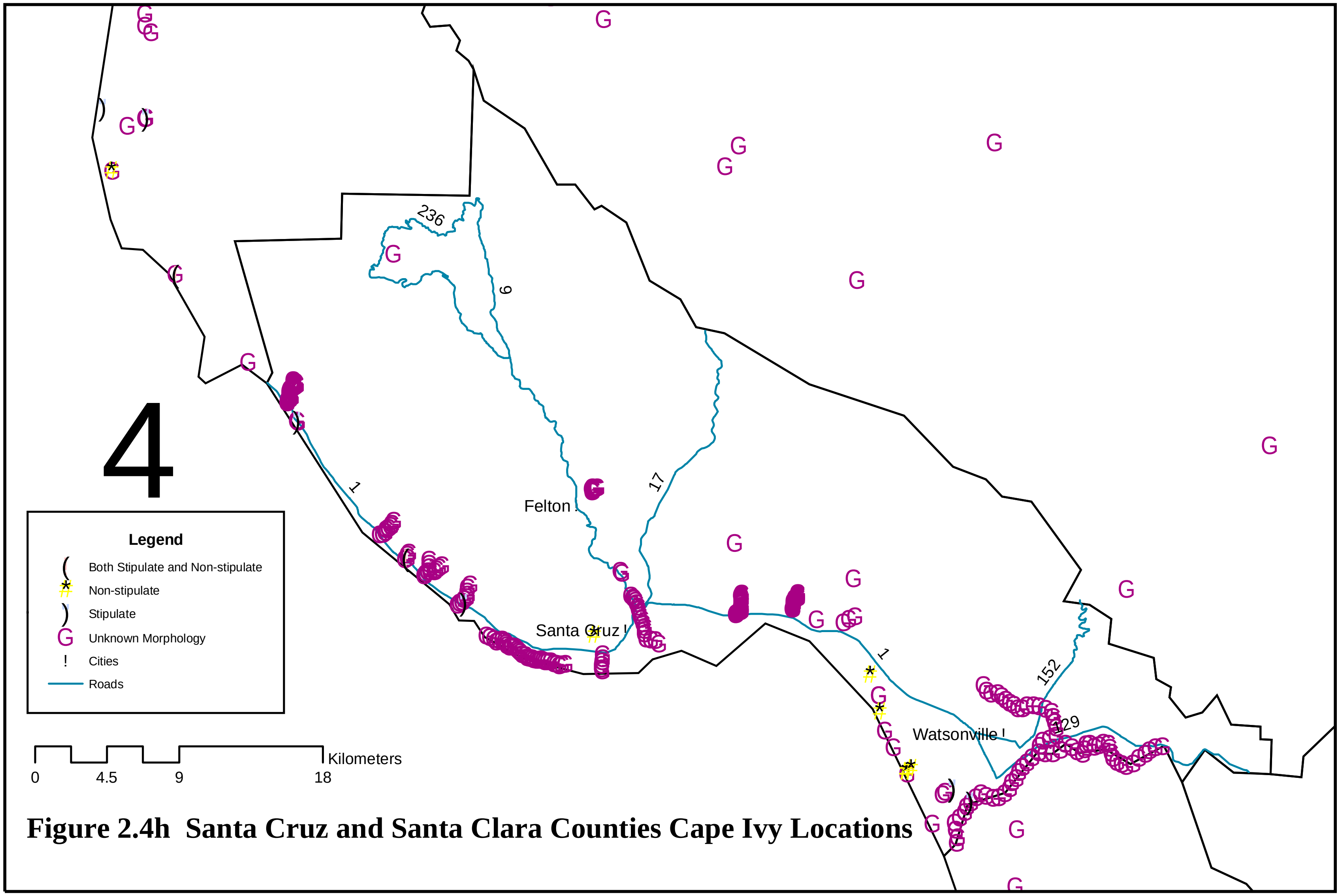


Figure 2.4h Santa Cruz and Santa Clara Counties Cape Ivy Locations

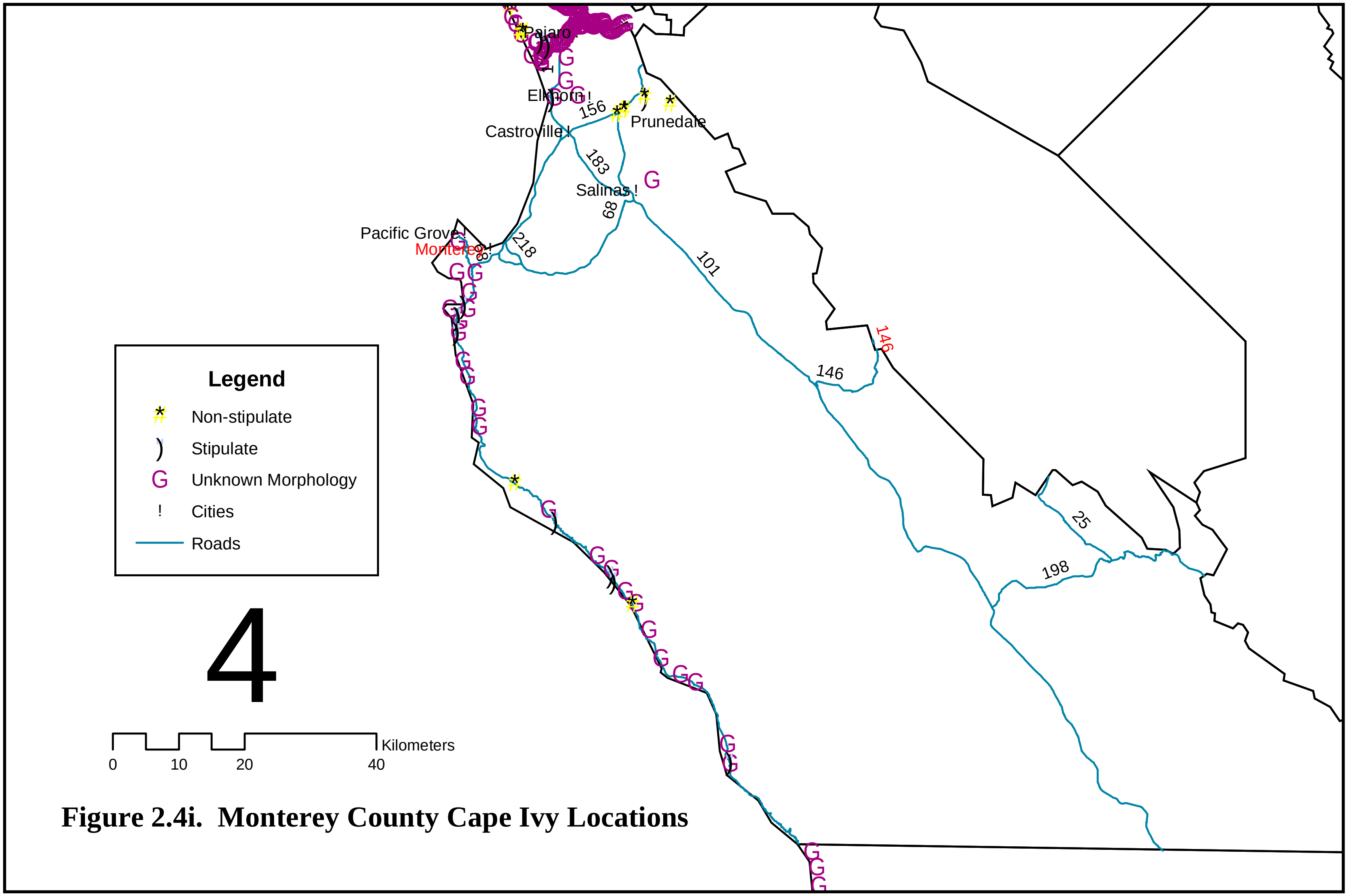


Figure 2.4i. Monterey County Cape Ivy Locations

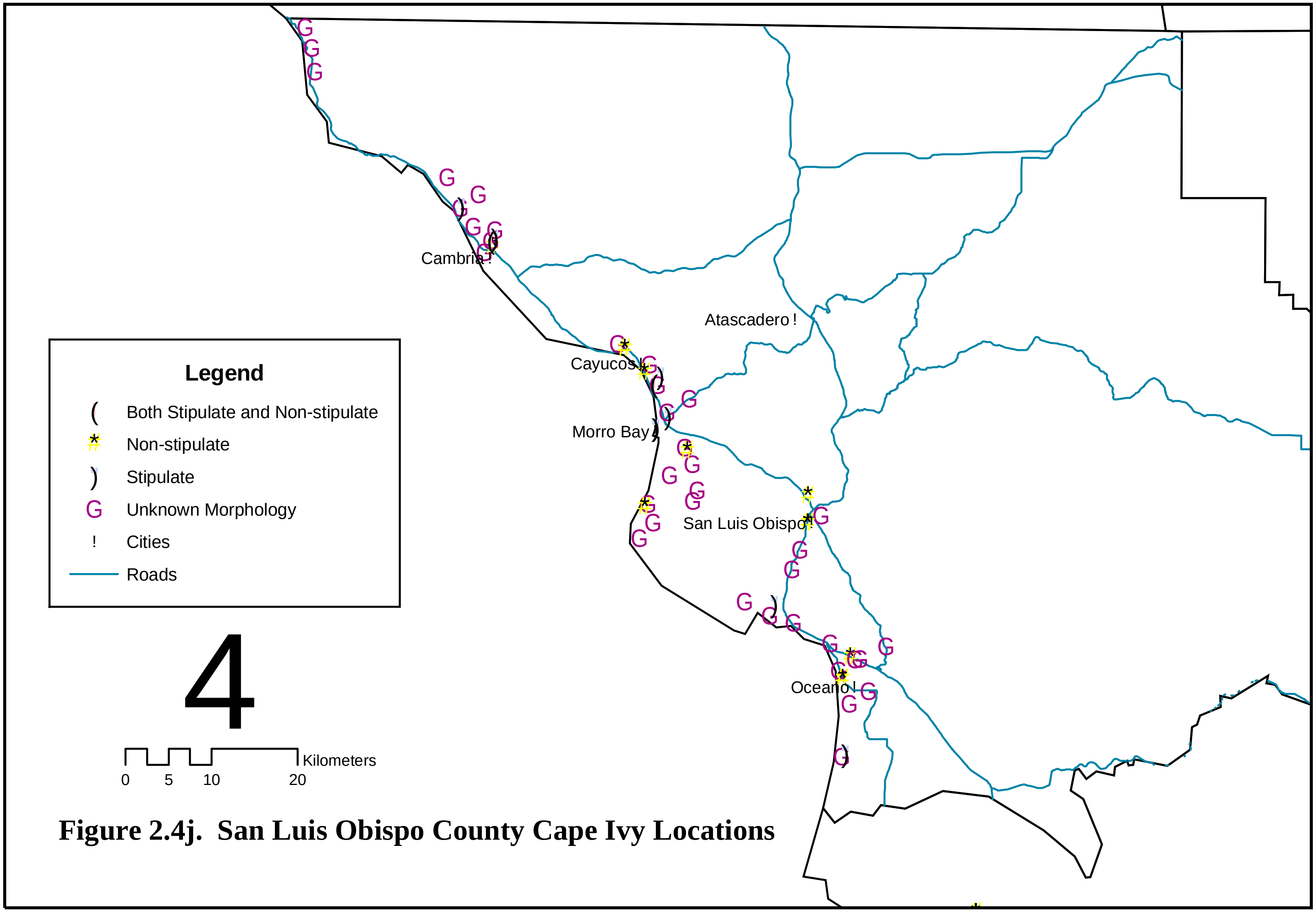


Figure 2.4j. San Luis Obispo County Cape Ivy Locations

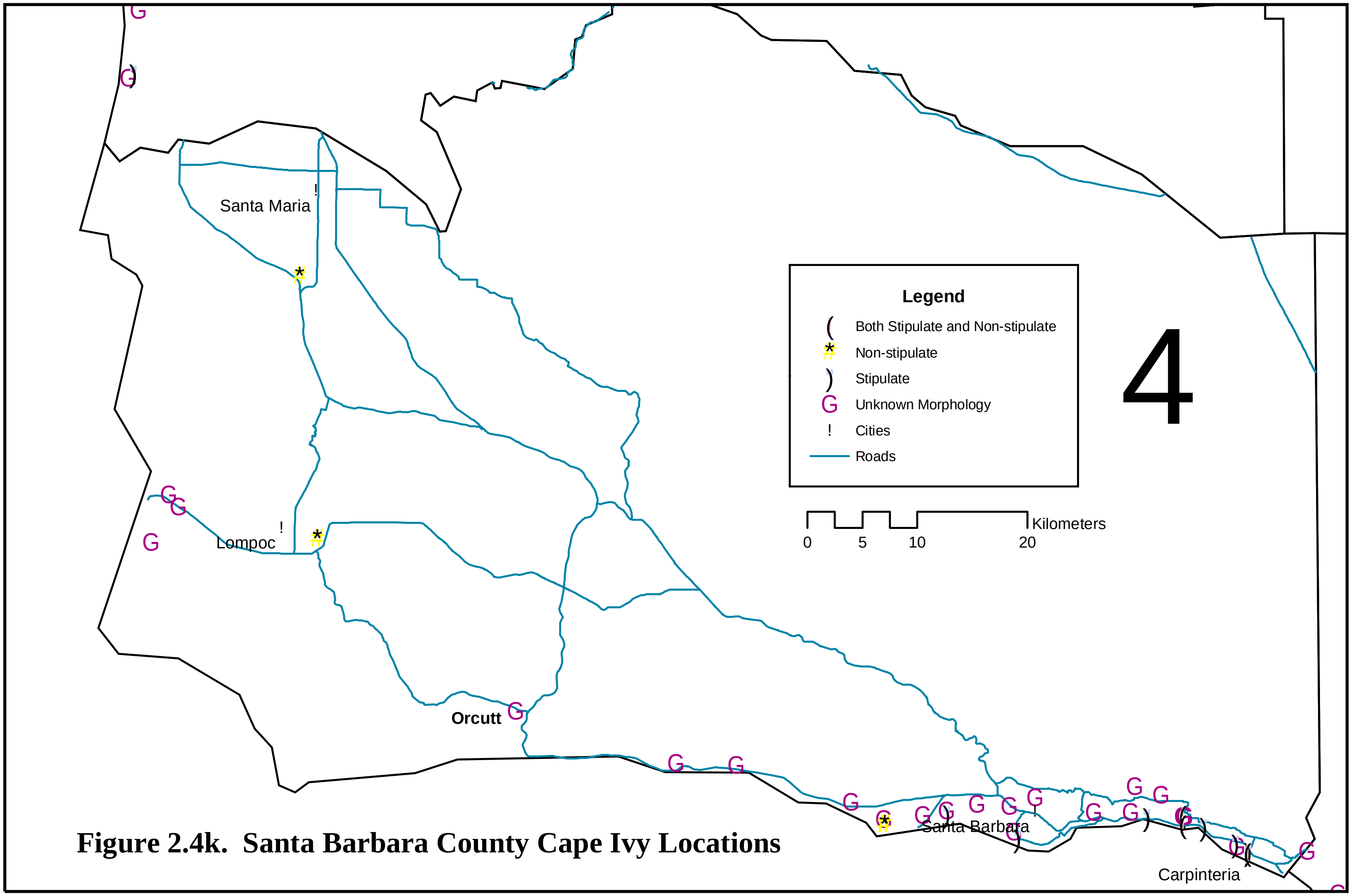


**Figure 2.4k. Santa Barbara County Cape Ivy Locations**

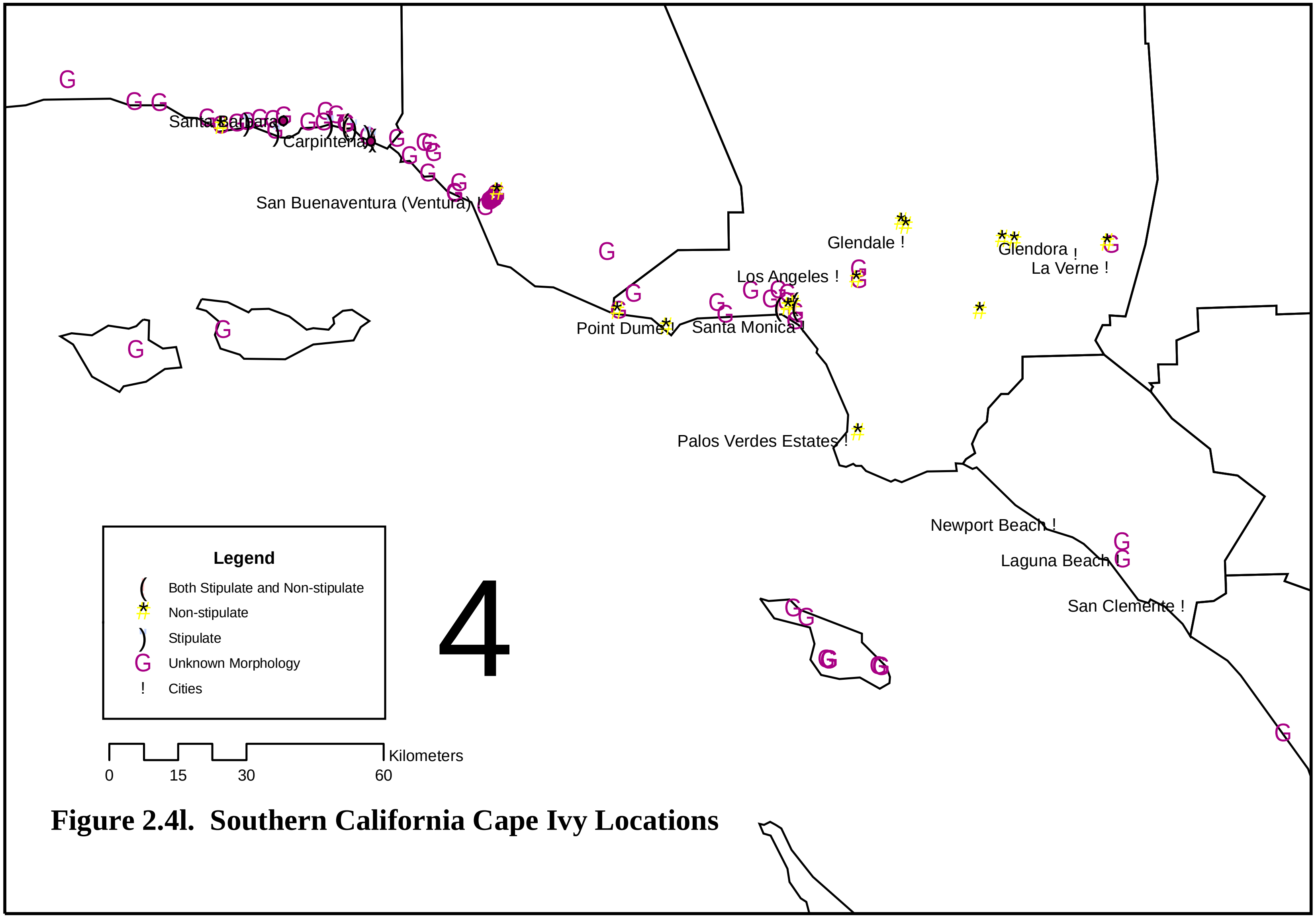


Figure 2.4l. Southern California Cape Ivy Locations

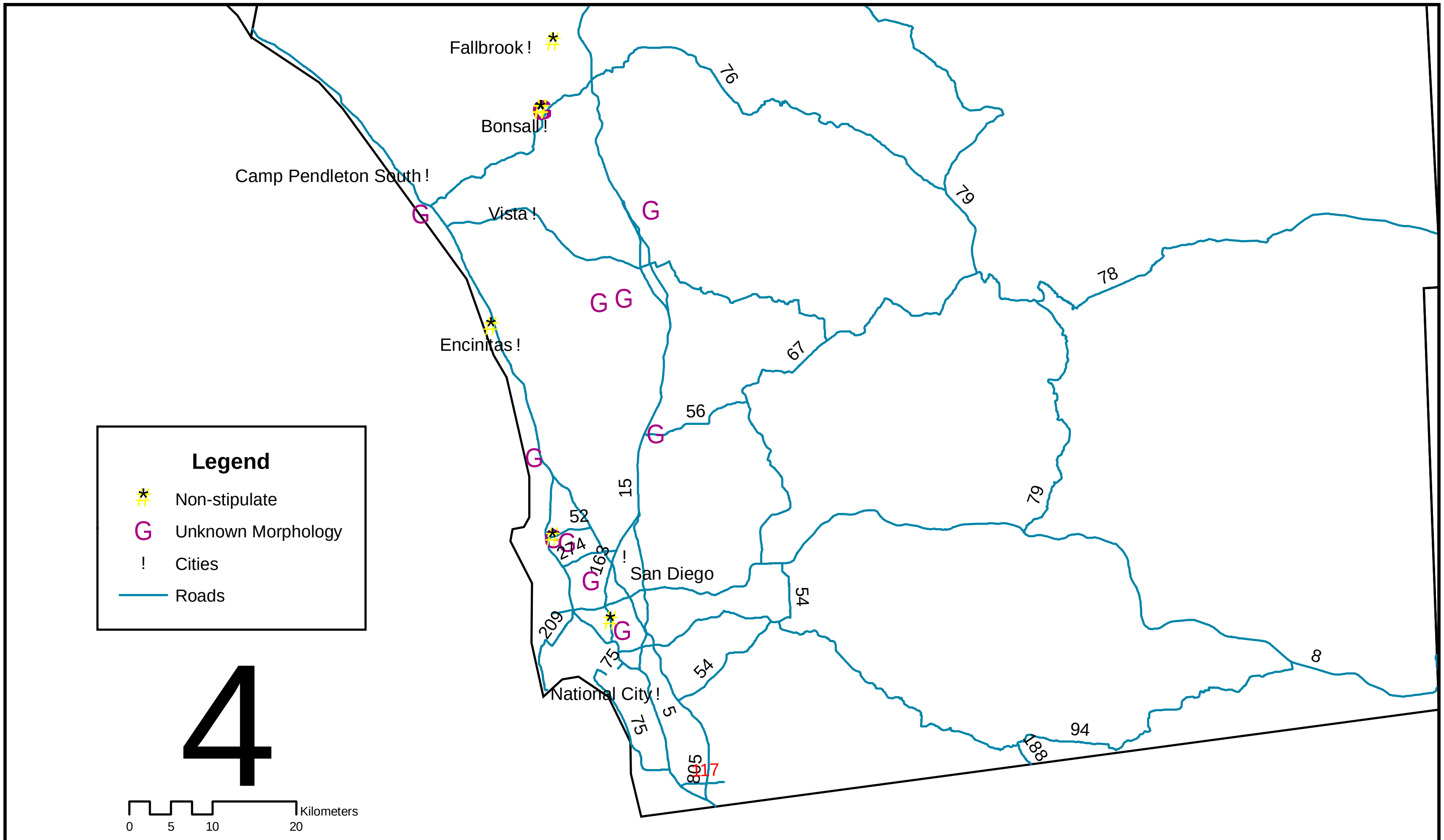


Figure 2.4m. San Diego County Cape Ivy Locations

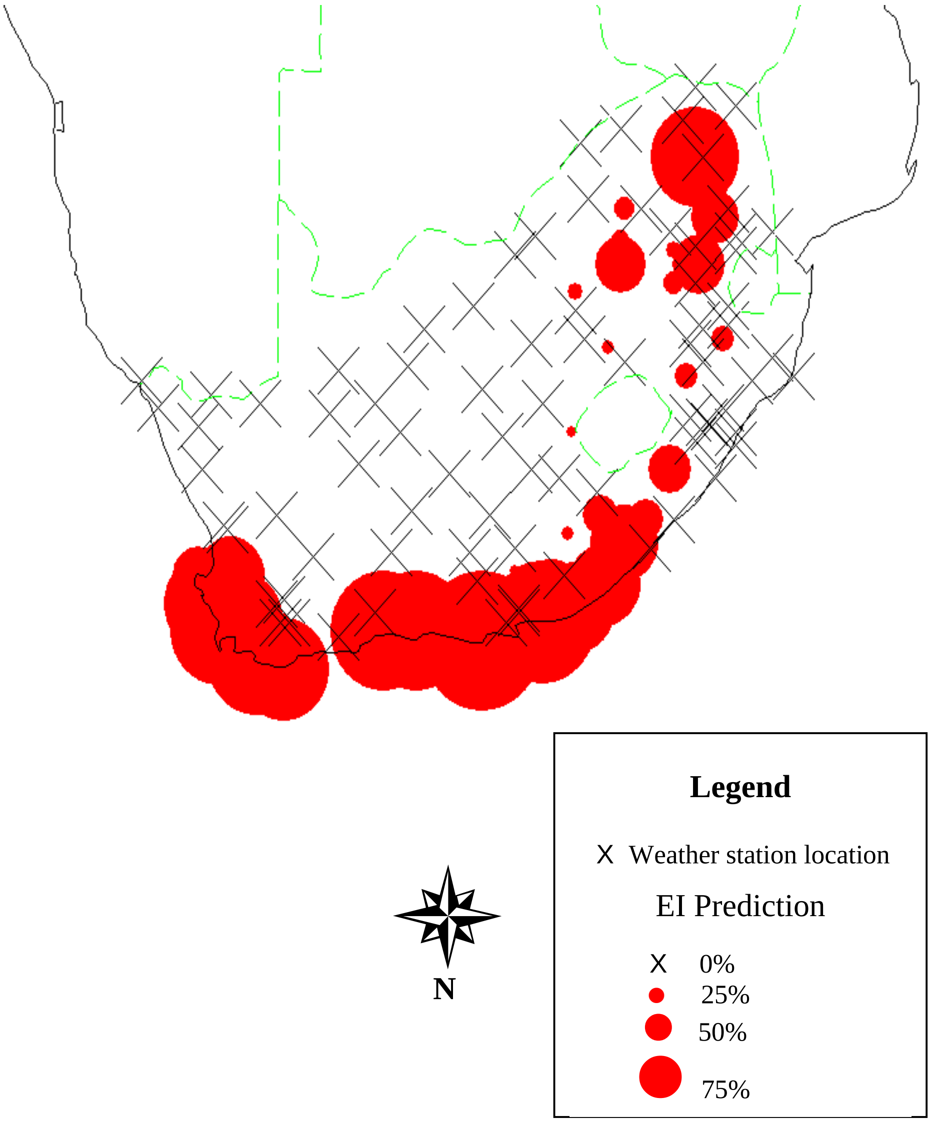


**Figure 2.5a. CLIMEX Ecoclimatic Index (EI) South Africa prediction for Cape ivy**

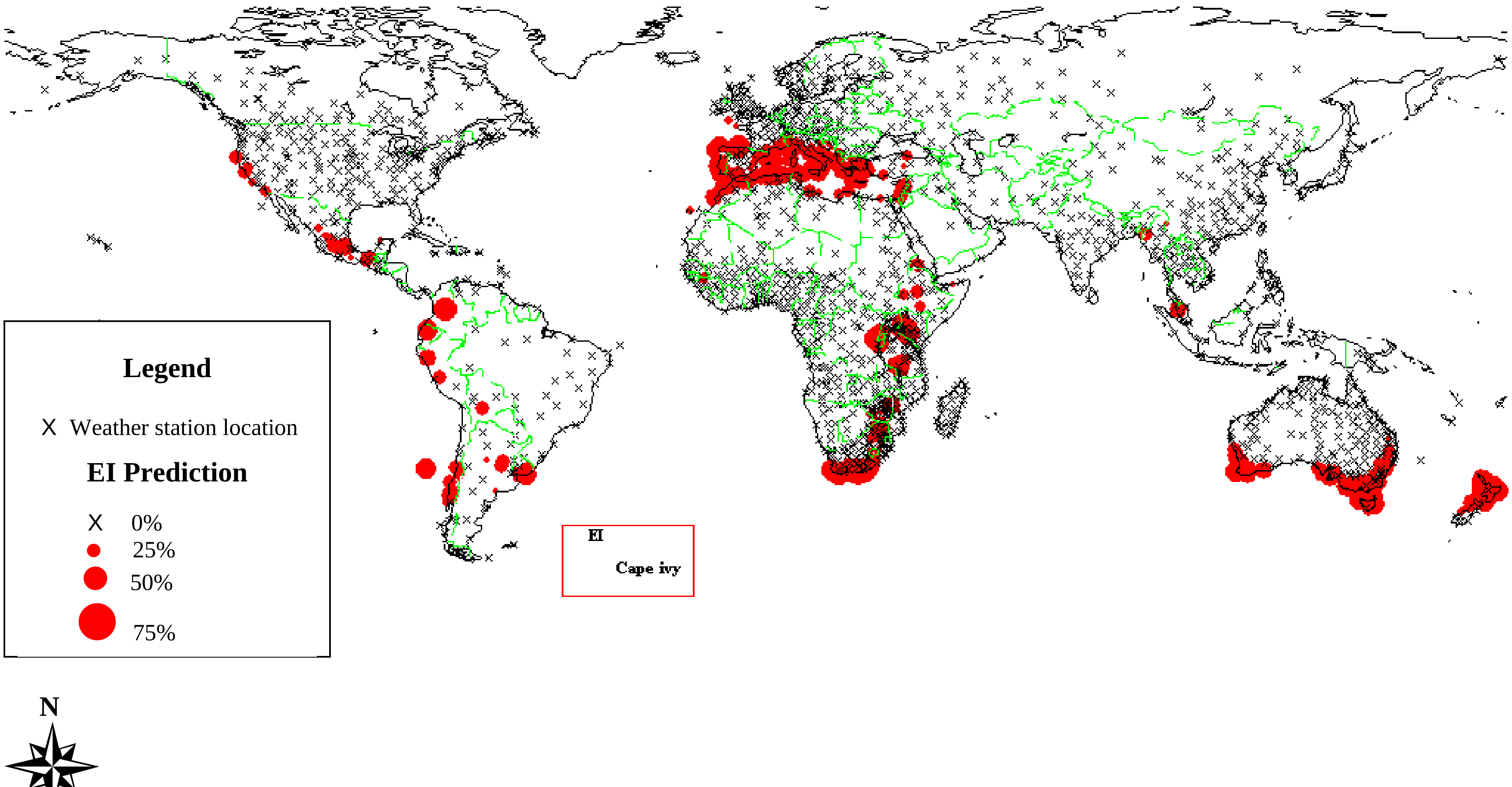


**Figure 2.5b. CLIMEX Ecoclimatic Index (EI) world distribution prediction for Cape ivy**

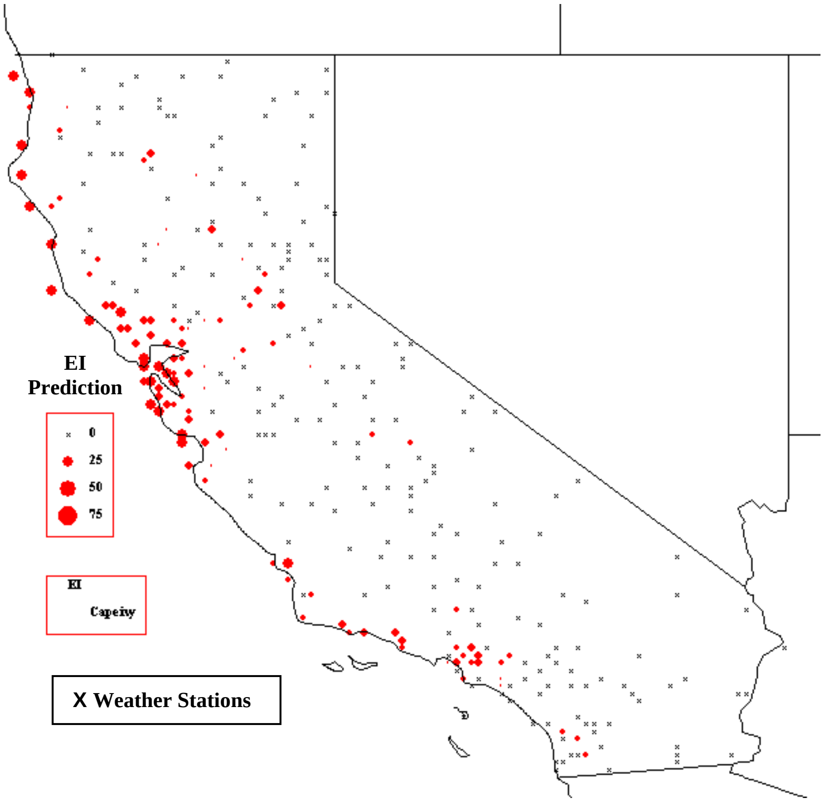


Figure 2.5c. Ecoclimatic Index (EI) prediction for California

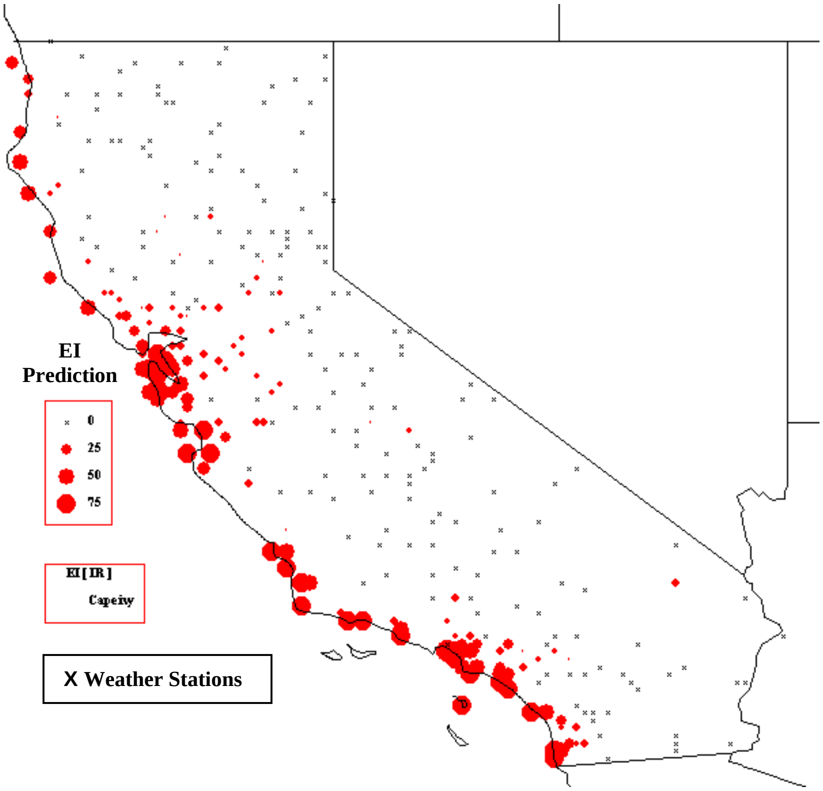


Figure 2.5d. Ecoclimatic Index (EI) prediction for California with added irrigation

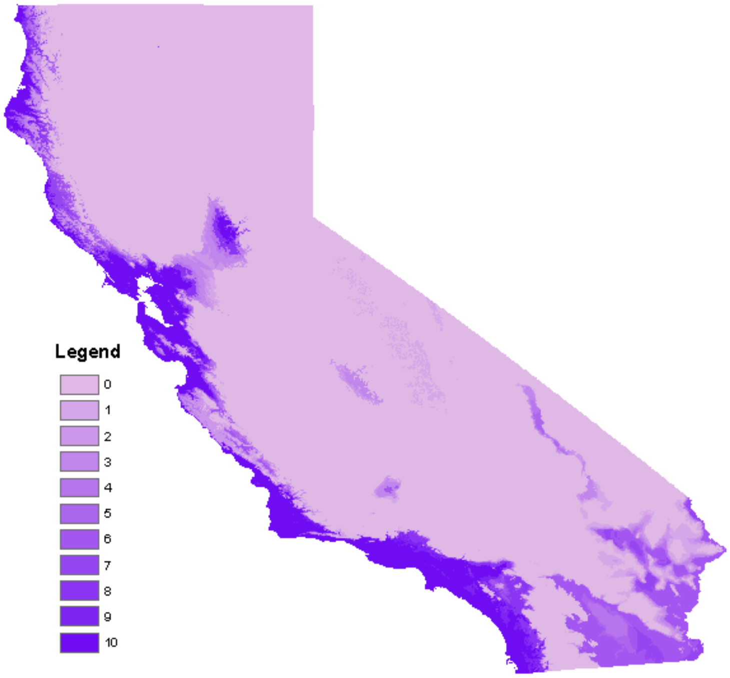


**Figure 2.6a. Sum of 10 Best Subsets of GARP model with elevation, maximum temperature of warmest month, minimum temperature of coldest month and mean annual precipitation.**

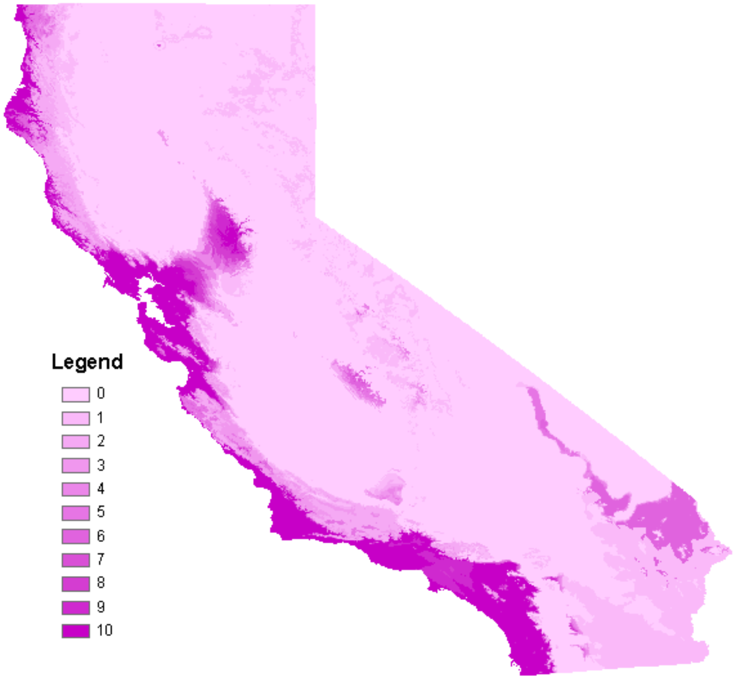


**Figure 2.6b. Sum of 10 Best Subsets of GARP model with annual mean temperature, annual mean precipitation, maximum temperature of warmest month, minimum temperature of coldest month and precipitation of driest month.**

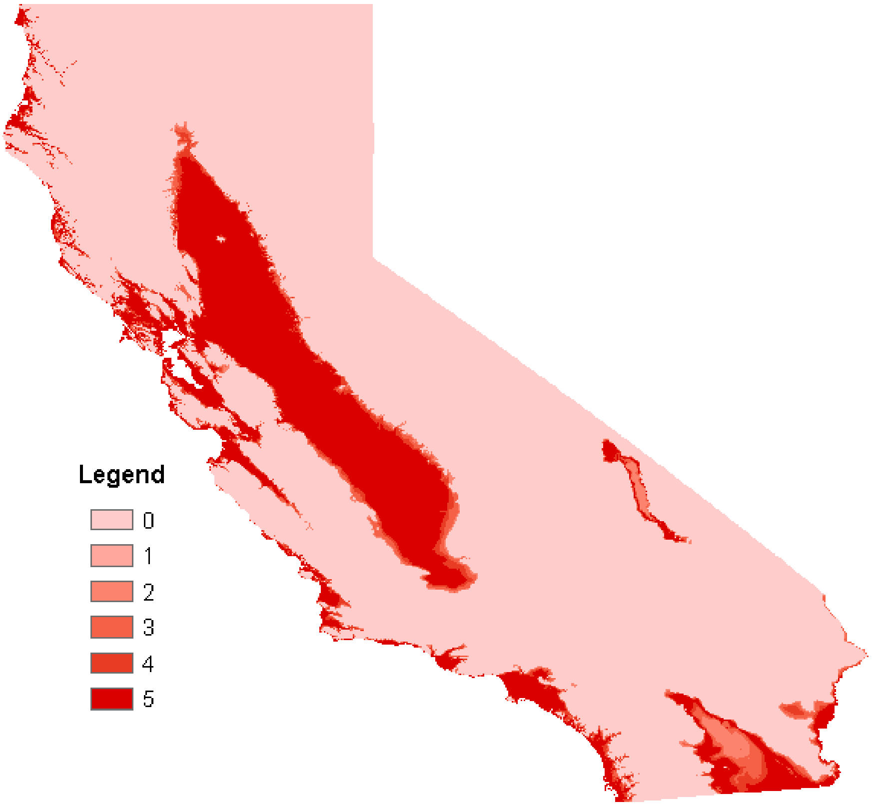


**Figure 2.6c. Sum of Five Best Subsets of GARP model run with elevation as only parameter**

# CHAPTER 3

## Growth Analysis

### ABSTRACT

Cape ivy from four different locations was grown in full sunlight and in shade (20% and 6% of full sunlight) to determine if genetic differences were present within or between source populations. The experiment was conducted in Davis, California, from May to July, 2003 (Experiment 1), and then repeated from September to November, 2003 (Experiment 2). Plant response data (length, number of internodes, number of leaves, final leaf area, and final weights of leaves, stems and roots) were analyzed as a split-plot design with percentage sunlight and population as the main plot factors and genotype as the within plot factor. Derived growth analysis parameters, including relative growth rate, specific leaf area, and absolute growth were also analyzed**.** The log of the final total biomass for Experiment 1 was significantly different for the main effects of population and percentage sunlight, as well as the interaction of population and percentage sunlight. This differed from Experiment 2, which only showed significance among treatments for percentage sunlight. In Experiment 2, biomass production was not significantly different among genotypes. There was a significant genotype by light interaction in Experiment 2, indicating that the expression of relative growth rate differences among genotypes within populations depended on light availability. Results thus indicate that for Cape ivy in California there is 1) phenotypic plasticity in growth response to light levels and 2) there exists genetic variation among and within populations for important fitness traits. The poor performance of Cape ivy in the full sunlight, summer Central Valley tests indicates

the species is unlikely to persist in areas with prolonged high intensity sunlight. The experiments did show that Cape ivy could survive in shaded areas of inland California that receive sufficient summer moisture.

## INTRODUCTION

In South Africa, Cape ivy is found in diverse habitats ranging from near desert to high mountain *Podocarpus* forest edges (Hilliard 1977, Grobbelaar et al. 1999, Rolando 2000), suggesting that there may be a high level of environmental tolerance within the species and perhaps genetic diversity as well. Cape ivy reproduces sexually in South Africa (Rolando 2000), also indicating that genetic diversity might be high there. However, there is no information available on the variation of Cape ivy populations in its native range or in other areas it has invaded. Prior to 2001, it was assumed that California Cape ivy was only capable of reproducing vegetatively and, therefore, it was possible that all plants there were genetically identical (Bossard et al. 2000, Young 2000). Since then, studies have documented viable seed production in California (see Chapter 4). Nevertheless, little is known about how much genetic or phenotypic diversity is present within or among California Cape ivy populations. In 2002, molecular approaches were attempted, but did not yield replicable results (see Appendix A). In order to examine patterns of genetic variation by a different approach, studies were conducted to compare the growth response of Cape ivy collected from four California populations. In its native range, Cape ivy grows primarily in moist, shady environments along forest edges (Rolando 2000) which receive varying levels of light intensity. Therefore, response to light availability was measured as a means to evaluate genetic and phenotypic variability in the species in California.

The only observable morphological difference between California Cape ivy populations is the presence or absence of stipules. In South Africa, all known locations are stipulate, with the exception of one located in the Hogsback State Forest in the Eastern Cape Province (J. Balciunas, personal communication). In California, both stipulate and non-stipulate types are common (see Chapter 2). Plants of both morphological types were grown in a "common garden" to evaluate genetic diversity within and between the populations. When genetic replicates (e.g., clones) are raised in a common environment, patterns of phenotypic response (norms of reaction) for each individual can be measured (Thompson et al. 1991, Pigliucci et al. 1996, Sultan 2003). We were interested in determining whether genetic diversity was present in California Cape ivy for two reasons. If genetic diversity is present between and within populations in California, then the potential for Cape ivy to expand its range in California would be increased. Also, if populations were not genetically uniform clones it could indicate either multiple introductions had occurred or successful genetic recombination through sexual reproduction was occurring. Genotypic diversity within populations can facilitate the range expansion of invasive species (Baker 1974, Barrett and Richardson 1986, Bazzaz 1986). Genetically diverse invaders have an advantage in adapting to new environmental conditions in their invaded ranges. Because Cape ivy is a highly successful invader with a long history of introduction, it would be surprising to find that populations are genetically uniform unless sexual reproduction was not occurring.

Genetic diversity was measured in these experiments using classical growth analysis approaches. Relative growth rate (RGR) can be defined as the rate of increase in plant mass per unit of plant mass already present (Hunt 1978, Lambers et al. 1998). RGR is composed of two components, net assimilation rate (NAR) and leaf area ratio (LAR). NAR is the rate of increase of plant mass per unit leaf area and LAR is the amount of leaf area per unit total plant mass (Lambers et al. 1998). Leaf area ratio can be further broken down into two components, specific leaf area (SLA) and leaf mass ratio (LMR), which is the fraction of total biomass allocated to leaves. SLA is the amount of leaf area per unit of leaf mass, a measure of the relative density or leaf thickness (Hunt 1978). This component is thought to be the most important factor in explaining variation in RGR (Poorter and Garnier 1999). RGR and other growth analysis components can be measured non-destructively over the course of an experiment, or destructively with successive harvests.

In addition to investigating the genotypic diversity of Cape ivy populations in California, this study sought to assess the potential geographical limitations to Cape ivy's expansion in California by growing it under summer conditions in the Central Valley where it currently does not occur. These experimental results were expected to help explain the distribution modeling predictions presented in Chapter 2.

## MATERIALS AND METHODS

During February and March, 2003, Cape ivy stems were collected from four populations. Two populations were growing in open habitats and two populations were under tree canopy. In addition, two of the populations consisted of only stipulate plants and two populations consisted of only non-stipulate plants (See Figure 3.1 for collection locations). The northernmost collection (2/28/03) was from Curry County, Oregon, in the coastal town of Pistol River. The location was in full sun and the plants were of the non-stipulate morphological type. The second population, from Mendocino County at Schooner Gulch (2/25/03), was stipulate and grew in full sun in a coastal environment. It was in a mixed community with a dense growth of big periwinkle (*Vinca major*) and poison-hemlock (*Conium maculatum*). The third population, from Marin County, along Highway 1 north of Bolinas (3/27/03), was comprised of plants that were stipulate and growing in the shade of willows (*Salix* spp.). The southernmost population collected was from Marian Bear State Park in San Diego County (2/9/03). These plants were non-stipulate and grew in the shade of coast live oak (*Quercus agrifolia*). At each population five stem pieces were collected at least five meters apart. Each piece was four or more nodes long. Stem pieces were kept cool until they could be propagated in the greenhouse at UC Davis.

To minimize site--specific maternal environmental effects, each collection was vegetatively propagated and grown in the same greenhouse. The five daughter plants from each population are referred to here as “genotypes” even though it was not certain when the experiment started whether they were genetically different individuals. Two-node sections from each genotype were cut and planted in greenhouse soil (modified UC mix[1]), one node below and one node above the soil surface. No rooting hormone or other treatment was necessary to propagate the Cape ivy segments. These “stock” plants were placed on a mist bench with bottom heat until roots were established. The mist bench operated five times a day for one minute each time and the bottom heat was between 21 and 27 ºC. After roots established, plants were moved to another greenhouse and placed in plastic trays flooded daily by drip emitters until the initiation of the experiment.

The first experiment began on April 26, 2003. The stock plant stems were cut into two node segments, with a total of nine plants propagated from each stock plant. The nine plants produced from each genotype are referred to as clones since they were genetically identical. This insured that a copy of each clone could be placed in each treatment. Each two node starting segment was weighed and the length recorded. The cuttings were planted in 3.8 liter pots filled with modified UC mix as described above. The mean weight of cuttings was 0.7 g (± 0.2 g SD) and the mean length was 15.6 mm (± 3.2 mm SD). Plants were grown in a lath house for two weeks before exposure to the full sunlight or shade treatments on May 12, 2003. During the experiment, plants were watered to saturation four days a week with an automatic watering system that also delivered nutrients (GrowMore 10-15-20 No Boron). The temperatures in Davis ranged between 41.7 and 7.2°C during the experiment (see Figure 3.2a). The mean maximum temperature was 32.4°C and the mean minimum temperature was 12.8°C.

The experiment consisted of three light treatments replicated three times in a completely randomized design. This included a full sunlight treatment and two shade level treatments, 20% and 6% of full sunlight (see Figure 3.3). Each replicate contained five plants (genotypes) from the four populations for a total of 20 plants per replicate. In order to determine the appropriate shade treatments, light levels were measured with a Decagon Sunfleck Ceptometer[2] for Cape ivy populations in Marin County on March 27, 2003. The light levels were between 4% and 22% of full sunlight. Using shade cloth, the light treatments were established at 6% and 20% full sunlight. This was achieved with a single layer of shade cloth in the 20% sunlight treatment and a double layer in the 6% sunlight treatment. A taupe colored shade cloth was chosen to minimize heat build-up within the structures. The shade structures were built on top of two wooden benches 0.86 m wide and 8.4 m long. The enclosures were 1.1 m tall on the northern bench and 1.4 m tall on the southern bench, and each was 2.13 m by 0.86 m. The enclosures were wooden frames with the shade cloth stapled on, and flaps were built into the southern end of each enclosure for access. The location of each enclosure or full sunlight treatment was randomly chosen, and the full sunlight treatments that fell between the shade treatments were placed on immediately adjacent benches to minimize shading from the enclosures.

Starting on May 12, 2003, the number of leaves was recorded and the length of the main stem, branches and internodes was measured. Measurements were repeated every eight days for the duration of the experiment. During experiment 1, plants appeared slightly nutrient stressed around the third week after transfer to the shade structures, so one teaspoon (equivalent to 6 grams) of Scotts Osmocote® fertilizer was added to all pots on June 6. The formulation was 17% total nitrogen, 7% available phosphate, and 12% soluble potash. A similar nutrient stress was observed during the second experiment, but fertilizer was not added.

Plants were harvested between 64 and 77 days after propagation, and an attempt was made to minimize the time of harvest within each replication. At harvest the length of the main Cape ivy vine as well as the lengths of any branches were recorded. This “total length” was then analyzed for both experiments. The total number of internodes at the end of the experiment were calculated and analyzed. Leaves were counted and then stored on ice or in a refrigerator and then used to estimate leaf area. Leaf area was determined for the shade grown plants with a Li-Cor 3100 Area Meter[3]. By harvest time, many of the full sun plants had died. After measurement of leaf area, the leaves, stems and roots were dried for at least 24 hours at 70ºC and weighed.

The experiment was repeated a second time starting on September 4, 2003, using the same stock plants for cuttings as described above. In this experiment the mean cutting weight was 0.3 g (± 0.2 g SD) and the mean cutting length was 11.0 mm (± 4.2 mm SD). The propagated plants were kept in the lath house until September 21, when they were transferred to the experimental treatment locations. Again, measurements were taken every eight days, but in this experiment only the number of internodes was counted. Fertilizer was not added during the experiment even though plants initially exhibited signs of nutrient stress. After the third week the plants recovered and grew vigorously. The experimental plants were harvested between 67 and 75 days after propagation, again with an attempt to minimize the within replicate harvest time. The final measurements and dry weights were taken as described above. Temperatures in Davis ranged between 0.6°C and 40°C during the experiment (see Figure 3.2b). The mean maximum temperature was 26.0°C and the mean minimum temperature was 8.7°C.

## ANALYSIS

Plant response data (total stem length, number of internodes, number of leaves, final leaf area, and final biomass of leaves, stems and roots) were analyzed as a split-plot design within each sunlight treatment with percentage of sunlight and population as the main plot factors and genotype as the within plot factor. Initial weight of cuttings was included as a covariate in ANOVA analyses. Relative growth rate was obtained by using the slope of the regression line generated by graphing the total length data for all of the measurement intervals (as described in Hunt 1978). Specific leaf area, considered the most dominant factor in explaining variation in RGR (Poorter and Garnier 1999), was calculated by dividing final leaf area by final leaf dry weight (Hunt 1978). Absolute growth was calculated by dividing the change in total biomass over the course of the experiment by the total number of days.

Data were tested for the ANOVA assumptions of homogeneity of variances, independence and normality. Many of the variables tested were non-normal and/or heteroscedastic and could not be transformed to meet the assumptions, so a ranks averaged transformation was performed on the raw data and ANOVA analyses were completed on ranked values (Conover and Iman 1981). In the case of total dry biomass, analyses were performed on log transformed values. Experiments 1 and 2 were analyzed separately. The analyses were performed with JMP IN version 5.1 (SAS institute 2004). The main model tested included all the variables listed in Tables 3.1 and 3.2. A separate ANOVA analysis was necessary to test the correct denominator for Sunlight% as the JMP IN program tested the Sunlight% crossed with population nested within genotype in the larger analysis as the denominator, generating an incorrect degree of freedom. The model used for the Sunlight% ANOVA was Replicate (Random), Replicate (Random) crossed with Sunlight%, and Sunlight%.

Genetic variation among and within populations was determined by examination of the population and clone effects response from the common garden experiment.

Variation in phenotypic plasticity among genotypes was compared by analyzing variation in their growth response to different light levels.

The norm of reaction was computed for the RGR of each genotype in Experiment 2. As an index of plasticity, the coefficient of variation was calculated for several of the variables. First, the mean of each genotype's response at each sunlight level was calculated for the parameter of interest, then the mean and standard deviation for all five genotypes were used to calculate the coefficient of variation.

## RESULTS

Growth responses of Cape ivy genotypes differed both between and within populations. After a brief presentation of the survival data, this section presents the significant results for between-- and within--population genetic variation. Cape ivy exhibited classic "shade avoidance syndrome" behavior (Smith and Whitelam 1997). In response to shade, plants produced less dry matter, retained photosynthate in the shoot at the expense of root growth, developed longer internodes and petioles, and produced larger thinner leaves (Grime 1979). The shade avoidance response meant that light percentage alone was significant in most of the Experiment 1 and 2 analyses. Therefore significance of the light response is not discussed unless a significant result was obtained when sunlight percentage was crossed with population.

## Survival

The number of plants surviving in each sunlight level in Experiments 1 and 2 are listed in Table 3.3. The plants in the full sunlight were much smaller than the others that we assumed at first that mortality was higher. Using a $X^2$ analysis, we found that survival was not significantly different between sunlight levels in Experiment 1 or 2. We had also assumed that plants would grow better in the cooler temperatures of the second experiment, but found the overall mortality was higher in this experiment. Using a heterogeneity $X^2$ analysis the two experiments were not found to be significantly different.

## Between Population Genetic Variation

The differences in the growth of plants among the sunlight level treatments were dramatic. Figure 3.4 shows photographs of Experiment 1 plants from each treatment at the time of harvest. The size differences are obvious, as are the larger number of leaves in the 20% sunlight treatment as compared with 6% sunlight. In the photographs, plants were arranged by population, starting with Curry on the left and continuing to the right with Mendocino, Marin and San Diego. Although it is not observable in the photographs, the Experiment 1 ANOVA analyses revealed significant differences between populations for log of the total biomass, RGR, leaf area and leaf number (Table 3.1). Population differences were not significant in Experiment 2. Experiment 1 also showed significance for population crossed with light percentage for the log total biomass and the RGR.

A comparison of the mean total biomass for both experiments by sunlight level and population source is shown in Figure 3.5. Differences are evident between

Experiments 1 and 2, as well as within populations and sunlight levels. Plants in the 20% sunlight treatment were consistently larger than plants in 6% or full sunlight treatments for each population. In the full sunlight treatment, plants were larger in the second experiment than in the first. Plants were also larger in the 20% sunlight level for Curry, Mendocino and Marin counties in the second experiment, but not for San Diego. San Diego plants were larger in the first experiment in the 6% and 20% sunlight levels.

The expression of population differences was dependent on the light level in Experiment 1 as shown by above and below ground allocation of biomass in each sunlight level (Figure 3.6). The proportion of biomass in the 20% sunlight level was larger in all populations, and the full sunlight treatments had the lowest biomass. San Diego had the largest total mass at 20% sunlight, followed by Curry, Marin and Mendocino counties. Differences in biomass between populations were much smaller at 100% and 6% sunlight. Below ground allocation was small in all cases, but showed the same trend with higher allocation in plants grown under 20% sunlight and with San Diego having the largest biomass at that light level.

Relative growth rate for Experiment 1 showed a trend similar to log total biomass -- significant differences were found for population alone and for the interaction of sunlight level and population. The least squares means of the relative growth rate for the four populations and three sunlight percentages in Experiment 1 are shown in Figure 3.7. Similar to the total biomass, San Diego plants had the greatest relative growth rate at 20% and 6% sunlight. Unlike total biomass, however, population effects on RGR varied with light level. The Marin population grew the slowest at 20% light, but was the second fastest in growth at 6% light.

During the first experiment there was significant herbivore damage to Cape ivy plants within shade structures 8 (20% sunlight) and 9 (6% sunlight) from *Plusia biloba*[3] larvae (See Appendix B, Figure B-1). The larvae damage was almost entirely to leaves. *Plusia biloba* is a common moth with multiple yearly generations and, given the right conditions, could cause significant damage to Cape ivy plants. In Experiment 1, leaf area was calculated only for the shade plants that were un-damaged or slightly damaged by *P. biloba*.

For leaf area, only the 20% and 6% sunlight treatments were included in Figure 3.8**,** as most of the plants in the full sun treatments in Experiment 1 had no living leaves by the end of the experiment. In both experiments, the leaf area was larger for the 20% light than the 6% light treatment regardless of the population. Population effects on leaf area were not consistent across experiments. Experiment 1 plants from San Diego in 20% light had the largest overall leaf area, and for the other three populations the largest leaf areas were in Experiment 2. Leaf area ANOVAs were also not performed on the full sunlight treatment. In Experiment 1, population differences were highly significant for leaf area and leaf number, but the trend was not repeated in Experiment 2 (Tables 3.1 and 3.2).

Length per day, total length, number of internodes and absolute growth were significantly different at the population level in Experiment 1 **(**Table B-1, Appendix B**)**. Total length was divided by the number of days to harvest to obtain “length per day,” which is depicted in Figure 3.9 and Table 3.4. The values in Figure 3.9 are means of the treatments. The highest value was 226.5 mm/day obtained for a San Diego plant in 20% sunlight during Experiment 1.

## Within Population Genetic Variation

Final biomass differences among genotypes nested within population were significant in Experiment 1, but not in Experiment 2 (Table 3.1 and 3.2). For RGR in Experiment 1, there was a main genotype effect indicating that the expression of within population variation was consistent across light treatments. In contrast, the expression of within-population genetic variation in Experiment 2 was dependent on the light environment.

As an illustration of the within-population genetic variation, the least squares means for Curry County genotypes in Experiment 2 are listed in Table 3.5 (least squares means for the other populations are not shown). Table 3.5 shows that the relative growth rate of each Curry County genotype (clones 1 through 5), responded differently in each sunlight level. Genotypes 1 and 4 grew best in 6% sunlight, while genotypes 2, 3, and 5 grew better in 20% sunlight. Mendocino genotypes all grew most rapidly in 20% sunlight, and Marin had one genotype growing fastest in 6% sunlight and the rest doing better in 20% sunlight. San Diego had three genotypes growing best in 6% sunlight and two growing best in 20% sunlight.

In order to further illustrate the significant effect of the percentage light on the expression of genetic variation at the genotype level, a norm of reaction diagram showing the phenotypic state at each point along the light gradient was developed for RGR data in Experiment 2 (Figures 3.10a and 3.10b). The norm of reaction depicts the mean of each genotype’s response at each light level (Sultan and Bazzaz 1993). Although growth rates were generally low in the full sunlight treatment, variation in the RGR of genotypes differed among the populations sampled. One overall trend was the small growth rates at the full sunlight level. At 20% sunlight populations from all of the populations showed the largest variability in response, but were not consistent in their response at the other light levels. As an example, relative growth rate for Curry County genotypes was most variable at 20% sunlight, but genotypes 1 and 4 showed opposite behavior at 20% and 100% sunlight.

In Experiment 1, genotype nested within population was significantly different for leaf area, leaf number, and absolute growth in addition to total biomass and RGR (Tables 3.1 and B-2, Appendix B). Table 3.6 shows the coefficient of variation for Experiment 1 in all the cases where genotype nested within population was significant (Tables 3.1 and 3.2). It indicates that the genetic variation was lower overall in Curry and San Diego, at the northern and southern end of the distribution, than it was in the middle of the distribution. Since these were the two non-stipulate locations sampled, the expression of genetic diversity in these populations was lower than in the stipulate populations sampled. This result would match with the presence of many stipulate and only one known non-stipulate population in Cape ivy's native range (See Chapter 1). It also appears that genetic variation was highest in the Mendocino population for leaf area, leaf number and absolute growth.

## DISCUSSION

Cape ivy was found to be genetically diverse within and among populations; detection of patterns of genetic variation in this species was the main question posed in this research. This section discusses the implications of those findings and relates them to Cape ivy's invasive behavior. Discussion is also included on the sources of the Cape ivy populations, their sexual reproductive status and the possible founder effects of multiple introductions. Given Cape ivy's genetic diversity and phenotypic plasticity, it may have the potential to expand its range in California through continued local adaptation.

Common garden experiments are often used to detect genetic variation among plant populations. No common garden experiments have previously been conducted with Cape ivy, but Rolando (2000) conducted a growth analysis experiment in South Africa with stem fragments and exposed them to varying light levels (71, 45 and 17% available sunlight). She eliminated the effects of genetic variation by collecting stolons from a 2 by 2 meter plot within a single population. Therefore the emphasis of the study was on the inherent phenotypic plasticity present in one Cape ivy genotype for response to light level. Cape ivy grew best at the intermediate light level of 45% and showed differences at each light level in many of the characters measured. Flowering was also higher in the 45% sunlight treatment. Rolando's study demonstrated that Cape ivy has inherent adaptive plasticity which may be able to be transferred between generations through differential reproduction.

The Cape ivy populations sampled in my study were also biogeographically distinct. They differed in their morphology, sexual reproduction and climate as listed in Table 3.7. Adaptive differentiation in this case could be occurring for the colder minimum temperatures in the two northern populations, or for the higher maximum temperatures at the southern distribution edge. Adaptation to lower precipitation may also be occurring at the southern end of the range. All of the collection locations were in areas where there was either current or historic human settlement. This supports the theory that multiple introductions have occurred over time and contributed to the genetic diversity observed in this study. The two sexually reproducing populations, in Curry and Marin counties, would also be expected to become more genetically diverse over time depending on the success of seedling recruitment.

A pairwise correlation analysis of the Cape ivy data revealed that most of the variables measured were positively correlated, except for specific leaf area which was negatively correlated. Schlichting (1989) showed that phenotypic correlations among morphological characteristics are often altered by environmental conditions. Similar findings have been reported by other researchers studying *Xanthium strumarium* (Lechowicz and Blais 1988). In contrast, Winn found similarity among correlation structures among environments (Winn and Evans 1991). It would be useful in understanding the population biology of Cape ivy to investigate traits directly related to fitness such as seed production or seedling recruitment to determine how the correlation structure of fitness related traits respond to environmental heterogeneity.

### Between Population Genetic Variation

In this study, Cape ivy exhibited genetic differences among populations based on the final total biomass and RGR regardless of the light level. These genetic differences may result from the historic introduction of multiple genotypes. Cape ivy was historically introduced as an ornamental, and it is assumed that multiple introductions occurred randomly as house plants were discarded in gardens, or it was directly planted as a ground cover and seeds escaped to form new populations. Genetic bottlenecks or founder effects can limit levels of genetic variation within new populations (Bazzaz 1986, Rice and Mack 1991), but multiple introductions of Cape ivy appear to have reduced bottleneck effects.

Two other invasive plants and one native have shown population variation based on a comparison of growth characteristics (Moran et al. 1981, Schlichting and Levin 1990, Rice and Mack 1991). The two invasive species, *Bromus tectorum* and *Xanthium strumarium*, are self-compatible annuals, while the native, *Phlox drummondii,* is a self-incompatible annual. Although phenotypic plasticity explained part of the adaptive response in all three cases, differences were also detected that were genetically based.

When response to light level was investigated, population differences were also detected in final biomass production. The observed variation was not dependent on whether plants were initially collected from sun or shade. These differences suggest that local adaptation may be occurring as a selective response to light level.

A number of common garden experiments with *Polygonum* and other species have been conducted in which varying light levels were used to assess the plasticity of populations (Zangerl and Bazzaz 1983, Winn and Evans 1991, Sultan and Bazzaz 1993, Pigliucci et al. 1995, Nicotra et al. 1997, Sultan et al. 1998, Sultan 2001). Studies that found genotype by light interactions are presented first, followed by studies that reported contrasting findings.

Sultan and Bazzaz (1993) looked at *Polygonum persicaria* growth at three light levels and found that each genotype studied expressed a set of diverse phenotypes in response to contrasting light levels that matched assumptions about growth in high or low light conditions.  These results were similar to those observed for Cape ivy.  In another study comparing early and late-successional *Polygonum* species, researchers found variation in photosynthetic response within populations (Zangerl and Bazzaz 1983).  The variables measured and the species involved determined the extent of the genotype response.  In a short-lived annual species, genetically diverse populations of *Arabidopsis thaliana* grown in a common garden showed widespread phenotypic plasticity and some genotype by environment interaction at four light levels (Pigliucci et al. 1995).  Genetic variation was detected in plastic responses to differing light and nutrient levels, and the genotype by environment effects for light level were mostly shown in amount of fruit production.

In contrast to the findings of Pigliucci (1995) and the other studies summarized above, Winn found a lack of significant population by environment interaction in *Prunella vulgaris* response to light levels (Winn and Evans 1991).  They speculated that if other traits were measured population variation in plasticity may have been detected. Nicotra (1997) also studied light response by genotypes of *Piperia* and found little genotypic variation in light response to photosynthesis (Nicotra et al. 1997).

### Within Population Genetic Variation

During the first experiment, differences in biomass production and RGR among genotypes were consistent across light levels.  This evidence supports the conclusion that multiple introductions have occurred at the sites.  The potential for further local adaptation is also suggested because natural selection will be able to act on the genetic variation already present at the sites.  The genotype by light environment interactions observed in Experiment 2 suggest genetic variation in norms of reaction and thus the capacity to evolve different patterns of plasticity. Crimson fountaingrass (*Pennisetum setaceum*) in Hawaii provides an example of a population with low genetic diversity due to a limited number of introduced genotypes. This is probably a contrasting scenario to Cape ivy's introduction, but it provides an example of the evolution of phenotypic response in a weedy species. Williams et al. (1995) found low genetic variation within Hawaiian crimson fountaingrass populations even though the species is a highly successful invader there and elsewhere, including California. The study included reciprocal transplants from three altitudes into common gardens and measured a wide variety of growth and fitness characters. They found little clonal variation and attributed the broad ecological amplitude of the species to phenotypic plasticity. They concluded that the original immigrants to the island possessed little genetic variation; indeed there is only one known historical introduction. Therefore the observed population differences reflect phenotypic plasticity and not genetic differentiation; a situation that may have resulted because of an extreme genetic bottleneck that occurred during introduction of crimson fountaingrass to Hawaii.

Invaders can adapt to selection pressures in their new range with two distinct strategies; either high genetic variation within introduced populations can lead to local adaptation or adaptive plasticity may arise in genetically depauperate introductions (Mack 1992). High within population genetic variation is often a result of multiple introductions whereas low genetic diversity in invasive populations is due to a limited founder effect (Barrett and Richardson 1986, Bazzaz 1986, Williams et al. 1995). Cape ivy's success as an invader may result from a “mixed strategy” that results from a combination of genetic adaptations as well as adaptive plasticity. It possesses within population genetic variation that facilitates local adaptation, most likely due to repeated introductions, and it also exhibits inherent phenotypic plasticity in response to light (Rolando 2000). Plasticity allows a plant to adapt to environmental heterogeneity and has been associated with invasive potential (Huthchings and DeKroon 1994, Mack 1996, Vermeij 1996, Sultan 2000, 2003). If a number of genotypes are present in a population and are able to exhibit plastic responses to variable environmental conditions, the population would have a better chance of surviving and thriving over time (Sultan 2000, 2003).

A well known example of another invasive vine with smothering clonal growth and sexual reproduction is kudzu (*Pueraria lobata*). It is a semi-woody, perennial vine in the pea family which is naturally found throughout China, and in Korea and Japan (van der Maesen 1985, Sun et al. 2005). Two molecular genetic studies conducted with kudzu found high levels of within population genetic diversity in its invasive range. The first study used allozymes to compare genetic variability and clonal diversity of 20 populations in the southeastern US (Pappert et al. 2000). They found genetic diversity was high within the populations, and the proportion of genetic variation explained by among population variation ($G_{ST}$) was similar to out-crossing, animal dispersed species with both sexual and asexual reproduction. There were no geographic patterns and little overlap of genotypes between populations; evidence for multiple introductions followed by gene flow and recombination. Sun et al. (2005) compared the genetic diversity of kudzu between introduced populations in the US and populations in its native range in China using inter-simple sequence repeat (ISSR) variation. This study found high within--population genetic diversity, but low differentiation among populations. The amount of genetic diversity found in the Chinese populations was similar to that found in the US populations, indicating that genetic differentiation occurred after introduction into the US.

Both of the kudzu studies above emphasize the importance of the history of introduction to explain the genetic structure observed in the US populations. Kudzu is known to have viable seed production and seedling recruitment in the US (Abramovitz 1983, Forseth and Teramura 1986). Kudzu has a well documented history of repeated intentional introduction by the Soil Conservation Service and others as an ornamental, or for fodder and erosion control (Pappert et al. 2000). This would help explain the high within population genetic diversity resulting from selective breeding and multiple introductions. We do not know how much genetic diversity is present in South African populations of Cape ivy, but the number of native populations is certainly fewer than those in the native distribution of kudzu. Other intentionally introduced ornamentals have high within population genetic diversity (Godt and Hamrick 1991, Schierenbeck et al. 1995). Cape ivy is sometimes referred to as the “kudzu of the west,” a nickname which seems appropriate given the similarities in its history of introduction and within--population genetic diversity.

In contrast to the findings for kudzu and other ornamentals, some studies have shown that invaders have low within or between population genetic diversity in their introduced range (Warwick and Black 1986, Novak and Mack 1993, Hermanutz and Weaver 1996). It is then presumed that the invasive success of these introduced species is due to adaptive phenotypic plasticity. Hermanutz et al. (1996) found that all populations of a weedy *Solanum* displayed significant levels of plasticity in vegetative and reproductive traits and that colonization appeared to be dominated by general-purpose genotypes rather than selection for specialized genotypes. Using a molecular analysis, *Bromus tectorum* was shown to have the greatest genetic differentiation in its native range (Novak and Mack 1993). The genetic differences between introduced and native populations were presumed to have arisen from founder effects as well as multiple introductions. Velvetleaf (*Abutilon theophrasti*) was also shown to have low levels of allozyme variation among populations sampled, although based on morphological and reproductive characteristics differences between populations were observed (Warwick and Black 1986).

## CONCLUSIONS

When Cape ivy was grown in a common garden at three different light levels, four populations exhibited differential growth. The differences among populations were observed for final total biomass and relative growth rate in Experiment 1. The differences in the relative growth rate of genotypes also indicate a presence of within--population genetic variation that should promote response to the diverse selection pressures experienced by a species expanding its geographic range. In Experiment 2 there was a significant genotype by light interaction, indicating that the expression of relative growth rate differences among genotypes within populations depended on light availability. The poor performance of Cape ivy in the full sunlight, summer Central Valley conditions indicates the species is unlikely to persist in areas with prolonged high intensity sunlight. The experiments did show that Cape ivy could survive in shaded areas of inland California that receive sufficient summer moisture.

One trait that was not examined in this experiment was the capacity of Cape ivy to compete for light or other resources. While Cape ivy would be able to survive in shaded Central Valley conditions, there may be other ecological barriers to its initial establishment. For instance, in areas where it was growing with big periwinkle (*Vinca major*), big periwinkle was often dominant in full sun and Cape ivy was dominant in the shade (personal observation). Light levels the populations are exposed to obviously vary during the year (spatially and temporally), and the proximity to the coast means that fog and clouds are present more than they would have been in the Central Valley. In this case, plasticity in response to light level is likely to be adaptive.

## FOOTNOTES

1. UC Davis soil mix composed of 0.22 $m^3$ compressed peat moss, 0.23 $m^3$ sponge rock, 0.11 $m^3$ #2 vermiculite, 0.17 $m^3$ sand, 2.27 kg dolomite, 0.7 kg 14-14-14 fertilizer, 0.7 kg Micromax™ micronutrient fertilizer, Sierra Chemical Co., 1001 Yosemite Drive, Milpitas, CA 95035.
2. Decagon Sunfleck Ceptometer, model SF-80. Manufactured by Decagon Devices, Inc., Pullman, Washington, 99163. http://www.decagon.com.
3. Li-Cor 3100 Area Meter. Manufactured by Li-Cor Biosciences, Lincoln, Nebraska, 68504. http://www.licor.com.
4. Specimens identified by Dr. Art Shapiro, UC Davis.

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## Table 3.1. Abbreviated Analysis of Variance for Experiment 1.

| Source | DF Num | SS | MS Num | F Ratio | Prob > F |
|---|---|---|---|---|---|
| **Log Total Biomass** | | | | | |
| **Population** | **3** | **17** | **5.7** | **8.0** | **0.0015**** |
| **Light percentage[1]** | **2** | **283** | **141.3** | **74.4** | **0.0007***** |
| **Light percentage x Population** | **6** | **5** | **0.9** | **3.6** | **0.0071**** |
| **Genotype nested within Population** | **16** | **12** | **0.8** | **3.0** | **0.0030**** |
| Light percentage x Genotype nested within Population | 32 | 8 | 0.2 | 0.6 | 0.9704 |
| **Initial weight of cutting[2]** | **1** | **6** | **5.9** | **13.8** | **0.0003***** |
| **Relative Growth Rate (Ranks Averaged)** | | | | | |
| **Population** | **3** | **15976** | **5325.3** | **3.7** | **0.0340*** |
| **Light percentage[1]** | **2** | **293595** | **146797.3** | **70.1** | **0.0008***** |
| **Light percentage x Population** | **6** | **19708** | **3284.7** | **9.2** | **<0.0001***** |
| **Genotype nested within Population** | **16** | **23716** | **1482.2** | **4.0** | **0.0003***** |
| Light percentage x Genotype nested within Population | 32 | 11427 | 357.1 | 0.4 | 0.9982 |
| **Leaf Area (Ranks Averaged) with full sunlight treatment excluded** | | | | | |
| **Population** | **3** | **13643** | **4547.5** | **9.5** | **0.0005***** |
| Light percentage[1] | 1 | 1569 | 1568.5 | 0.6 | 0.5209 |
| Light percentage x Population | 3 | 295 | 98.4 | 0.5 | 0.6588 |
| **Genotype nested within Population** | **16** | **7744** | **484.0** | **2.9** | **0.0190*** |
| Light percentage x Genotype nested within Population | 16 | 2643 | 165.2 | 0.4 | 0.9821 |
| **Leaf Number (Ranks Averaged)** | | | | | |
| **Population** | **3** | **13371** | **4456.9** | **8.0** | **0.0014**** |
| **Light percentage[1]** | **1** | **39610** | **39609.6** | **21.4** | **0.0437*** |
| Light percentage x Population | 3 | 26 | 8.6 | 0.04 | 0.9868 |
| **Genotype nested within Population** | **16** | **9006** | **562.9** | **3.0** | **0.0153*** |
| Light percentage x Genotype nested within Population | 16 | 2946 | 184.1 | 0.4 | 0.9672 |

1. Light percentage values calculated using separate JMP analysis (see text for description)
* F < 0.05; ** F < 0.01; *** F < 0.001
2. Initial weight of cutting only shown when significant.

**Table 3.2. Abbreviated Analysis of Variance for Experiment 2.**

| Source | DF Num | SS | MS Num | F Ratio | Prob > F |
|---|---|---|---|---|---|
| **Log Total Biomass** | | | | | |
| Population | 2 | 1 | 0.6 | 0.6 | 0.5643 |
| **Light percentage[1]** | **2** | **154** | **76.9** | **103.2** | **0.0003*** ** |
| Light percentage x Population | 5 | 6.8 | 1.4 | 0.8 | 0.5581 |
| Genotype nested within Population | 15 | 15 | 1 | 1 | 0.8594 |
| Light percentage x Genotype nested within Population | 31 | 53 | 1.7 | 1.4 | 0.1146 |
| **Initial weight of cutting[2]** | **1** | **17** | **17** | **13.6** | **0.0004*** ** |
| **Relative Growth Rate (Ranks Averaged)** | | | | | |
| Population | 3 | 7340 | 2446.6 | 0.7 | 0.5536 |
| **Light percentage[1]** | **2** | **130241** | **65120.4** | **38.4** | **0.0025** ** |
| Light percentage x Population | 6 | 10200 | 1700.1 | 0.6 | 0.7365 |
| Genotype nested within Population | 16 | 55221 | 3451.3 | 1.2 | 0.3186 |
| **Light percentage x Genotype nested within Population** | **32** | **92334** | **2885.5** | **1.8** | **0.0109*** |
| **Initial weight of cutting[2]** | **1** | **7116** | **7115.7** | **4.5** | **0.0360*** |
| **Leaf Area (Ranks Averaged) with full sunlight treatment excluded** | | | | | |
| Population | 3 | 2482 | 827.3 | 0.8 | 0.5037 |
| **Light percentage[1]** | **1** | **23607** | **23607** | **20.7** | **0.0445*** |
| Light percentage x Population | 3 | 4157 | 1385.7 | 1 | 0.4264 |
| Genotype nested within Population | 16 | 16188 | 1011.8 | 1 | 0.7563 |
| Light percentage x Genotype nested within Population | 16 | 23082 | 1442.6 | 1.3 | 0.2461 |
| **Leaf Number (Ranks Averaged)** | | | | | |
| Population | 2 | 181 | 90.5 | 0.1 | 0.9024 |
| **Light percentage[1]** | **2** | **88637** | **44318.5** | **65.7** | **0.0008*** ** |
| Light percentage x Population | 5 | 5195 | 1039.1 | 0.7 | 0.6006 |
| Genotype nested within Population | 15 | 12673 | 844.9 | 0.6 | 0.8408 |
| Light percentage x Genotype nested within Population | 31 | 44293 | 1428.8 | 1.5 | 0.06717 |
| **Initial weight of cutting[2]** | **1** | **16980** | **16979.6** | **18.1** | **0.0001*** ** |

1. Light percentage values calculated using separate JMP analysis (see text for description)
* F < 0.05; ** F < 0.01; *** F < 0.001
2. Initial weight of cutting only shown when significant.

**Table 3.3. Number of Plants Surviving to the End of Experiment 1 and 2 in each Sunlight Percentage**

| Sunlight Precentage | n | Experiment 1 | Experiment 2 |
|---|---|---|---|
| 100 | 60 | 52 | 40 |
| 20 | 60 | 55 | 47 |
| 6 | 60 | 55 | 35 |

**Table 3.4. Mean Length per Day for Experiments 1 and 2 (mm/day)**

| | n | Mean | SE | Maximum | Minimum |
|---|---|---|---|---|---|
| **Experiment 1** | 114 | 41.6 | 3.8 | 226.5 | 0.75 |
| **Experiment 2** | 146 | 16.4 | 1.8 | 102.03 | 0 |

### Table 3.5. Least Squares Means for Genotype nested within Population crossed with Sunlight Percentage, for Curry County, Experiment 2

| Genotype, Light Level | Least Squares Mean | SE |
|---|---|---|
| 1,6 | 0.1169 | 0.0224 |
| 1,20 | 0.0941 | 0.0229 |
| 1,100 | 0.0032 | 0.0233 |
| 2,6 | 0.0819 | 0.0229 |
| 2,20 | 0.1261 | 0.0225 |
| 2,100 | 0.0371 | 0.0224 |
| 3,6 | 0.0959 | 0.0224 |
| 3,20 | 0.1229 | 0.0224 |
| 3,100 | 0.0201 | 0.0224 |
| 4,6 | 0.0759 | 0.0225 |
| 4,20 | 0.0324 | 0.0224 |
| 4,100 | 0.0232 | 0.0225 |
| 5,6 | 0.0633 | 0.0224 |
| 5,20 | 0.1308 | 0.0224 |
| 5,100 | 0.0295 | 0.0225 |

### Table 3.6. Coefficient of Variation for Genotype Nested within Population for Experiment 1

| Population | Log Total Biomass | RGR | Leaf Area | Leaf Number |
|---|---|---|---|---|
| Curry | 21 | 6 | 11 | 11 |
| Mendocino | 39 | 20 | 59 | 28 |
| Marin | 39 | 22 | 40 | 24 |
| San Diego | 24 | 12 | 36 | 24 |

## Table 3.7. Population Information for Growth Analysis Experiment Locations

| Location | Morphology Type | Collected from Sun or Shade | Sexually Reproducing?[3] | Mean Annual Precipitation (mm)[1] | Mean Annual Temperature Range (ºC) Min/Max[1] |
|---|---|---|---|---|---|
| Curry County, Oregon | Non-Stipulate | Full Sunlight | Yes | 2020[2] | 4.8/20.3[2] |
| Mendocino County | Stipulate | Full Sunlight | No | 1279 | 3.9/20.3 |
| Marin County | Stipulate | Shade | Yes | 1026 | 5.0/21.8 |
| San Diego County | Non-Stipulate | Shade | No | 322 | 7.5/25.9 |

1. Values for mean annual precipitation and temperature ranges obtained from BIOCLIM raster data as described in Chapter 2 Methods.
2. Data for Curry County location obtained from http://www.ocs.oregonstate.edu/page links/climate data zones/info sheets/gold beach ranger.html
3. See Chapter 4 for seed viability studies.

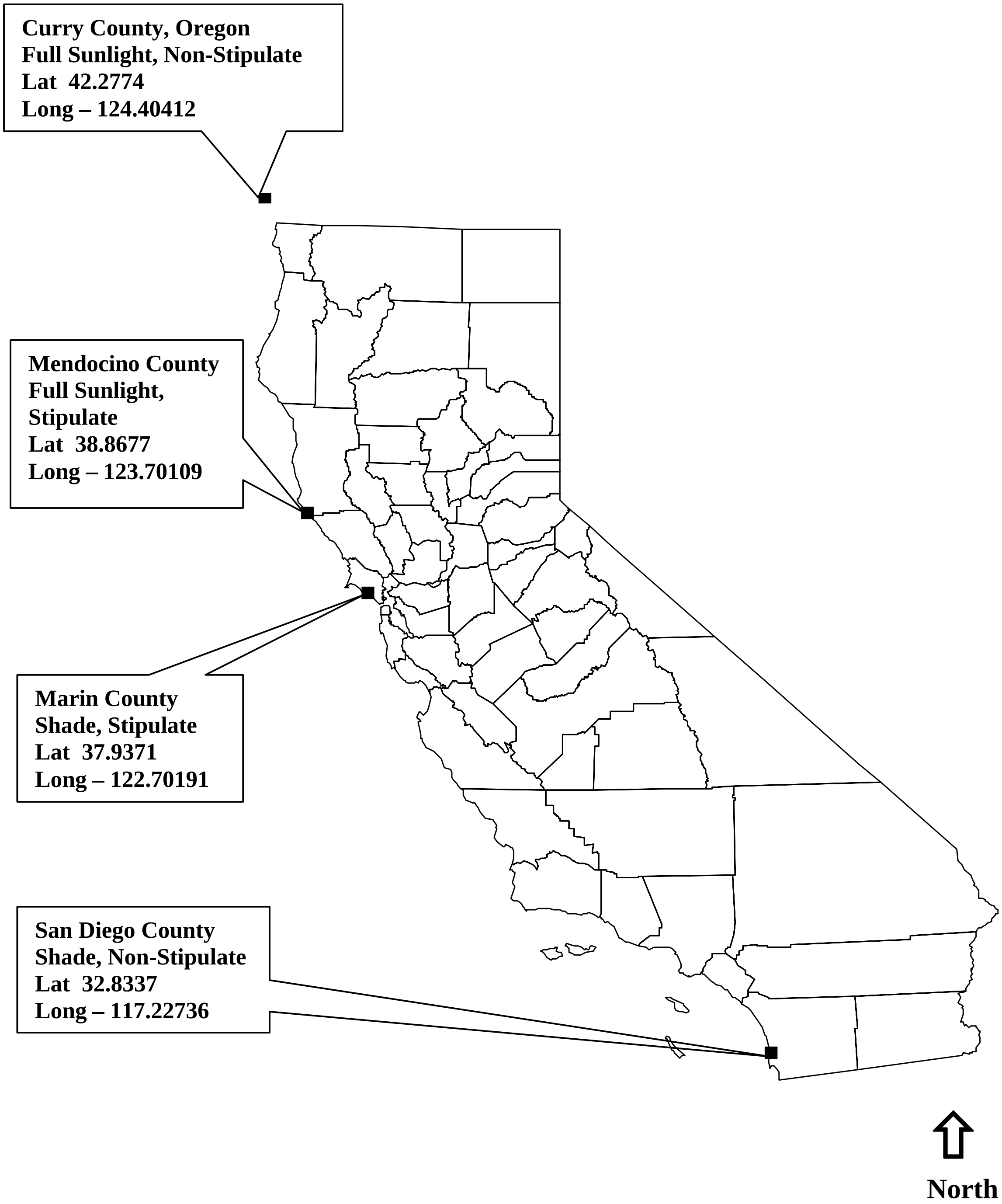


**Figure 3.1. Sources of Cape Ivy Cuttings for Growth Analysis Experiments**

**Figure 3.2a. Daily Maximum and Minimum Temperatures During Experiment 1**

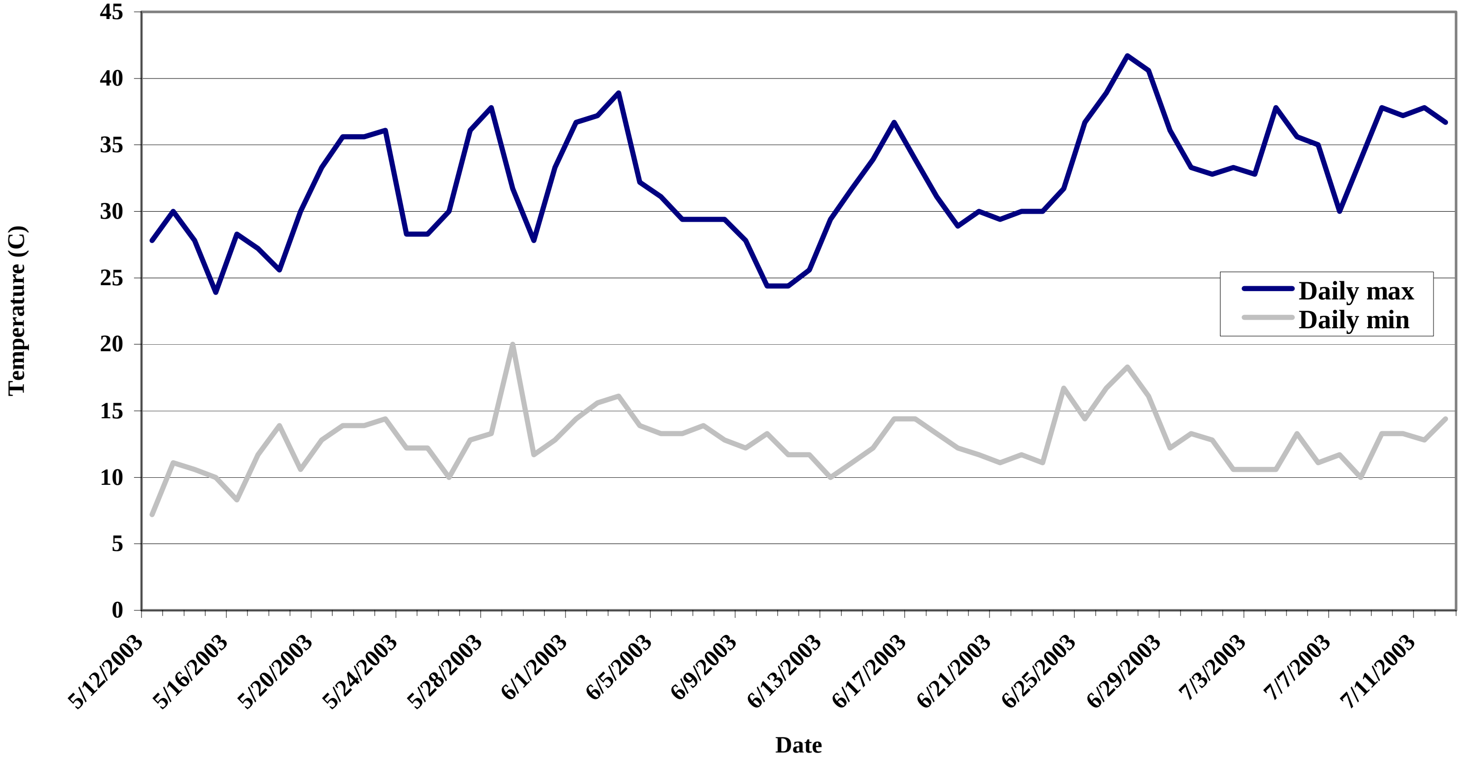
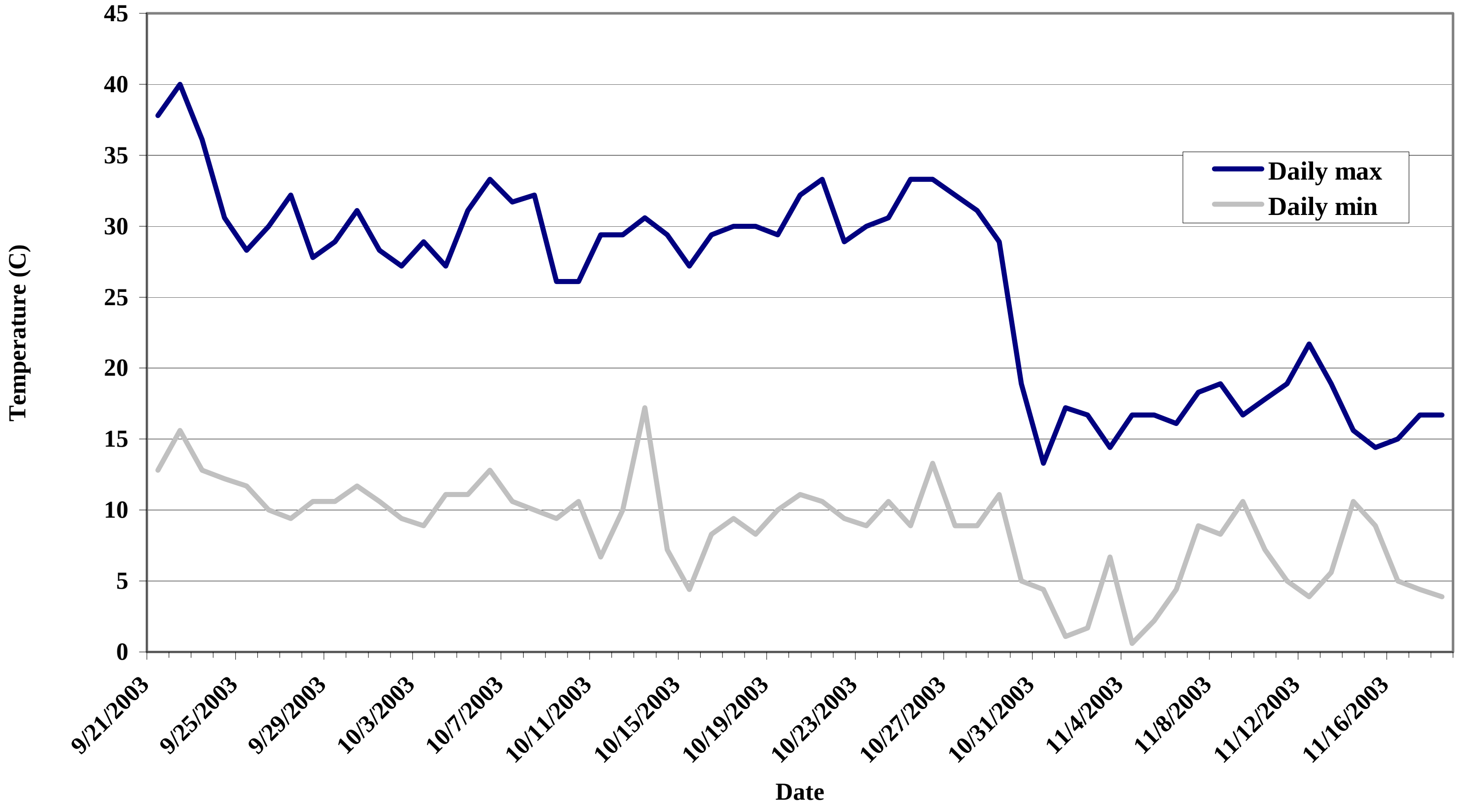


Figure 3.2b. Daily Maximum and Minimum Temperatures During Experiment 2



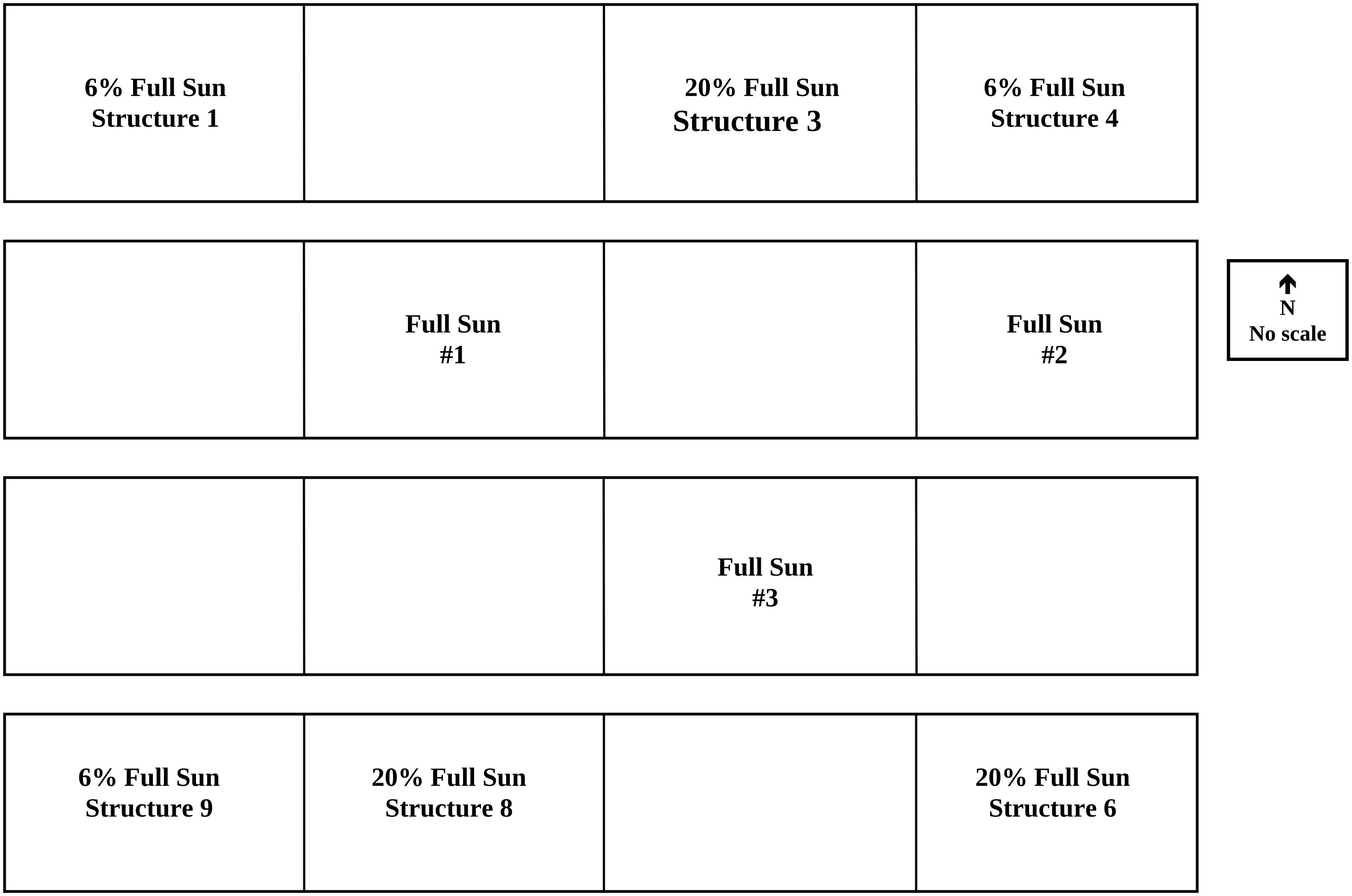
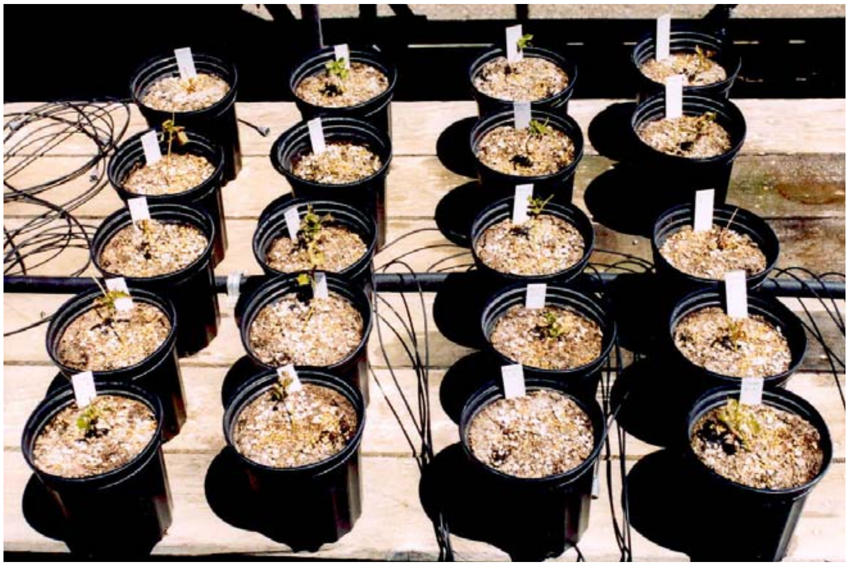


**Figure 3.3. Cape Ivy Growth Analysis Experimental Design**

**Figure 3.4. Photographs of Light Treatments at End of Experiment 1**

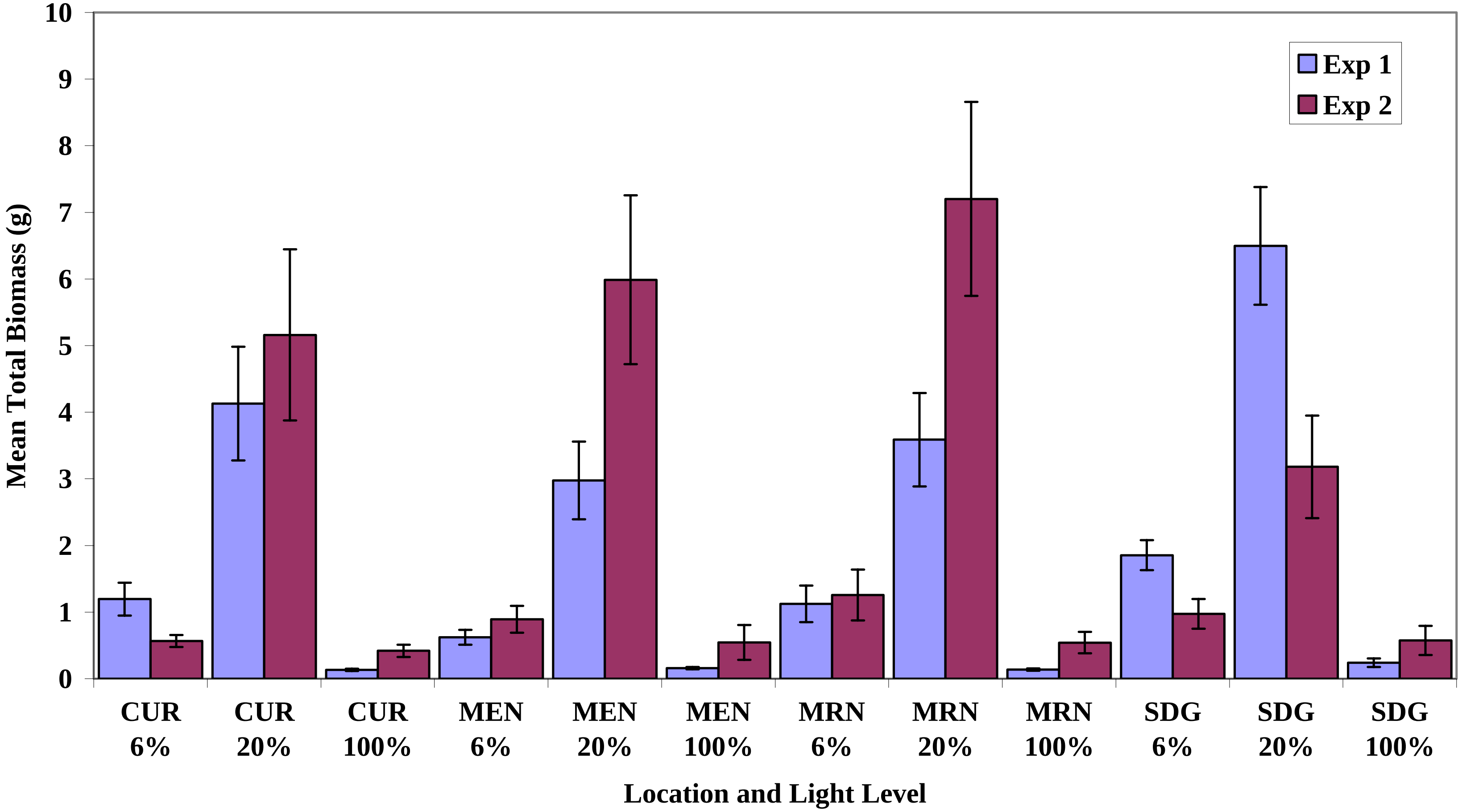
**6% Sunlight**

**20% Sunlight**



**Full Sunlight**

Figure 3.5. Mean Total Biomass Comparison for Both Experiments by Light Level and Location



Bars are Standard Error.

**Figure 3.6. Comparison of Above and Below Ground Total Biomass for Experiment 1. Bars are Standard Deviation.**

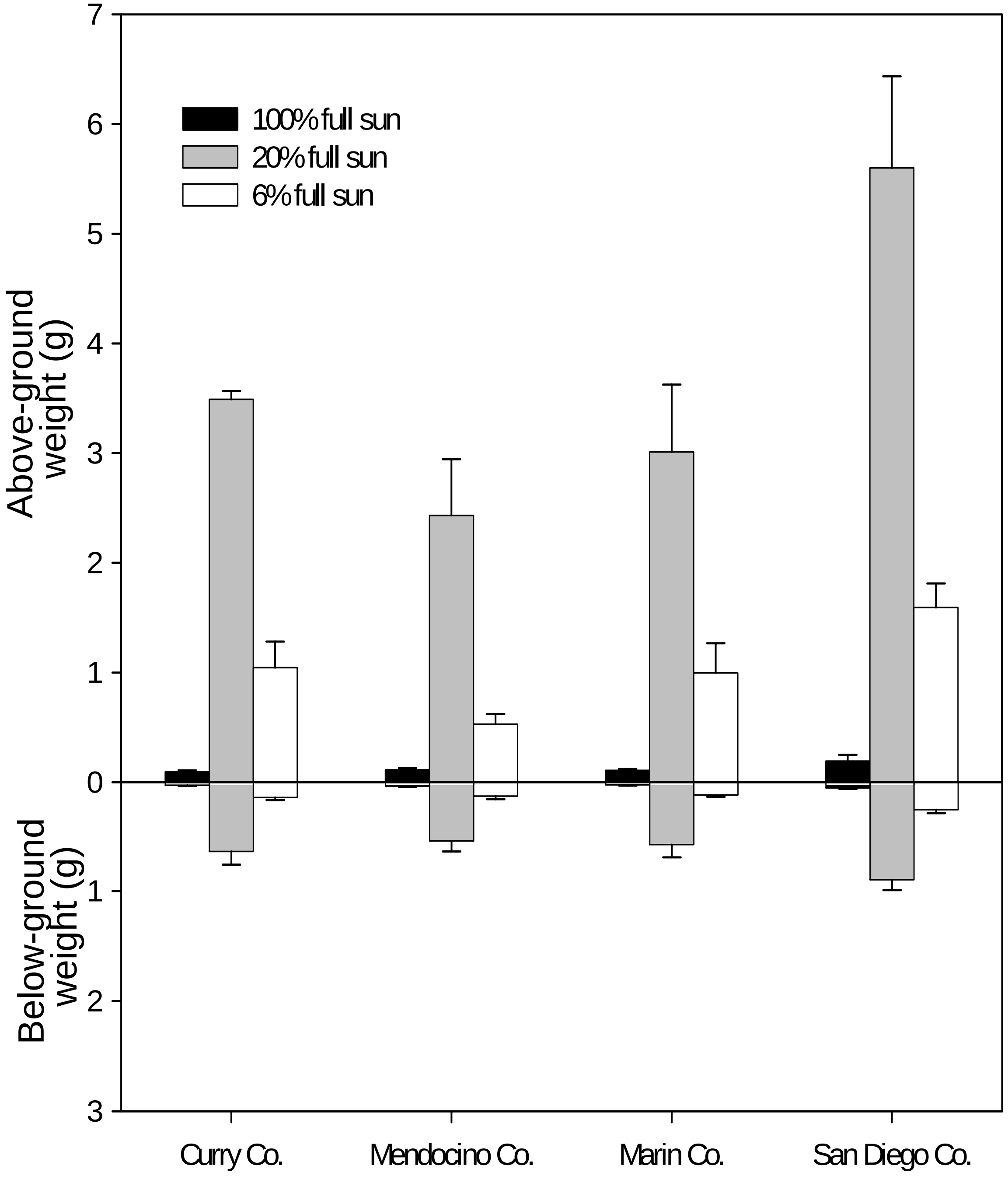
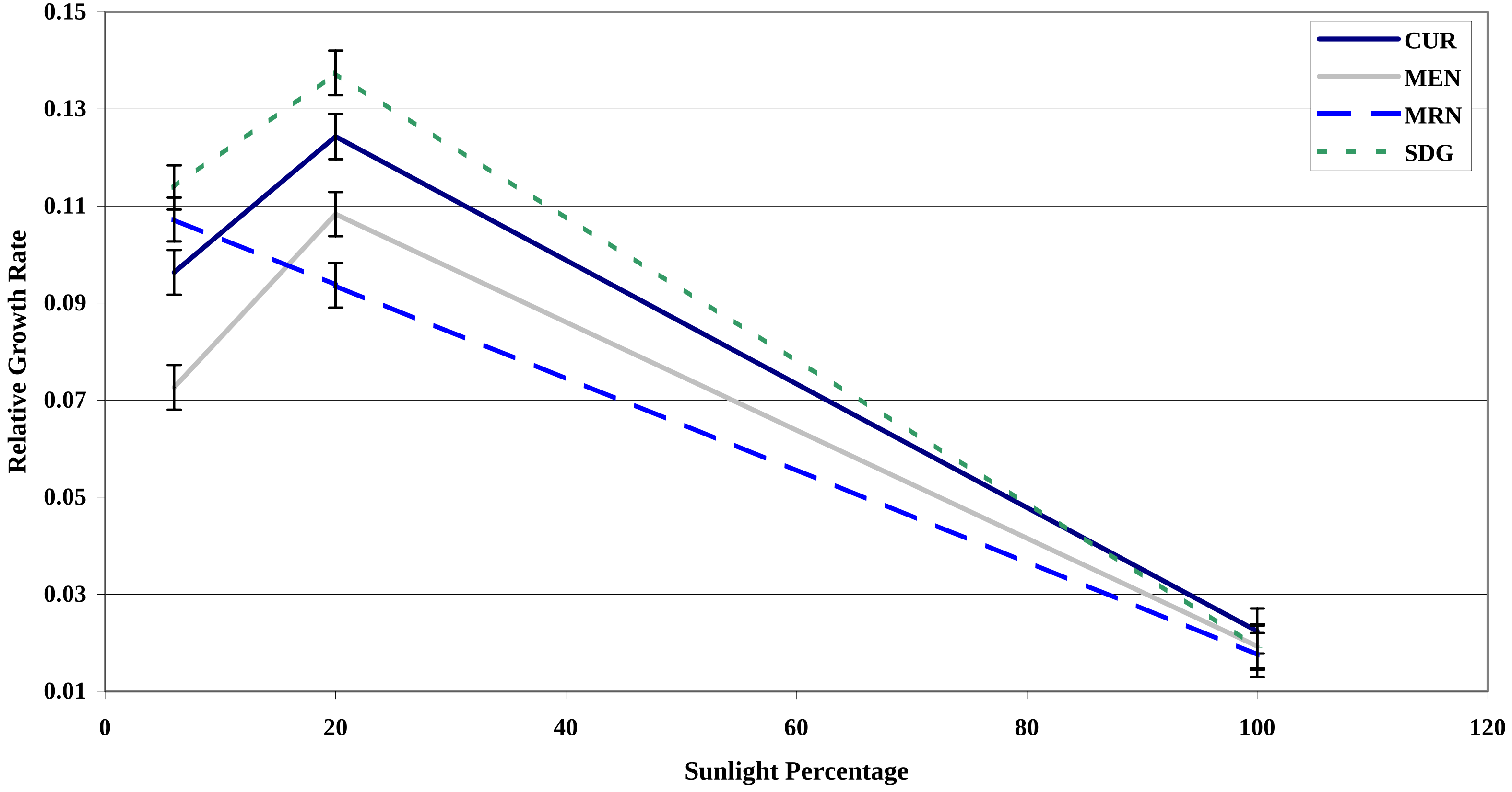
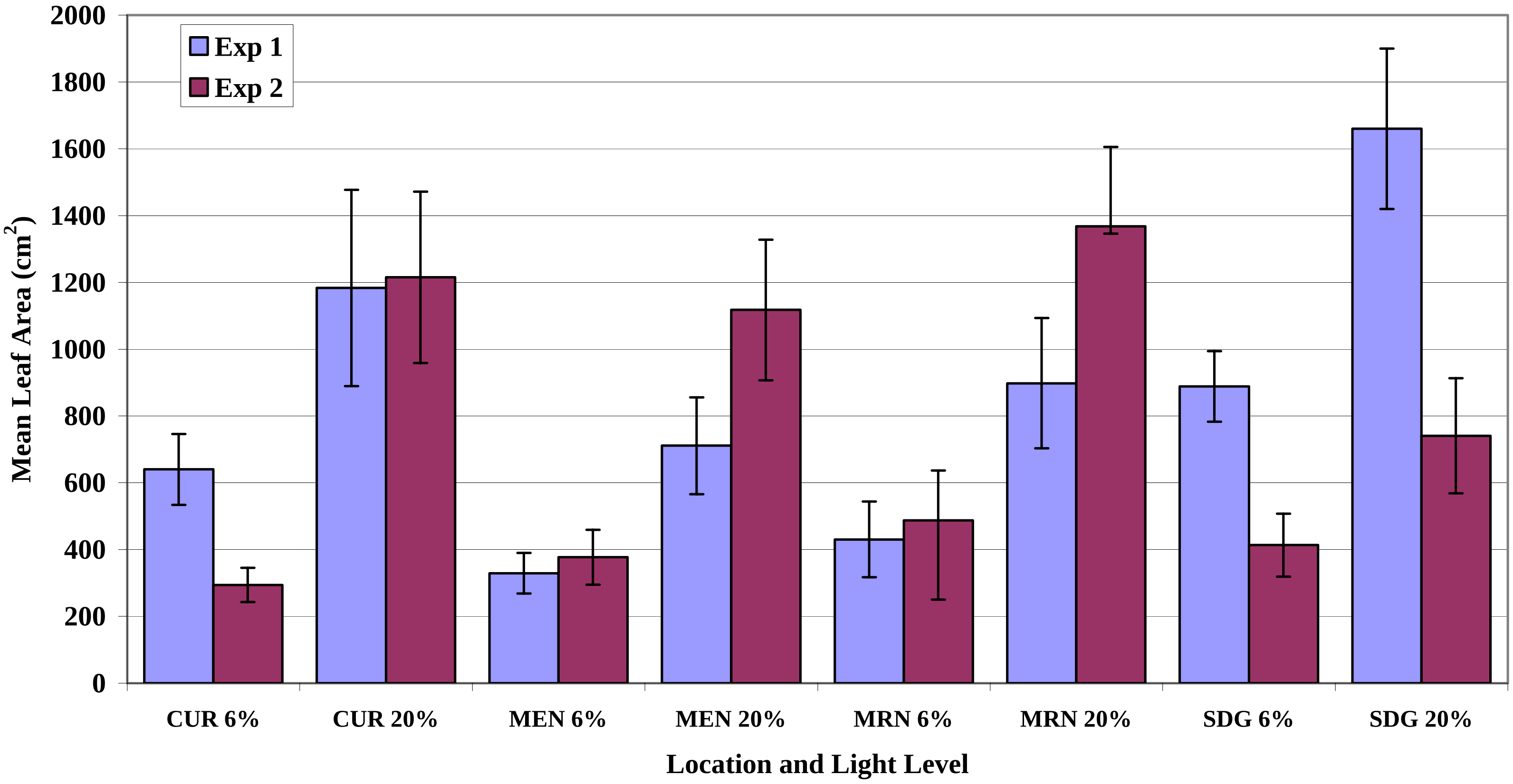


Figure 3.7. Experiment 1 Least Squares Means for Relative Growth Rate, by Population and Sunlight Percentage



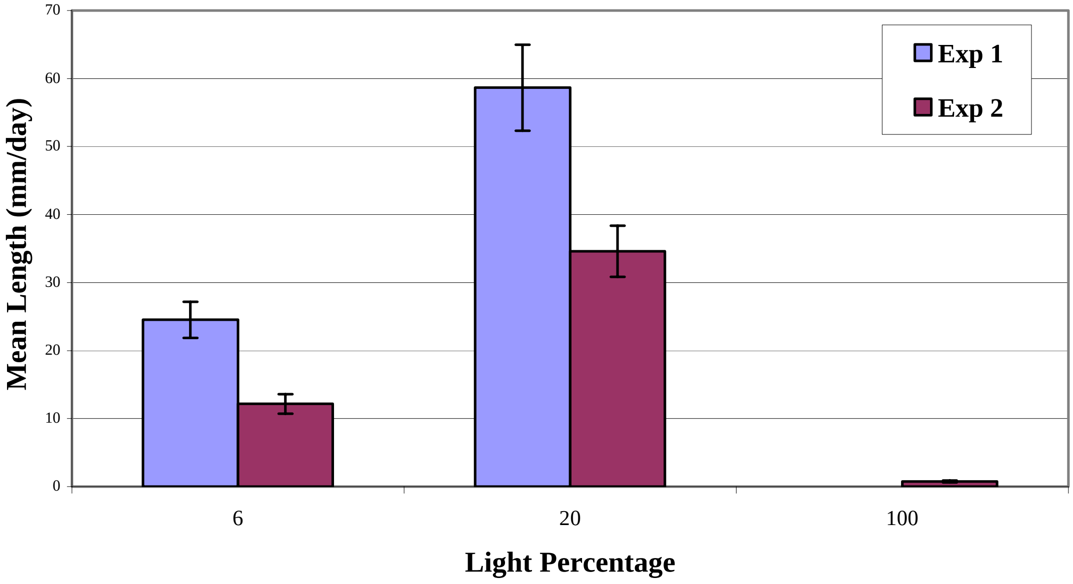
Bars are Standard Error of Least Squares Means.

Figure 3.8. Mean Leaf Area by Location and Light Level



Bars are Standard Error.

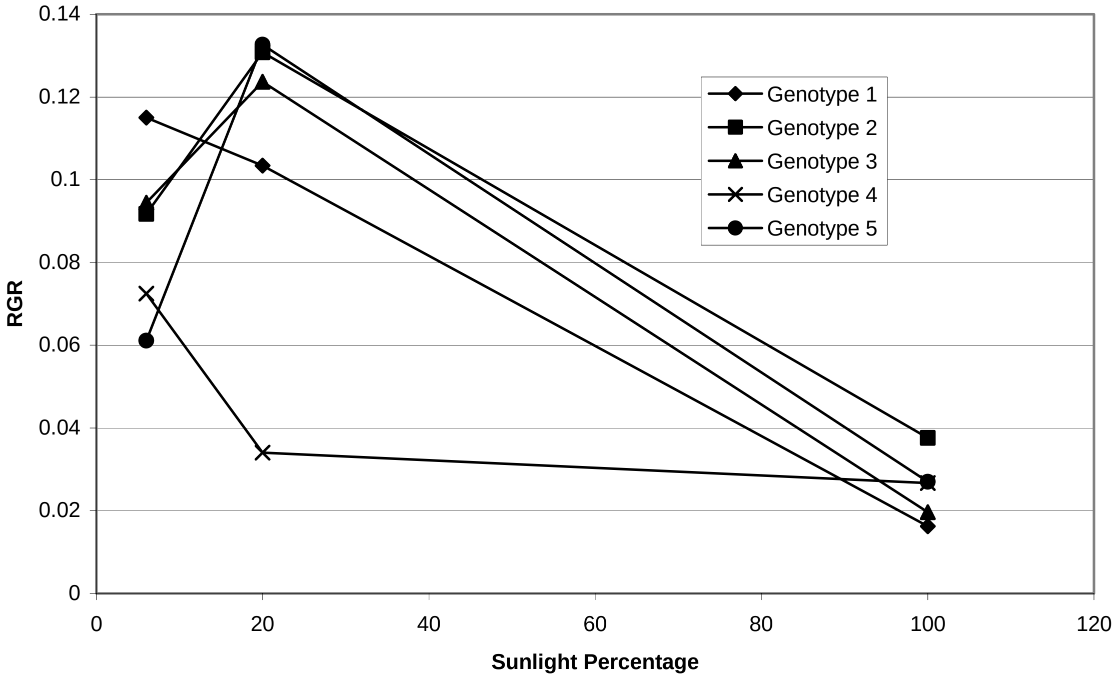
**Figure 3.9. Mean Length Per Day by Light Percentage**



Bars are Standard Error.

**Figure 3.10a. Experiment 2 Norm of Reaction for Relative Growth Rate of Genotypes at each Sunlight Percentage**

**CURRY**



**MENDOCINO**

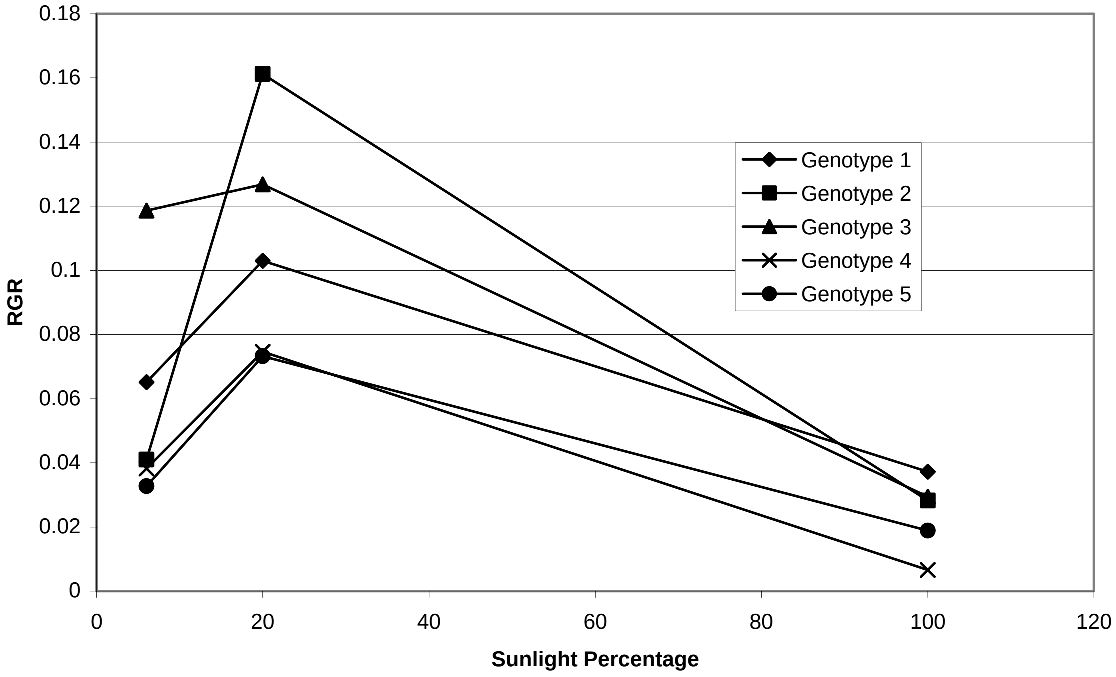
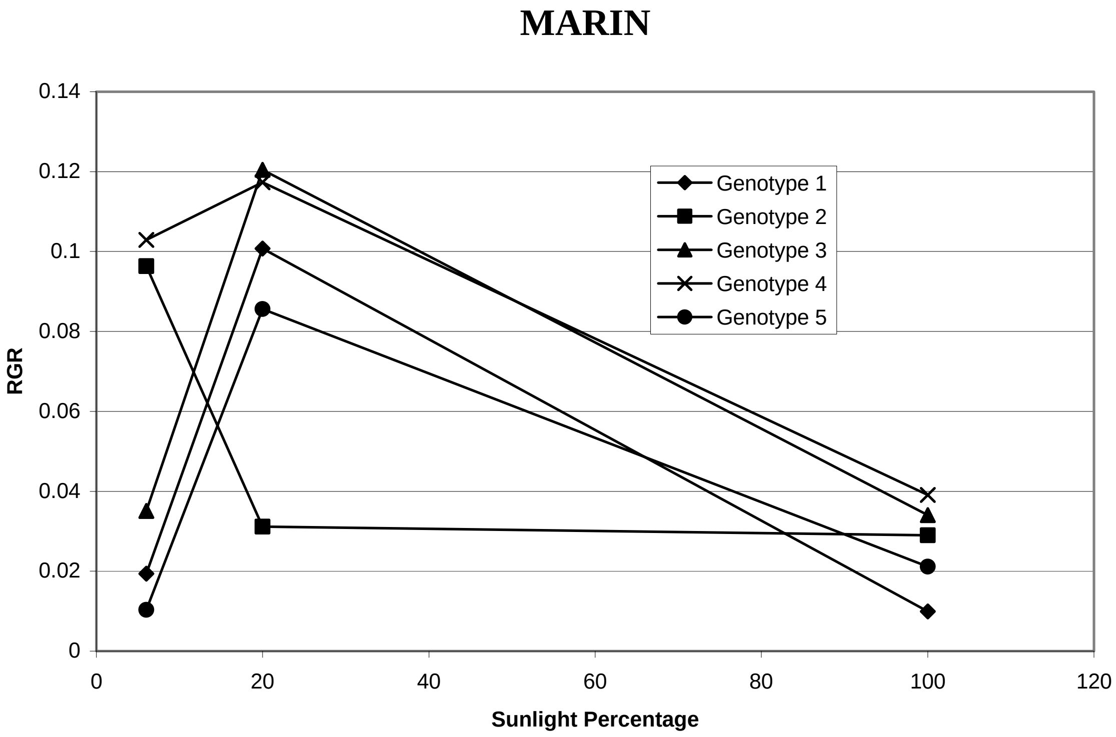
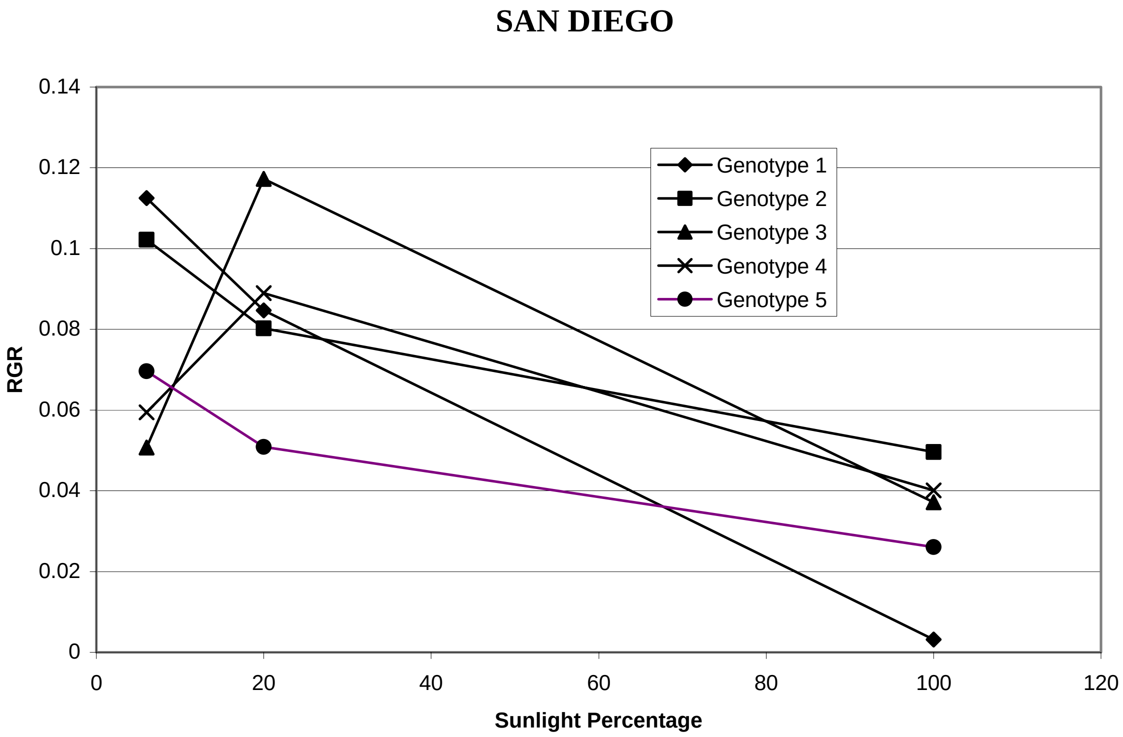


**Figure 3.10b. Experiment 2 Norm of Reaction for Relative Growth Rate of Genotypes at each Sunlight Percentage (Continued).**





# CHAPTER 4

# Reproductive Biology

## ABSTRACT

Studies on the reproductive biology of Cape ivy were conducted to better understand mechanisms underlying the potential spread of this species. Reciprocal crossing experiments were carried out to determine whether flowers from individual plants were self-compatible. Seed biology studies were also done to determine germination requirements and seed production characteristics. Cape ivy was shown to be self-incompatible in California because plants that were artificially cross-pollinated produced a larger percentage of filled (viable) seed than those that were self-pollinated. Seed from a wide geographic range of populations was sampled and 66% of 104 locations produced viable seed. Seed weights ranged from 0.02 mg to 0.39 mg, and the highest percentage of germination occurred in seeds weighing above 0.20 mg. Optimal germination occurred between 17 and 25ºC and seeds germinated in both light and dark treatments. Seeds germinated when planted on the soil surface or when buried 1 cm, but did not emerge when buried to depths of 2, 3, or 4 cm. One and two-node stem fragments planted on the soil surface or buried 2 cm emerged, but those buried at 4, 6 or 10 cm did not. This study demonstrates that Cape ivy is self-incompatible and, contrary to previous reports, produces viable seeds in most locations throughout California.

## INTRODUCTION

Cape ivy (*Delairea odorata*, syn *Senecio mikanioides*), originally from South Africa, is an invader of California’s coastal forests and scrublands. It is a brittle vine that is able to invade relatively undisturbed habitats through vegetatively propagating fragments and wind-dispersed seed. As presented in previous chapters of this dissertation, it is widespread in California and occupies a number of coastal vegetation communities. In Chapter 2, it was predicted to have a negative impact on 17 sensitive species based on an overlay analysis of Cape ivy point locations with data in the California Natural Diversity Database. Some of these sensitive species were plants with restricted distributions (less than 42 occurrences worldwide) and up to 73 percent of their occurrences could be negatively affected by Cape ivy. Given the threats to native species biodiversity, the current study was undertaken to gather more information on the seed and reproductive biology of Cape ivy, with the intention of contributing to more biologically-based management strategies.

Cape ivy produces 20 or more bisexual, discoid flower heads terminally or axillarily in a corymbose inflorescence (Lawrence 1985). The flower heads are each composed of rayless “disk” flowers enclosed by black-tipped phyllaries. The fruit produced is an oblong, dark colored achene formed from a single fertilized flower. The plump, viable achenes have longitudinal striations covered with minute strigose hairs, and the achene is topped by a pappus of stiff-haired bristles (Lemaire 1844, Harvey 1894, Hickman 1993).

In California, Cape ivy blooms from September to February (autumn to winter). By comparison, in its native range in South Africa, it flowers from May to July (also autumn to winter), indicating that flowering may be induced by short day-lengths. However, experimental attempts to artificially induce flowering using growth chambers were unsuccessful. Cape ivy is known to produce viable seed in its native South Africa as well as Hawaii and Australia (Wagner et al. 1990, Blood 2003), but there are no previous reports of viable seed production in California.

In addition to seed production, Cape ivy has two readily distinguishable morphological types. Some of the vines have a pair of stipules located at the base of the stem nodes, and other vines lack stipules. This is an interesting characteristic given that in its native range all but one population are stipulate (J. Balciunas, personal communication). In California we have a mixture of both types (see Chapter 2). The northern and southern ends of the distribution in California are predominantly non-stipulate, while the center of the distribution has a mix of both types, sometimes occurring in one location.

Baker (1974) proposed a list of 12 characteristics defining the ideal weed. Most of those characteristics relate to reproductive biology and dispersal. Cape ivy is known to possess the characteristics of an ideal weed in regards to its vegetative reproduction, but little is known about its reproductive biology and specifically its seed biology and self-compatibility. Baker and others (Allard 1965, Olivieri et al. 1991) have hypothesized that the plants with the most invasive potential are self-compatible, but not completely autogamous or apomictic (Baker 1965, 1974). Their reasoning was that a long-distance dispersal event could be followed by seed set even without suitable pollinators. Although it was long assumed that only self-compatible species have weedy potential, more recent studies have shown that the type of breeding system does not necessarily determine the ability of a species to become invasive (Price and Jain 1981, Reichard and Hamilton 1997).

The earliest information available on Cape ivy's reproductive biology comes from experiments performed in Australia in the 1980s (Lawrence 1985). These studies found that Cape ivy was self-incompatible and its potential seed set was between 20,000 and 40,000 per plant. A number of experiments were also conducted on Cape ivy's seed and reproductive biology in its native South Africa (Rolando 2000), where it was also found to be self-incompatible. A few preliminary studies have been conducted in California. USDA researchers in Reno, Nevada, evaluated the germination of Cape ivy seed from one population in Albany, California (Young 2000). They tested 100 seeds at temperatures between 5 and 40°C using various treatments to determine their germination percentage. Only one seedling germinated in the entire testing procedure in a plate with an equal mixture of $10^{-2}$ mmol potassium nitrate and 250 ppm gibberellin ($GA_3$). When the seedling was transported to the greenhouse the cotyledons never turned green and the seedling died (Young 2000). In 1994, Bossard and O'Connell tested thousands of seeds from 26 populations throughout California and did not find any germinable seed (Bossard 2000, Bossard et al. 2000). Based on these two studies, it was assumed prior to 2001 that Cape ivy was not producing viable seed in California and that populations were self-incompatible.

Reproductive biology, and seed production in particular, are important factors in invasive species success and spread (Baker 1965, 1974, Mooney et al. 1986, Newsome and Noble 1986). To test the assumptions about California Cape ivy self-compatibility and seed viability, seed from several sites were collected. Once viable seeds were discovered, further experiments were designed to examine the seed biology and environmental requirements for germination. Reproductive biology experiments were also undertaken to determine if California Cape ivy is self-compatible, and to determine the crossing potential of various populations throughout the state.

The three main areas of this portion of the research were: seed collection, seed biology and reproductive biology. Some of the specific questions addressed are summarized below.

Seed collections were conducted to answer the question, “Where is Cape ivy seed being produced in California?” Once viable seed was discovered, questions about seed viability followed. First we asked, “Are large, “filled” seeds more viable than small, “unfilled” seeds, and can the designation of viable or not viable be made based on weight or visual inspection?” The seed germination by weight class experiment was designed address this question. Previous studies (Lawrence 1985, Rolando 2000), had assumed that the large “filled” seed would have the highest viability, but they did not specifically test that assumption. Next we asked, “What is the optimal temperature germination range of Cape ivy seed?” This question was asked to determine whether the range of Cape ivy is being limited by the ability of its seed to germinate either at low or high temperatures.

Two environmental questions were also asked. Currently it is not known whether sexual or asexual reproduction contributes more to the spread of Cape ivy. Tests were designed to determine if Cape ivy seed or stem fragments could germinate or emerge when buried at different depths. This might have some use in the management of Cape ivy populations since a common mechanical control technique is vegetation removal followed by clearing of the soil surface. This practice exposes seeds or stem fragments and could stimulate their germination or emergence.  Conversely, it was not known whether burial of seeds or stems would prove to be an effective management technique.

Reproductive biology experiments were designed to answer the questions, (1) Is Cape ivy self-compatible in California and (2) When two morphological types are crossed will they produce viable seeds?  Rolando (2000) also conducted reproductive biology experiments in South Africa to examine whether Cape ivy is self-compatible or an obligate out-crosser, if plants were pollen limited, and if seed set were different in wild versus hand-pollinated plants.

## MATERIALS AND METHODS

### Seed Collections

Seed collection began in 2001 in what appeared to be an exceptional year for Cape ivy seed production in California.  The climate was relatively dry during January and February and seeds were able to mature and disperse before being damaged by storms.  Cape ivy seeds were collected from February 7 to March 21, 2001, from field sites throughout California.  Seeds from Southern California matured and were collected earlier than seeds from northern California.  Seeds from 52 locations were collected ranging from San Diego County to Humboldt County, California, and seeds were collected from one population in Curry County, Oregon.  The driest, most mature seeds were gathered, and all seeds from a given location were pooled and placed in paper bags or envelopes.  The bags were kept at room temperature and seeds were allowed to dry under ambient conditions.  Seeds from these collections were used in the greenhouse viability tests discussed below. Table 4.1 contains a list of seed collection locations and an estimate of the percentage of small, medium and large seeds in each sample. Seed sizes were estimated visually and filled seeds were selected for germination tests. Large seeds were dark colored, plump or “filled,” small seeds were light colored, flat or “unfilled”, and medium seeds were intermediate between the two. In Figure 4.1, seeds in the 0 to 0.1 mg category would be considered small, seeds from 0.2 to 0.3 mg were classified as medium, and 0.3 mg+ would be scored as large.

Seeds were again collected in 2002 between January 16 and April 21. As with the first collection, seeds from each location were pooled in one bag. Seeds were collected from fewer locations in 2002, with 19 locations sampled between San Diego and Humboldt counties. Twelve locations from 2001 were sampled again in 2002, while seven locations were new.

Seed collections in 2003 were extensive and represented areas not previously sampled. Ninety-nine locations were sampled between February 6 and March 16. Collections started in Southern California and continued up the California coast, ending in southern Oregon. In 2003, seeds were collected at each location by placing individual inflorescences in separate envelopes. These envelopes were stored in paper bags at room temperature to allow seeds to dry.

Collection locations for 2001 to 2003 are pictured in Figure 4.2 and dates are listed in Table C-1, Appendix C. A total of 104 different locations were sampled during the three year period. In addition to a description of the locations, Table C-1 contains latitude and longitude in the NAD 83 datum.

Figure 4.3 shows yearly cumulative precipitation at Half Moon Bay (Figure 4.3a), and Santa Barbara (Figure 4.3b**)** from July 1, 2000, to June 30, 2003. Daily precipitation data was obtained from the University of California Integrated Pest Management Online weather database http://www.ipm.ucdavis.edu/WEATHER/wxretrieve.html.

## Seed Biology

### 2001 Seed Germination

Germination tests were conducted in 2001 in a temperature controlled greenhouse in Sacramento, California. Seeds were cleaned and large or medium sizes (as described above) were separated. Twenty seeds from each location were placed in a 10.2 cm (4 inch) plastic pot on top of sterilized potting soil, and a small amount of soil was sprinkled on top. This initial experiment began on May 16 and included 23 locations. A second trial began on May 25 and included 15 locations, and a third trial started on June 28 with the same 15 locations tested as in the May 25 trial. All three trials were terminated on August 8, 2001. Greenhouse maximum and minimum temperatures and humidity were recorded. The temperature range during the experiments was 12.2 to 37.8ºC. Relative humidity was between 32 and 98%; light levels were not measured.

### 2002 and 2003 Seed Collection Location Analysis

Seed collections in 2002 and 2003 were examined for filled seed by visual inspection. For the 2002 collections, in which seeds were pooled in one envelope, at least 100 inflorescences from each envelope were inspected to determine if any large seeds were produced. The presence of large seeds was recorded after visual inspection under a dissection microscope. For the 2003 collections, in which inflorescences were collected in separate envelopes, at least five envelopes were examined for the presence of large seeds.

### Seed Viability by Weight

To determine the weight distribution of seeds from wild populations, seeds from two locations were weighed. One hundred seeds from Avila in San Luis Obispo County and 73 seeds from Monrovia in Los Angeles County were weighed using a Perkin–Elmer AD-4 Autobalance[2]. Avila seed weights ranged from 0.05 to 0.33 mg and Monrovia weights ranged from 0.02 to 0.39 mg. Based on these ranges, I established weight classes of 0 to 0.10 mg, 0.101 to 0.20 mg, 0.201 to 0.30 mg, and above. These weight classes were used in seed germination and viability experiments described below. Photos of seeds in the four weight classes are shown in Figure 4.1.

In order to determine viability of all seed weight classes, tetrazolium tests were performed on seeds from Volunteer Canyon, Marin County (105 seeds); Purisima Creek, San Mateo County (100 seeds); and Toro Canyon, Santa Barbara County (216 seeds). Seeds were first weighed as described above, placed in deionized water for 12 to 24 hours, then soaked in 1% solution of 2,3,5 tri-phenyl tetrazolium chloride (TZ) for another 12 to 24 hours. After exposure to TZ, respiring tissues stain red, indicating viability (Hartmann et al. 1997). Treated seeds were cut open and scored as viable or not viable depending on the color of various tissues. If the embryo stained red and the endosperm remained unstained, the seed was considered viable. If the embryo did not stain, was partially stained, or if the endosperm was stained instead of or in addition to the embryo, the seed was considered non-viable.

Optimum Seed Germination Temperature

A seed germination temperature response study was conducted in 2001. Large seeds (0.2 mg or greater) were used from populations in Humboldt, Marin, Los Angeles and San Diego counties. Twenty filled seeds from each location were placed in sterile 8.5 cm diameter petri dishes containing a sterilized piece of Anchor Steel Blue Seed Germination Blotter[3] and 8 ml deionized water. The dishes were sealed with parafilm "M" to prevent desiccation and reduce microbial contamination, and then put on a temperature gradient table ranging from 8 to 34ºC. Cooling was provided by a VWR Scientific refrigerated recirculator at one end of the table and a heater at the opposite end, creating the temperature gradient. The table consisted of eight parallel lanes (each 10 cm wide, 24 cm long and 15 cm deep) separated by clear acrylic and oriented perpendicular to the temperature gradient. Each lane contained a mercury thermometer (-20 to 110ºC). Around the clear acrylic lanes were 5 to 8 cm of styrofoam insulation and two more layers of clear acrylic covered the top of the table. Four petri dishes, one with seeds from each County, were placed in each lane adjacent to the thermometer, and temperatures immediately outside the dishes in each lane were recorded. Seeds were exposed to a 12 hour light/12 hour dark cycle from four cool white florescent lights placed 46 cm above the table. The number of seeds germinating each day was recorded and the experiment was terminated after seven days.

In 2003 and 2004 a more extensive seed germination temperature study was conducted using populations from Purisima Creek, San Mateo County; Toro Canyon Creek, Santa Barbara County; Monrovia Canyon County Park, Los Angeles County; and Bonsall Preserve, San Diego County. The experiment was conducted three times for the four populations using the methods described above. Treatment temperatures varied between test dates and that was taken into account during the analysis. The first test was conducted between August 11 and August 19, 2003 (temperature range 8, 12, 17, 20, 25, 30, 32, and 38ºC); the second between October 13 and 24, 2003 (temperature range 8, 13, 16, 19, 25, 30, 32, and 39ºC); and the third between January 7 and February 3, 2004 (temperature range 8, 12, 15.5, 18, 24, 28, 30, and 36ºC). Seeds from the Bonsall location were re-tested starting on February 3, 2004, and ending on February 19, 2004 (temperature range 8, 12, 15, 18, 24, 28, 30 and 36ºC). The number of seeds germinating was recorded every two to three days.

### Seed Germination by Weight Class

All seeds used for this experiment and the remainder of the seed biology tests were from the Toro Canyon population in Santa Barbara County. Toro Canyon is located in a riparian woodland in an urban area, and in that sense it was similar to many other collection locations. It was chosen because it produced enough filled seed to run all the experiments, while most of the other populations collected in 2003 did not.

The first seed weight class germination test started on December 17 and ended on December 31, 2003. The experiment was repeated between December 31, 2003, and January 15, 2004. During each experiment three replicates of ten seeds from each of the four weight classes described above were placed in sterile 85 mm diameter petri dishes containing a sterilized piece of Anchor Steel Blue Seed Germination Blotter[3] and 8 ml deionized water. The dishes were sealed with parafilm “M” to prevent desiccation and reduce microbial contamination. The plates were placed in a 20ºC growth room with 24 hour artificial lighting. The number of germinated seeds was recorded every few days.

Additional sterilized deionized water was also added as necessary to maintain filter paper saturation.

## Seed Germination in Light and Dark

Cape ivy seeds were tested for germination response to light. Three petri dishes were prepared for the light and dark treatments with Anchor Steel Blue Seed Germination Blotter[3] and 8 ml of deionized water. Six replicates of ten large seeds from the Toro Canyon population were selected and placed in small coin envelopes. In a darkroom with the lights out, the seeds from three replicates were placed in a petri dishes. The dishes were then sealed with parafilm M and covered with tinfoil. Three replicates for the light treatment were also placed in petri dishes in the darkroom but were not covered in foil. All six petri dishes were placed in a 20ºC growth room with 24 hour artificial lights (same growth room used in seed weight class experiment). Dishes in the light treatment were examined periodically, but dishes in the dark treatment were not opened until the end of the experiment. The first experiment began on January 8 and ended on January 22, 2004. A second trial of this experiment was conducted between February 3 and February 19, 2004.

## Seed Germination at Different Soil Depths

Cape ivy seeds were buried in greenhouse soil (UC mix[1]) at five depths, including surface, 1, 2, 3, and 4 cm. Large, filled seeds were again used from the Toro Canyon population. Seeds were placed in 10.2 cm (4 inch) square pots, either sprinkled on the surface or buried at the selected depth. After seeds were sown, the pots were placed on a mist bench with bottom heat and checked every few days until the end of the experiment. The mist bench operated five times a day for one minute each time and the bottom heat was between 21 and 27ºC. The experiments took place between November 4 and December 9, 2003, and again from December 9 to January 9, 2004. An additional test of the surface and 1 cm depths was started on January 9 and ended on February 2, 2004.

### Effects of Burial Depth on Stem Fragment Sprouting and Emergence

Two sizes of Cape ivy stem fragments were planted at different depths to examine differential rates of node sprouting and emergence. The stem fragment sizes were either one or two nodes, with a centimeter of stem at the edges of the cutting beyond the outside node. Plants were propagated from greenhouse specimens originally collected from the same location in San Luis Obispo County. Fragments were planted at the surface, and at 2, 4, 6, 8, and 10 cm depths in 3.8 liter (1 gallon) round pots filled with UC mix[1] and placed in a temperature controlled greenhouse. A drip emitter was placed in each pot and the plants were watered each day to saturation with water containing nutrients in the ratio 4-18-38 (N-P-K) without added boron. The number of nodes sprouting was recorded periodically and at the end of the experiment. The first experiment began on November 4 and ended on December 9, 2003. Temperatures during this part of the experiment ranged between 16 and 28ºC with a mean maximum of 27 ± 0.9ºC and a mean minimum of 21 ± 3.4ºC. The experiment was replicated between December 9, 2003 and February 2, 2004. Temperatures during this part of the experiment ranged between 14 and 28ºC with a mean maximum of 26 ± 2.2ºC and a mean minimum of 18 ± 2.4ºC.

## Reproductive Biology

### 2002-2003 Self-Compatibility Field Test

Eight locations in Sonoma, Marin and San Francisco counties (see Table 4.2) were selected to test whether Cape ivy populations were self-compatible. Locations were chosen that contained stipulate, non-stipulate or both morphological types. On November 5, 2002, small fabric bags were placed on 10 unopened inflorescences within each population. The bags were made of white nylon tulle and were sewn along three sides with an interlocking stitch. The bags were approximately 5 by 7.5 cm squares. A bag was placed over the unopened flower heads and the open end was closed with a plastic twist-tie. The bags were monitored a few times during the experiment and were harvested on January 28, 2003. During the harvest at least 10 open-pollinated inflorescences were also collected from each location. The open-pollinated and the bagged inflorescences were each placed in a separate coin envelope, labeled with the location and date, and stored at room temperature. Seed fill was assessed visually, with seeds either scored as filled (plump) or not-filled (flattened). The number of flower heads present in the sample and the number of filled seeds were recorded.

Calculations were made of the mean number of flowers produced per inflorescence in order to estimate the percentage of seed set in the reproductive biology experiments. In the literature, Cape ivy is said to produce between eight and twelve flowers per discoid head (Lemaire 1844, Harvey 1894, Hickman 1993). Rolando (2000) used 10 flowers per head for her calculations, though she does not mention how she obtained this number. At least five flower heads were chosen from 12 populations throughout California, and the number of flowers or seeds present was recorded. The overall mean number of flowers per flower head for all 12 populations sampled was 11.2. This average value was used to estimate the percentage of seed set in the reproductive biology experiments.

### 2002-2003 Greenhouse Crosses

A greenhouse at Bodega Marine Laboratory in Bodega Bay, California, was used to conduct Cape ivy reproduction experiments because wild populations grow in the area, and the greenhouse there was closer to natural conditions. It provided no heating, artificial light or supplemental nutrients in the water supply. Populations were selected for greenhouse crosses based on location and morphological type (stipulate or non-stipulate). Plants were started in greenhouses at UC Davis on September 12, 2002. Two node stem cuttings were placed in 10.2 cm (4 inch) square pots filled with UC mix[1], one node above ground and one node below ground. Populations used in the crossing experiments were from Pistol River, Oregon; Toro Canyon, Santa Barbara County; and San Dimas, Los Angeles County. Five plants were started from each location. In addition to plants started from greenhouse specimens, some were started from wild plants collected from Jenner and Bodega Bay, Sonoma County; Stinson Beach, Marin County; Presidio, San Francisco County; and Pacifica, San Mateo County. Five plants were also started from each of these locations. After propagation, pots were placed in plastic flats and bottom watered with drip emitters. Flats were watered every other day to maintain constant moisture. Plants propagated at Davis were moved to the Bodega greenhouse on October 18, 2002, after roots had successfully established and new leaves were being produced. In the Bodega Bay greenhouse, pots were also placed in plastic trays and watered with emitters. One meter bamboo stakes were placed in each pot to train the vines up the stakes and keep them separated from each other. Growing plants were attached to the stakes with twist-ties. As the plants grew, strings were tied to the top of the stakes and attached to beams above the greenhouse benches to further extend the growing area.

Most plants from the UC Davis propagation did not flower, leaving the wild-collected locations as the source of the majority of the study specimens. Study locations that did flower and were used in the experiment are listed in Table 4.3. The methods used were similar to the field self-compatibility experiment described above. Fabric bags were placed on inflorescences before flowers opened. Some of the inflorescences were kept closed in bags, and others were opened, crossed with other morphological types, and then re-bagged until fruits matured. Cape ivy flowers were too small to be emasculated, so for the crosses an entire flower head with viable pollen was cut off the donor plant and then the anthers were rubbed onto the receptive stigmas of the recipient and the inflorescence was re-bagged. A number of inflorescences were allowed to mature without bagging and those were collected when mature. All harvested inflorescences were stored in coin envelopes and kept at room temperature. Seed fill was assessed visually, with seeds scored either as filled or not-filled. The number of flower heads present in the sample and the number of filled seeds were recorded.

### 2003-2004 Field Crosses

Following the greenhouse study, a field crossing experiment was conducted. A location in Marin County along Highway 1 near Volunteer Canyon was chosen that included stipulate and non-stipulate morphological types. Flowering was first observed on October 16, 2003, and fabric bags were placed on four stipulate and four non-stipulate inflorescences at that time. On December 16, 12 more bags were placed on inflorescences of both types and on December 27, 2003, crosses were made between and within stipulate and non-stipulate morphological types. In some cases crosses between individuals of the same type were possible without removing any flowers due to the length of the vines. For crosses between types it was necessary to remove a flower head of one type and transport it to the location of the pollen recipient. To make the cross, the anthers with pollen, while still attached to the parent flower head, were rubbed on the stigmas of the pollen recipient. Four crosses were made between stipulate plants, four crosses were made between non-stipulate plants, one cross was made with a male non-stipulate to female stipulate and two crosses were made with male stipulates to female non-stipulates.

Four closed pollinated (bagged) inflorescences and 10 open pollinated inflorescences were harvested on January 16, 2004, and the remaining 14 closed pollinated inflorescences were harvested on March 20, 2004. Also harvested in March 20 were 11 bags from crosses performed on December 27, 2003. The mature inflorescences were placed in coin envelopes and stored at room temperature. Seed fill was assessed visually, with seeds scored either as filled or not-filled. The number of flower clusters present in the sample and the number of filled seeds were recorded.

## ANALYSIS

### Seed Collections

For the 2001, 2002 and 2003 seed collections, filled seed percentages within the community and morphological types were compared using a chi-square analysis.

### Seed Biology

Percentage seed viability with tetrazolium was analyzed using paired t-tests, and ANOVA was used to compare the viability of the weight classes after pooling. Chi-square analysis was used to compare the seed viability between locations.

Germination data for each experiment were pooled, and a regression analysis was performed on the relationship between temperature and germination. Seeds from Monrovia and Bonsall in the first experiment were smaller than those from the other populations due to improper sorting technique, so those data were excluded from the regression analysis.

Means of seed germination by weight class, germination in light or dark, and germination at different soil depths for the pooled data from each experiment were compared using the Student's t and Tukey Kramer HSD tests.

The stem fragment depth and emergence data were tested for normality and failed the Shapiro-Wilk W test for goodness of fit. An arcsin transformation was performed and the data were still not normal, so a ranks average transformation was completed (Conover and Iman 1981) and an ANOVA was performed on the pooled data from both experiments. Results from the ranks average transformation ANOVA were similar to the ANOVA performed on the raw data.

### Reproductive Biology

For the 2002-2003 greenhouse crosses and the 2003-2004 field crosses ANOVA was used to compare the percentages of filled seeds for each treatment after similar treatment types were pooled from each sample location. The treatments were then compared using Student’s t and Tukey-Kramer HSD tests.

## RESULTS

### Seed Collections

Seed collection locations for 2001 to 2003 are shown in Figures 4.2a, b and c, and listed in Table C-1 in Appendix C. A total of 104 different locations were sampled during the three year period. The collection dates, community types and an estimate of the filled seed percentage are included in Table C-1. Populations with any filled seed were scored as “Yes” even if the filled seed percentage was small. In 2001, medium and large filled seed percentages were calculated and are presented in Table 4.1. In addition, populations collected in 2002 and 2003 with greater or less than 1% filled seed are indicated in Table C-1.

Filled seed percentages differed among populations and varied by collection year. In 2001, Monterey, San Diego and Los Angeles counties produced the largest percentages of filled seed, and filled seeds were produced from Curry County, Oregon to San Diego County (Table 4.1). Most Mendocino County locations produced unfilled seed with six locations producing only 1 or 2% medium sized seeds. Marin County had the highest percentage filled seed in northern California while southern California counties had the highest percentages overall. When the 2001 seed size percentage data were sorted into percentage categories (0, 1-5, 6-25, 26-50 and 50% plus) for each morphological type, there were no overall trends observed. Although all morphological types produced filled seeds, the populations with both morphological types produced a larger percentage of filled seed.

The data for all three collection years were pooled to create Figure 4.4. Populations were scored as either not filled, < 1% or > 1% filled seed for each year and populations collected more than once were scored for each year. For the chi-square analysis, the not filled and <1% filled categories were pooled and that is presented in Figure 4.4. In the chi-square contingency table the expected values for each of the seed size categories were 50 percent. The two cells which contributed the most to the total chi-square value were the < = 1% filled seed categories for non-stipulate and both types (see gray cells in contingency table with Figure 4.4). More than the expected number of non-stipulate and both types were < or = 1% filled seed size. While the number of populations sampled with both morphological types was relatively low (20), the difference between the number of filled and not-filled seed producing populations was more pronounced than in populations with only one morphological type. However, populations with only a single morphological type also produced > 1% filled seed in nearly half the sampled locations.

The percentage of locations with filled seed for each morphological type in each community are shown in Figure 4.5. There do not appear to be any striking trends, with most morphological types appearing to produce at least a small amount of filled seed in each community type in which they occur. The expected frequencies for the chi-square analysis table were 60 percent for the filled category and 40 percent for the unfilled category in each community type. The willow riparian community type had a larger percentage of filled seed than would be expected from the 60/40 ratio. Sycamore willow riparian also had a large percentage of filled versus unfilled seed, but the sample size was too low to contribute significantly to the total chi-square value. When the filled seed percentage results from riparian and non-riparian community types were pooled, the number of locations with filled and non-filled seed production was almost identical.

In 2002 and 2003, the percentage of filled seed per population was lower than in 2001 for many of the populations sampled, perhaps due to different methods used to estimate filled seed percentages. In 2001 small, medium and large seed percentages were estimated, and in 2002 and 2003 seeds were scored as filled or not filled. Only 19 populations were sampled in 2002 and 63% of those produced filled seed. Three populations had less than 1% filled seed and seven had greater than 1%. In 2003, 59 populations were sampled and 68% of those produced filled seed. Similar to 2002, 16 populations had less than 1% filled seed and 25 had more than 1% filled seed. Geographically, in 2002 and 2003, most of the seed production in the greater than 1% filled category occurred in San Mateo, Monterey, San Luis Obispo, southern Santa Barbara, and Los Angeles counties. In a trend similar to previous years, the northern part of Cape ivy’s range produced much lower filled seed percentages as compared to southern California.

## Seed Biology

In 1998, attempts to artificially induce flowering in Cape ivy in greenhouse or growth chambers at UC Davis were largely unsuccessful. The only plants that consistently flowered were those that had been pre-induced in the field and collected in September or October after flowering had started in wild populations.  When placed into greenhouse conditions, Cape ivy plants often aborted flowering and began vigorous vegetative growth.  Greenhouses at UC Davis were warmer than field conditions and received supplemental light and nutrients; all factors that could discourage flowering. Growth chamber studies were also unsuccessful in inducing flowering, perhaps due to the low light conditions present in most growth chambers.  After these unsuccessful artificial induction attempts, experiments were conducted under natural conditions or in greenhouses at Bodega Marine Lab, which had conditions closer to those of California wild populations of Cape ivy.

### Seed Germination Potential and Viability

Cape ivy seeds in California and Oregon were found to germinate either in soil or on moist filter paper (Figures 4.6a and 4.6b).  Figure 4.6a shows seeds from 2001 sprouting after being placed on the soil surface and watered.  In the photograph, populations 3, 5, 7, and 8 were from Los Angeles County, population 11 was from Curry County, Oregon, and population 12 was from Marin County.  Cape ivy seeds germinating in a petri dish with moist filter paper are shown in Figure 4.6b.  Seeds in this photograph were collected from Toro Canyon, Santa Barbara, in 2003, and were germinated in November, 2004.

For the 2001 seed germination tests, Table 4.4 lists the locations tested, the number of replications, the mean number of days to first germination, and the mean percentage germination.  The geographic range of Cape ivy seed germinability is well illustrated by the data in the table.  The mean number of days to first germination varied geographically, with the longest time to first germination in Curry County (16 days ± 3). However, no north to south trends were observed. The mean germination percentage ranged between 8 and 90 percent, with the lowest germination in Curry County. Southern California locations once again had the highest germination rates, similar to the results presented in Table 4.1.

A correlation was found between seed weight and germination (Figure 4.7). Seeds in the heaviest weight class (0.3 mg+) germinated at the highest percentage, and their germination was significantly different from the 0.2 to 0.3 mg and lighter classes. Notably, minimal germination was observed in the lightest weight class, 0 to 0.1 mg. There was also a correlation between seed weight and viability, as determined with tetrazolium tests (Figure 4.8). When seed weights of 0.1 mg and heavier were pooled for each of the three populations tested, and a chi-square analysis was performed, no significant differences were found seed viability. The viability in the 0 to 0.1 mg weight class depicted in Figure 4.8 was due to one seed from Volunteer Canyon. This result is comparable to the amount of germination observed in the same weight class in Figure 4.7.

## Environmental Requirements for Seed Germination or Fragment Emergence

The average maximum germination for four different populations in the optimum germination temperature tests occurred at 20.6°C (Figure 4.9). Germination also occurred at a range of temperatures, from 8 to 32°C. There were no significant differences between the germination percentages at temperatures between 8 and 37°C, or between the different test locations based on ANOVA and MRPP tests. An overall test for coincidental regressions (Zar 1999) was also performed and the F statistic was not significant (0.019), suggesting that the sample regressions estimate the same population regression.

In the light versus dark germination experiment I found between 20 and 60% germination in the dark (30% ± 16% SD), compared with 60 to 100% germination in the light (mean germination 80% ± 14% SD) at 20°C. For the depth of seed burial experiment I also observed high germination of surface seed (76% ± 4% SE), and much lower germination of 1 cm buried seed (6% ± 4% SE), with no emergence at 2, 3, or 4 cm burial depth **(**Figure 4.10**)**. The percentage of surface germination was significantly different from all the burial depths.

It is not known at this time whether sexual or asexual reproduction contributes more to the spread of Cape ivy. In this study, either one or two node fragments sprouted when placed on the soil surface (75% emergence) or when buried 2 cm (19% emergence), but no emergence occurred when fragments were buried 4, 6, 8, or 10 cm deep (Figure 4.11). There was no significant difference between one or two node cuttings at the surface or 2 cm burial depth. Surface node emergence was significantly different from 2 cm burial, and surface and 2 cm burial were significantly different from all other burial depths.

## Reproductive Biology

### 2002-2003 Self-Compatibility Field Test

The results of the field self-compatibility test are presented in Table 4.5. In all but one case the closed bags produced no filled seed, indicating that Cape ivy is self-incompatible in California. The population that did produce filled seed (0.04%) was at

Volunteer Canyon where both stipulate and non-stipulate types grew adjacent to each other. The seed set in closed bags could have been due to experimental error -- exclusion bags may have not been entirely impenetrable to insects with access to both types of pollen. It is also possible that Cape ivy is capable of low levels of self-compatibility. Rolando (2000) found 0 to 0.5% filled seed in self-pollinated flowers compared with 20 to 50% filled seed in either cross or open-pollinated flowers. Volunteer Canyon was the only population producing a significant amount (20%) of filled seed in open pollinated flowers. These results led to the design of a field crossing experiment in 2003-2004, which is described below.

### 2002-2003 Greenhouse Crosses

The results of a greenhouse crossing experiment are in Table 4.6. Plants from six locations were used in the experiment, and results for each type of cross were pooled in order to increase the power of the statistical tests. The pooled categories were: non-stipulate (NS) or stipulate (ST) open pollinated, non-stipulate closed (bagged), stipulate closed (bagged) or stipulate crossed with stipulate, and stipulate/non-stipulate cross. The mean percentage filled seed was highest in the ST/NS crosses (14.7%). Open pollinated flowers produced 8.4% filled seed for non-stipulate and 3.9% for stipulate plants. The other two treatments, closed NS and ST closed and ST cross, had the lowest percentage seed set. Using a one-way ANOVA treatments were significantly different ($p < 0.0001$). Using a Student's t test to compare treatments, the NS open and ST/NS cross were significantly different from the other treatments, NS open and closed were different from the other treatments, and ST open and the two closed pollinated treatments were significantly different from the others.

### 2003-2004 Field Crosses

Table 4.7 contains the results for the 2003-2004 field crossing experiment. As is evident in Table 4.7, the results were not conclusive and only serve to illustrate what was already evident from the 2002-2003 self-compatibility field test and the 2002-2003 greenhouse crosses – open-pollinated flowers produced more filled seed than either bagged or crossed and bagged flowers. The open pollinated filled seed percentages (10.7 for NS and 6.2 for ST) were less than for the same population in 2002-2003, when 20% filled seeds were produced. Using a one-way ANOVA a significant difference was found between the treatments (p = 0.0003). Using a Student's t test to compare treatments, the ST and NS open were not significantly different from each other, and the NS open was significantly different from the rest of the open and closed treatments.

## DISCUSSION

### Seed Collections

The most important result was that viable seed was found throughout Cape ivy's North American range, from Oregon to San Diego County (Figure 4.2, Table 4.4 and Table C-1). There were no discernable differences in the production of viable seed among plant communities or between morphological types. There was higher than expected filled seed production in willow riparian habitats based on a chi-square analysis. In the north, seed viability was quite low in Mendocino County where Cape ivy is abundant (compare Figures 2.4d and 4.2a). In San Mateo County, many of the sampled populations produced viable seed and seed production occurred in locations with stipulate, non-stipulate or both morphological types. In Southern California, a majority of the locations produced viable seeds (Figure 4.2c). This important finding has obvious implications for the management of Cape ivy in that area.

In addition to California and Oregon, viable Cape ivy seed is known to be produced in South Africa, Australia and Hawaii (Wagner et al. 1990, Rolando 2000, Blood 2003). The climate in the native range in South Africa is classified as both Temperate, Mediterranean (Cs) and Temperate, Mild Winter (C) (Dallman 1998). In Australia, as well as California, Cape ivy's distribution falls in both of those climate zones. Hawaii is composed of many climate zones, though the areas where Cape ivy occurs can be classified as wet tropical with no dry season.

## Seed Biology

In addition to the reproductive biology studies conducted by Lawrence (1985), Rolando also conducted Cape ivy seed biology research. She examined seed characteristics such as fruit weight, pericarp permeability, temperature requirements for germination, seed longevity, germination response to light and dark, and seedling emergence from different planting depths.

A correlation was found between seed weight and germination (Figure 4.7), and between seed weight and viability, as determined with tetrazolium tests (Figure 4.8). Rolando (2000) selected filled seeds for her germination tests, although no specific details were provided on the methodology. Lawrence (1985) also noted that fertile seed of *Senecio* spp. were always plump and variously colored, whereas sterile seeds were shriveled and white. Rolando (2000) weighed seeds in batches of 20 and recorded the mean weight of the batch, while seeds in this study were weighed individually. Rolando found a mean weight of 0.3 mg, which was much higher than the mean found in this study. The average weight of 173 seeds from two populations was 0.10 mg. The similarities in germination and viability percentages suggest that there is no primary dormancy mechanism for Cape ivy after seed dispersal.

In contrast to my findings, Rolando (2000) tested South African Cape ivy seed from one population and found maximum germination at 25°C. Her experimental temperatures were 10, 15, 20, 25 and 30°C and there were no significant differences in the final percentage of germination at those temperatures in multiple experiments. In her experiments, seeds tested at 30 °C did not germinate, but when returned to a 15°C environment, germination occurred. The difference between the maximum germination temperature for South African and California seed may have been based on the restriction of the South African experiment to a single population. However, both studies found germination occurring at a wide range of temperatures. The lack of germination at 30°C in the South African study may indicate a shift in environmental tolerance for California Cape ivy seed.

The response of Cape ivy seed germination to light or dark was similar for South Africa and California plants. In both cases Cape ivy seed germinated in darkness, but at a lower percentage than in the light. Rolando (2000) found between 40 and 70% germination of Cape ivy seed in the dark, whereas I found between 20 and 60% germination in the dark, compared with 60 to 100% germination in the light at 20°C. Both studies also examined germination of seeds at different burial depths. Rolando (2000) reported seed germinating most readily at the surface (76%) and only at small percentages when buried 1 cm (0.3%). I also observed high germination of surface seed (76%), and much lower germination of 1 cm buried seed (6%), with no emergence at 2, 3, or 4 cm burial depth.

Many other seed biology experiments with invasive plants have been conducted. One study that looked at a similar range of seed responses was for jubatagrass (*Cortaderia jubata*) (Drewitz and DiTomaso 2004). Viability, seed weight and germination, optimum germination temperature, light requirements and germination at different soil depths were studied. While jubatagrass seeds are much smaller than Cape ivy, many of the same responses to environmental conditions were observed as with Cape ivy seed. Seed production was high and seeds are wind dispersed. The authors found that the percentage of germination vs. seed viability as tested with tetrazolium was similar, indicating that jubatagrass does not have primary dormancy. The optimum temperature germination range was also similar to Cape ivy, with germination occurring between 8 and 35ºC with an optimum germination temperature of 20ºC. Jubatagrass germination percentages were lower in dark and also decreased when seeds were buried 1 cm or deeper. Jubatagrass is also a highly successful weed of the California coast, much like Cape ivy. Both species posses many of the characteristics found on Baker’s list of successful invaders.

Hsu and Chiang (2003) looked at the effects of temperature, planting depth and light on two species of *Mikania* found in Taiwan, one native (*M. cordata*) and one introduced (*M. micrantha*). This study offers an interesting comparison with Cape ivy seed biology because *Mikania* is closely related to *Senecio*. *Mikania* is a vine that produces wind dispersed seed, and some species in the genus are highly invasive (*M.*

*micrantha* and *M. scandens*). The temperature germination range was (8 to 32ºC) for *M. micrantha* and (12 to 28ºC) for *M. cordata*, and both species germinated at higher percentages in light than in dark. Seedling emergence was also lower for both *Mikania* species when seeds were buried 2.5 cm or more. The more vigorous growth of the introduced species *M. micrantha* under greenhouse conditions indicated that it would be able to out-compete the native *M. cordata.* The wide germination temperature range, ability to germinate in light and dark, and the vigorous vegetative growth, indicate the similarities of M. micrantha to Cape ivy. Unlike my studies, the *Mikania* study, compared growth of the native and introduced species in an effort to determine which would be more competitive in natural systems. Competition between Cape ivy and native or other introduced species was studied by Alvarez and Cushman (2002). They found that Cape ivy was also able to out-compete other species and form monocultures in three different habitat types.

These results of the seed biology experiments indicate that Cape ivy germinates more readily in light and on the soil surface. These are ideal characteristics for a weed that invades disturbed areas. Germination rates of many species have been shown to decrease at greater soils depths (Eastin 1983, Ayeni et al. 1997) and it is likely that Cape ivy’s small seed size is also not conducive to emergence from deep burial. Thompson et al. (1993) studied common groundsel (*Senecio vulgaris)* and other species as part of an attempt to predict the persistence of seeds in soil using seed size and shape. A common observation is that persistent seeds tend to be small and compact while short-lived seeds are larger and either flattened or elongate. Thompson et al. (1993) classified common groundsel as a species whose seed bank type could not be determined due to contradictory data. However, they did find that compact seeds weighing less than 3 mg were all persistent in the soil. Interestingly, the emergence of buried Cape ivy stem fragments appears to mirror the pattern of seed germination. Therefore, Cape ivy plants would be more likely to colonize disturbed, un-vegetated habitats either through vegetative fragments or seeds.

## Reproductive Biology

In addition to the studies conducted by Lawrence (1985), the only other research available on Cape ivy's reproductive biology is that of Rolando (2000). She examined the flowering phenology of Cape ivy in three locations across KwaZulu-Natal (Harding, Dargle, and Pietermaritzburg). The elevations ranged from 800 to 1300 m and the average monthly temperatures were between 19 and 22ºC. Dargle had the coldest average minimum temperature (0 to 5ºC) with frequent frosts during June and July. Rainfall is highest during the summer (November to February) and there is a dry season between May and August. She recorded four development stages (young bud, opening, full bloom, and withering/fruit set) of 50 immature inflorescences, and found that peak flowering occurred from April to May. Dispersal occurred by mid-July. As a comparison, California Cape ivy occurs at elevations between 0 and 891 meters, at annual mean temperatures between 10.5 and 17.7°C and in areas with annual precipitation ranging between 232 and 2270 mm (see Chapter 2).

Rolando (2000) conducted experimental pollinations at the three field sites and in a greenhouse. There were four treatments and a control: cross pollination, self-pollination, apomixis, and pollinator exclusion. Her cross-pollination experiments were carried out multiple times and the donor pollen was from plants in the same population at least 10 meters away from the pollen recipient. This differed from Cape ivy cross-pollinations which were conducted only once. All Rolando's experimental subjects were of the stipulate type. Self-pollination was also conducted several times; stigmas were brushed with the plant's own pollen and re-bagged. An apomixis treatment required removing the stigma after it became receptive and re-bagging the flower. Pollinator exclusion was accomplished by growing plants in a greenhouse. Pollination experiments showed fruit set was significantly lower for self-pollinated plants compared to the cross-pollinated plants at all three locations. Cross-pollinated fruit set was from 20 to 42% for all three locations, compared with 30 to 50% seed set in open-pollinated flowers. Self-pollinated plants produced either 0 or 0.5% filled seed. No filled seed was produced in the apomictic or pollinator exclusion trials. Rolando's results are more robust than those obtained for California Cape ivy due to the larger number of pollinations performed for each cross. However, a general comparison can be made between the open-pollinated plants and the self-pollinated plants. In both South Africa and California populations, plants were shown to be self-incompatible because the percentage of seed set in self-pollinated plants was negligible. The results from Rolando's cross-pollination studies also indicate that there are different genetic types among the stipulate populations that she used as study subjects.

Although there are no other reproductive biology studies on Cape ivy, there are some available that examine the breeding system of common groundsel (*Senecio vulgaris*) (Abbott et al. 1998, Wisskirchen 2000, Hoffmann 2001, Leiss and Muller-Scharer 2001b, a, Muller-Scharer and Fischer 2001, Jakobsson and Eriksson 2003). Common groundsel is an annual, but the flowers are similar to Cape ivy's and the seeds are wind dispersed. Wisskirchen (2000) studied the breeding systems of 57 taxa, including common groundsel, by bagging un-opened flowers. He found common groundsel to be self-compatible, in contrast to Cape ivy, which appears to be self-incompatible.

Because Cape ivy is a member of the Asteraceae, its incompatibility system is likely to be sporophytic (Lovett Doust and Lovett Doust 1988, Richards 1997, Li and Newbigin 2002). If this is indeed the case, all experimental crosses would be fully compatible or fully incompatible. Cape ivy flowers from California and South Africa, when bagged in self-compatibility tests, produced small seed viability percentages (0 to 0.2% in California and 0 to 0.5% in South Africa), indicating that Cape ivy either has a small amount of self-compatibility or that the methods used in both studies did not fully exclude non-self pollen. While many successful invasive species are self-compatible (Allard 1965), it is now recognized that both self-compatible and self-incompatible species can become successful invaders (Heywood 1989, Olivieri et al. 1991), and in some cases it has been shown that self-incompatibility can break down with floral age or environmental conditions (de Nettancourt 1977, Vogler et al. 1998).

## CONCLUSIONS

Cape ivy is an ideal weed. It is able to produce large amounts of wind dispersed seed and the seeds appear to have no induced dormancy mechanism. The seeds can germinate quickly in high or low light if they are near the soil surface and can do so at a wide range of temperatures. Cape ivy seed longevity was not estimated in this study, but seeds of common groundsel (*Senecio vulgaris*), when buried in a meadow for 50 years, remained viable (DiTomaso and Healy 2006). Another source indicated common groundsel seed can survive 16 years in soil (Baskin and Baskin 1998). Seeds of another weed, tansy ragwort (*Senecio jacobaea*), commonly live at least six years under field conditions, but have been reported to survive up to 20 years (DiTomaso and Healy 2006). This indicates that the Cape ivy seed bank is worth taking into account when planning long-term management.

Cape ivy's weedy characteristics differ only slightly from those reported by Rolando (2000) for South African Cape ivy seed. She found a higher optimum germination temperature (25 as opposed to 20.6°C in these experiments) and her seed did not germinate at 30°C as did ours. These differences may have been due to experimental methods, population variability, or may indicate a shift in environmental tolerance for California Cape ivy seed. In terms of reproduction biology, Rolando's results showed similarity in self-incompatibility and obligate cross-pollination for seed set to ours. However, our experiments resulted in lower success with cross-pollinations in the field, perhaps due to different methods used or the differences in climate during seed set in our region as compared to South Africa.

There appear to be no general trends regarding seed production in different vegetation types or by either morphological type. If both the stipulate and non-stipulate types are present, a higher percentage of viable seed was consistently produced, although viable seed was produced in populations containing either of the morphological types. The slightly drier and warmer climatic conditions in 2001 may have contributed to higher fecundity in central and southern California seed as compared to the seed production in 2002 and 2003.

The most important management implication of this study is the confirmation that viable wind-dispersed seed is produced throughout Cape ivy's range in the western United States. This important finding should be taken into account when developing management strategies for a given location. Obtaining this information for a particular location is not difficult. Seed viability can be estimated with visual inspection under a dissecting microscope, seed can be germinated directly in petri dishes or on moist soil at room temperature or under field or greenhouse conditions.

## FOOTNOTES

1. UC Davis soil mix composed of 0.22 $m^3$ compressed peat moss, 0.23 $m^3$ sponge rock, 0.11 $m^3$ #2 vermiculite, 0.17 $m^3$ sand, 2.27 kg dolomite, 0.7 kg 14-14-14 fertilizer, 0.7 kg Micromax™ micronutrient fertilizer, Sierra Chemical Co., 1001 Yosemite Drive, Milpitas, CA 95035.
2. Perkin–Elmer AD-4 Autobalance, Perkin–Elmer, 17 West 350 22nd Street, Oak Brook, IL 60523.
3. Anchor Steel Blue Seed Germination Blotter, 3 3/8" round. Anchor Paper Company 480 Broadway, St. Paul, Minnesota 55101. http://www.seedpaper.com.

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### Table 4.1. 2001 Cape Ivy Seed Germination Study
### Percentage of Small, Medium and Large Seed by County

| County | Sample Size | Mean% Small ± SE | Mean % Med ± SE | Mean % Large ± SE |
|---|---|---|---|---|
| Curry | 1 | 77 | 21 | 2 |
| Humboldt | 3 | 85 ± 15 | 4 ± 4 | 11 ± 11 |
| Mendocino | 14 | 99 ± 0.2 | 0.6 ± 0.2 | 0 |
| Sonoma | 3 | 96 ± 3 | 2 ± 2 | 2 ± 1 |
| Marin | 2 | 60 ± 19 | 15 ± 3 | 26 ± 17 |
| San Francisco | 1 | 87 | 5 | 8 |
| Alameda | 1 | 100 | 0 | 0 |
| San Mateo | 4 | 75 ± 14 | 9 ± 4 | 17 ± 10 |
| Santa Cruz | 6 | 81 ± 11 | 9 ± 5 | 10 ± 6 |
| Monterey | 4 | 40 ± 10 | 16 ± 3 | 44 ± 11 |
| San Luis Obispo | 2 | 46 ± 9 | 18 ± 7 | 36 ± 3 |
| Los Angeles | 9 | 54 ± 5 | 20 ± 1 | 25 ± 6 |
| San Diego | 1 | 42 | 40 | 18 |

**Table 4.2. Cape Ivy Self-Compatibility Field Test Locations 2002-2003**

| Location | County | Stipulate or Non-Stipulate |
|---|---|---|
| Bodega Bay, Whale Ship Road | Sonoma | Non-Stipulate |
| Marshall | Marin | Stipulate |
| North of Bolinas turn-off on Highway 1 | Marin | Stipulate |
| Volunteer Canyon, Bolinas Lagoon | Marin | Non-Stipulate and Stipulate |
| Stinson Beach<br>Near Beach and Eskoot Creek | Marin | Stipulate |
| Muir Beach | Marin | Non-Stipulate |
| Rodeo Valley | Marin | Stipulate |
| Presidio off Battery | San Francisco | Stipulate |

**Table 4.3. Greenhouse Crossing Experiment Test Locations 2002-2003**

| Location | County | Stipulate or Non-Stipulate |
|---|---|---|
| Jenner | Sonoma | Non-Stipulate |
| Bodega Bay, Whale Ship Road | Sonoma | Non-Stipulate |
| Stinson Beach | Marin | Stipulate |
| Presidio off Battery | San Francisco | Stipulate |
| Pacifica | San Mateo | Non-Stipulate |
| Toro Canyon | Santa Barbara | Stipulate |

# Table 4.4. 2001 Cape Ivy Greenhouse Germination Results

| **COUNTY**<br>**Location** | **Number of Trials** | **Mean Number of Days to First Germination ± SE** | **Mean % Germination ± SE** |
|---|---|---|---|
| **CURRY** | | | |
| Pistol River Schoolhouse | 3 | 16 ± 3 | 8 ± 2 |
| **HUMBOLDT** | | | |
| McKinleyville, School Road | 3 | 14 ± 2 | 38 ±17 |
| **MARIN** | | | |
| Rodeo Valley Creek, GGNRA | 3 | 9 ± 2 | 72 ± 7 |
| Rodeo Valley Maintenance Station | 1 | 8 | 65 |
| **SAN FRANCISCO** | | | |
| Presidio off Battery | 1 | 8 | 30 |
| **SAN MATEO** | | | |
| McNee Ranch south of Pacifica | 3 | 10 ± 1 | 32 ± 9 |
| San Bruno Mountain, bottom | 3 | 13.5 ± 0.5 | 18 ± 3 |
| **SANTA CRUZ** | | | |
| Watsonville Slough off San Andreas Rd. | 1 | 13 | 75 |
| Pajaro River | 1 | 13 | 65 |
| **MONTEREY** | | | |
| Elkhorn Slough near Moss Landing | 3 | 8 ± 1 | 75 ± 5 |
| San Jose Creek near Pt. Lobos | 3 | 10 ± 1 | 30 ± 15 |
| Gibson Creek, Pt. Lobos | 3 | 10 ± 1 | 62 ± 6 |
| **SAN LUIS OBISPO** | | | |
| Chorro Flats in Morro Bay State Park | 3 | 9 ± 1 | 38 ± 17 |
| High Street, San Luis Obispo | 3 | 14 ± 2 | 32 ± 6 |
| **LOS ANGELES** | | | |
| Temescal Canyon | 3 | 10 ± 1 | 18 ± 3 |
| Palisades Drive | 3 | 10 ± 1 | 67 ± 6 |
| Will Rogers State Historic Park, near entrance | 3 | 8 | 60 |
| Will Rogers State Historic Park, below entrance | 3 | 10 ± 1 | 90 ± 10 |
| San Dimas Canyon | 1 | 8 | 50 |
| Glendale, Elinita Rd. | 3 | 8 ± 1 | 75 ± 13 |
| Monrovia Canyon | 3 | 9 ± 1 | 52 ± 11 |
| **SAN DIEGO** | | | |
| Bonsall Preserve | 1 | 13 | 15 |

### Table 4.5. 2002-2003 Self-Compatibility Field Test Results

| Location | ST/NS | Closed Bags % Filled Seed | Open Pollinated % Filled Seed |
|---|---|---|---|
| Bodega Bay, Whale Ship Road | NS | 0 | 0.3 |
| Marshall | ST | 0 | 0 |
| North of Bolinas turn-off on Highway 1 | ST | 0 | 0 |
| Volunteer Canyon | ST/NS | 0.04 | 20 |
| Stinson Beach<br>Near Beach and Eskoot Creek | ST | 0 | 0 |
| Muir Beach | NS | 0 | 0.6 |
| Rodeo Valley GGNRA | ST | 0 | 0 |
| San Francisco Presidio off Battery | ST | 0 | 0 |

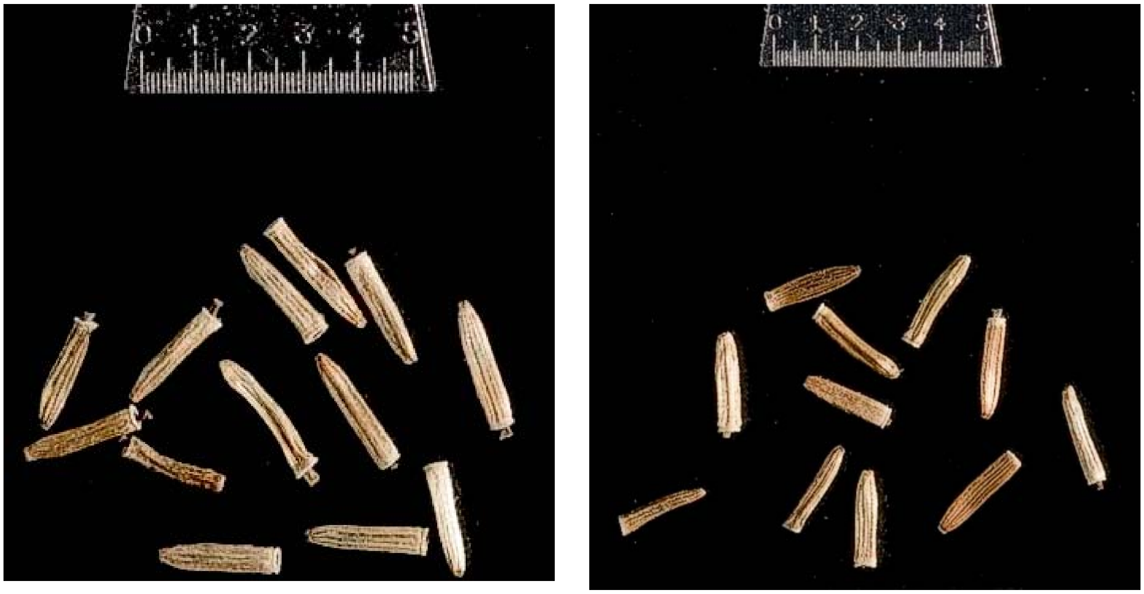
**Table 4.6. 2002-2003 Greenhouse Crossing Experiment Results**

| ST/NS | Open, Closed or Cross | N | # Flower Clusters | # Large Seeds | % Filled Seeds and Significance | |
|---|---|---|---|---|---|---|
| ST | Open | 52 | 404 | 174 | 3.9 | C |
| NS | Open | 10 | 95 | 88 | 8.4 | AB |
| NS | Closed (bagged) | 7 | 107 | 1 | 0.1 | BC |
| ST | Closed<br>(and ST cross) | 27 | 547 | 12 | 0.2 | C |
| ST/NS | Cross | 12 | 92 | 149 | 14.7 | A |

**Table 4.7. 2003-2004 Field Crossing Experiment Results**

| ST/NS | Open, Closed or Cross | N | # Flower Clusters | # Large Seeds | % Filled Seeds and Significance |
|---|---|---|---|---|---|
| ST | Open | 10 | 782 | 457 | 6.2 AB |
| NS | Open | 10 | 554 | 554 | 10.7 A |
| ST | Closed (bagged) and ST cross | 15 | 358 | 2 | 0.03 B |
| NS | Closed (bagged) and ST cross | 11 | 356 | 6 | 0.1 B |
| ST/NS | Cross | 3 | 89 | 0 | 0 Excluded from analysis |

Figure 4.1.  Photographs of Cape Ivy Seeds in Four Weight Classes



**0 to 0.1 mg**

**0.1 to 0.2 mg**

**0.2 to 0.3 mg**

**0.3+ mg**

Photographs by Jack Clark

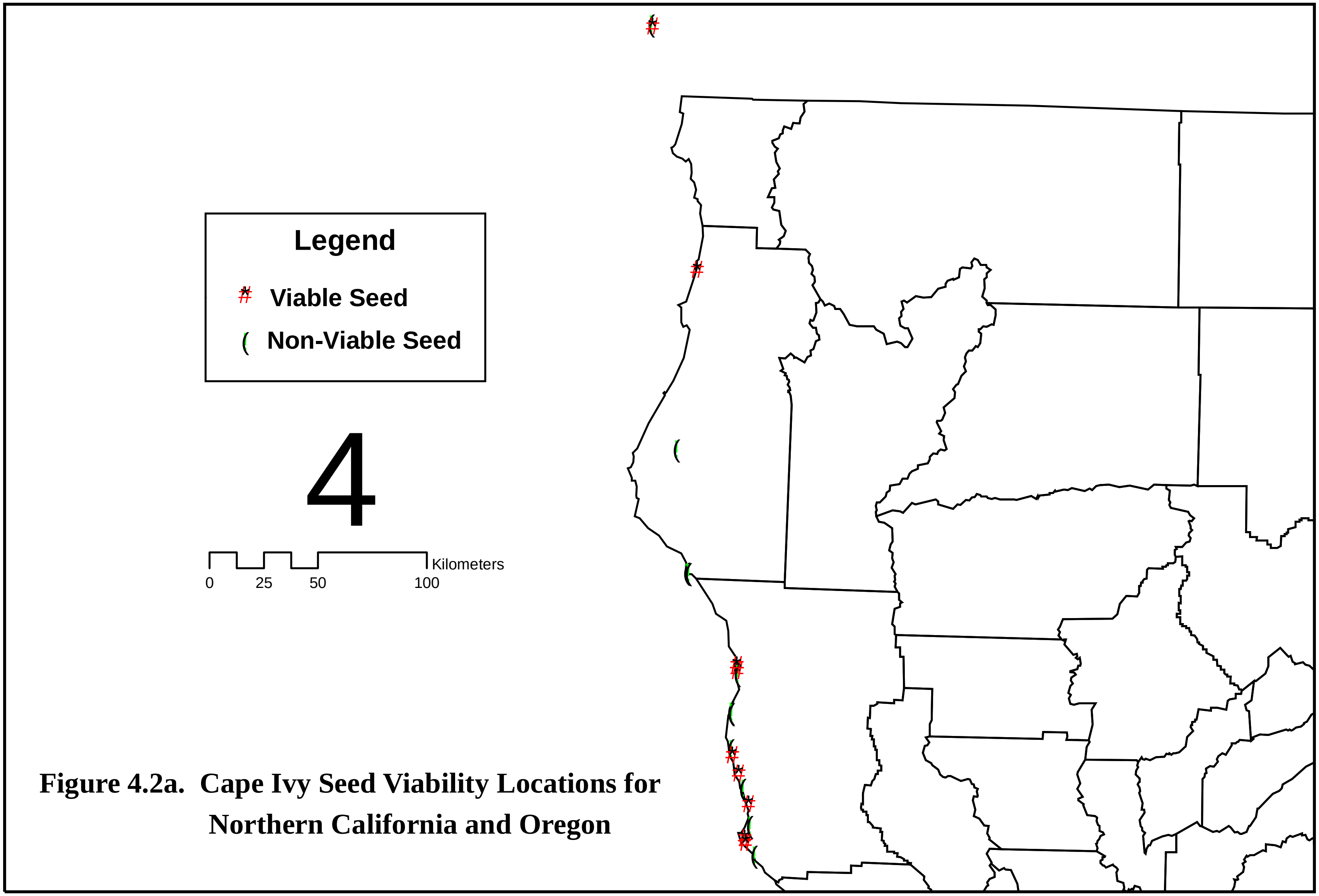


Figure 4.2a. Cape Ivy Seed Viability Locations for Northern California and Oregon

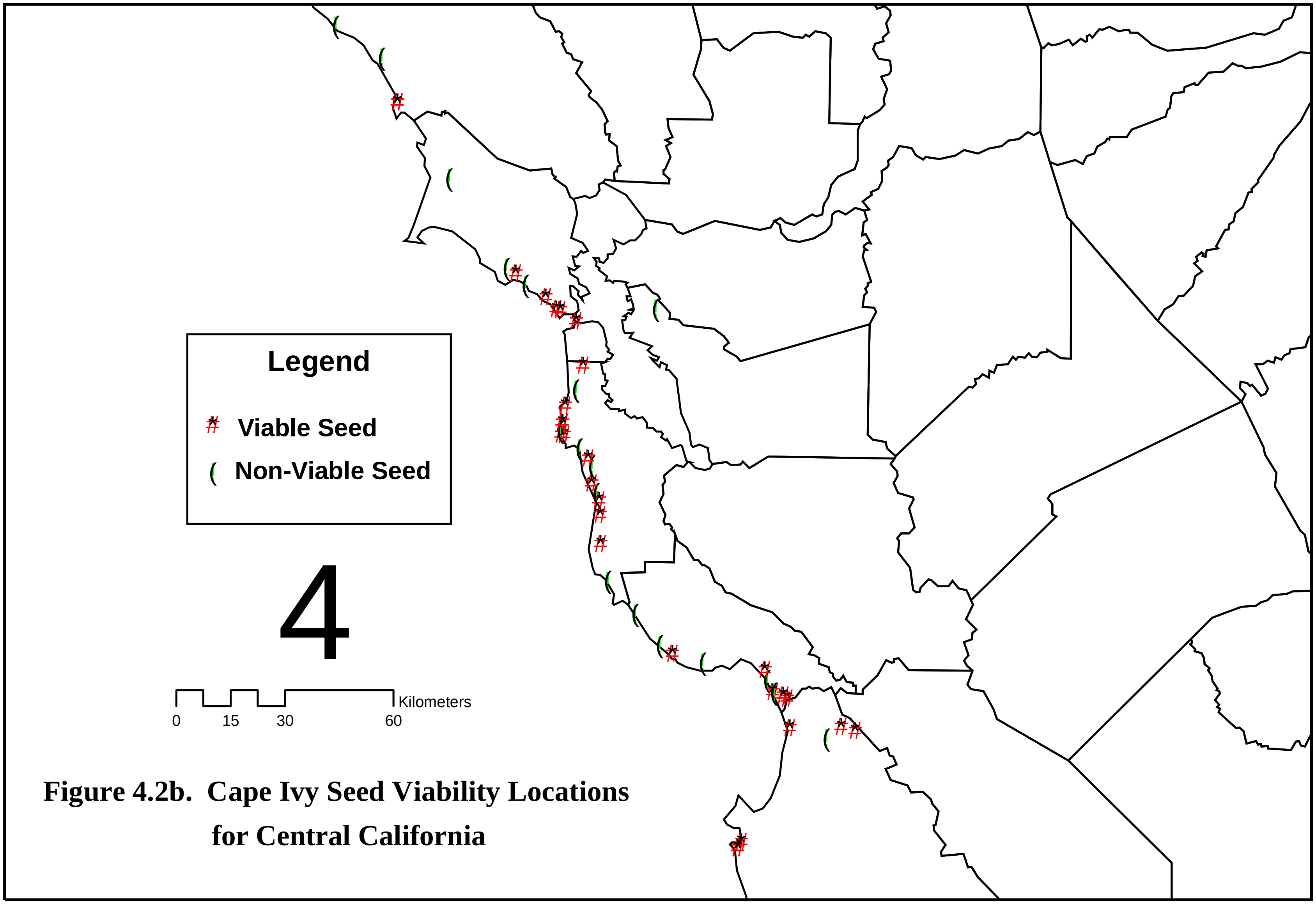


Figure 4.2b. Cape Ivy Seed Viability Locations for Central California

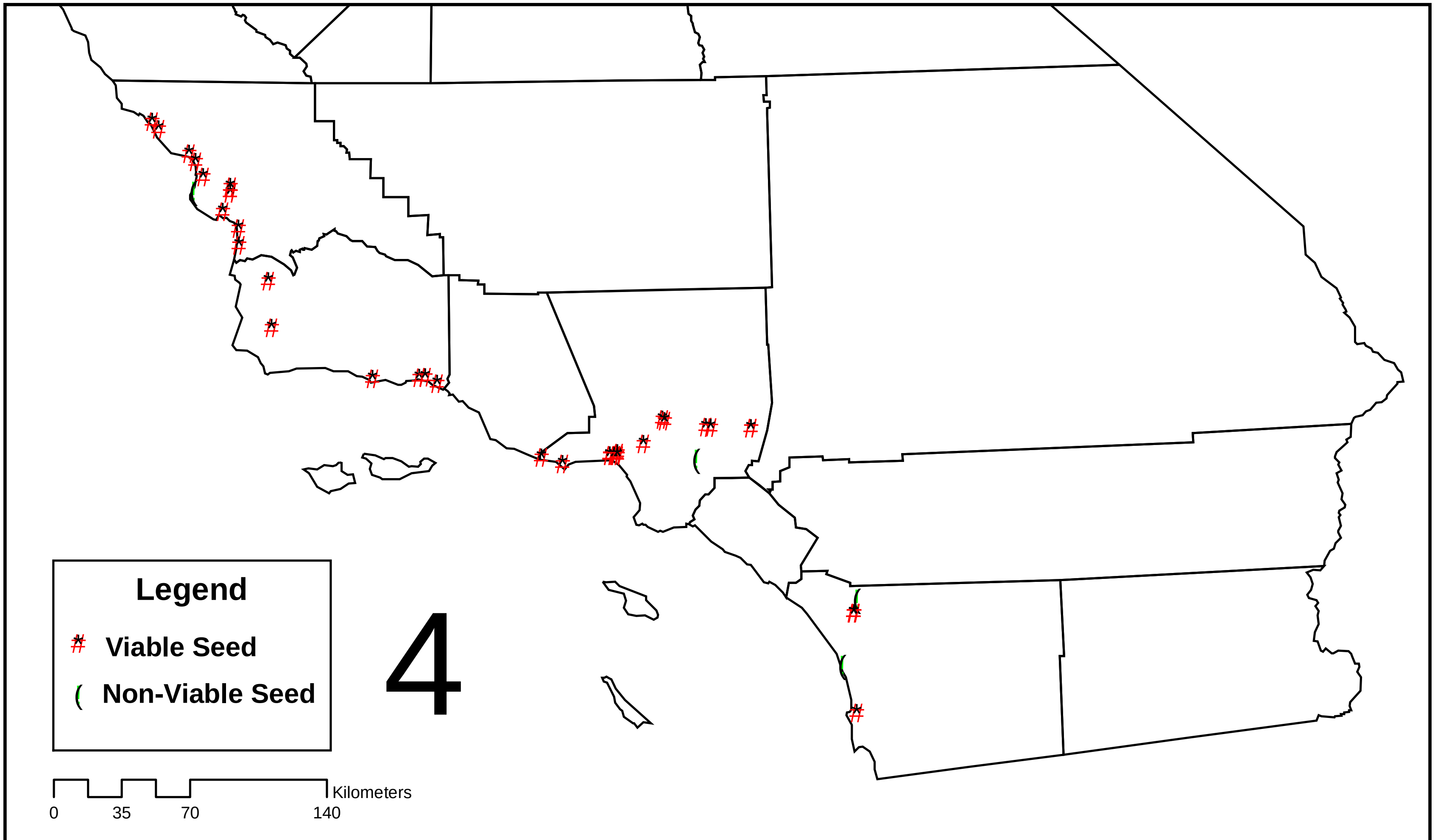


**Figure 4.2c. Cape Ivy Seed Viability Locations for Southern California**

Figure 4.3a. Cumulative Yearly Precipitation for Half Moon Bay, California

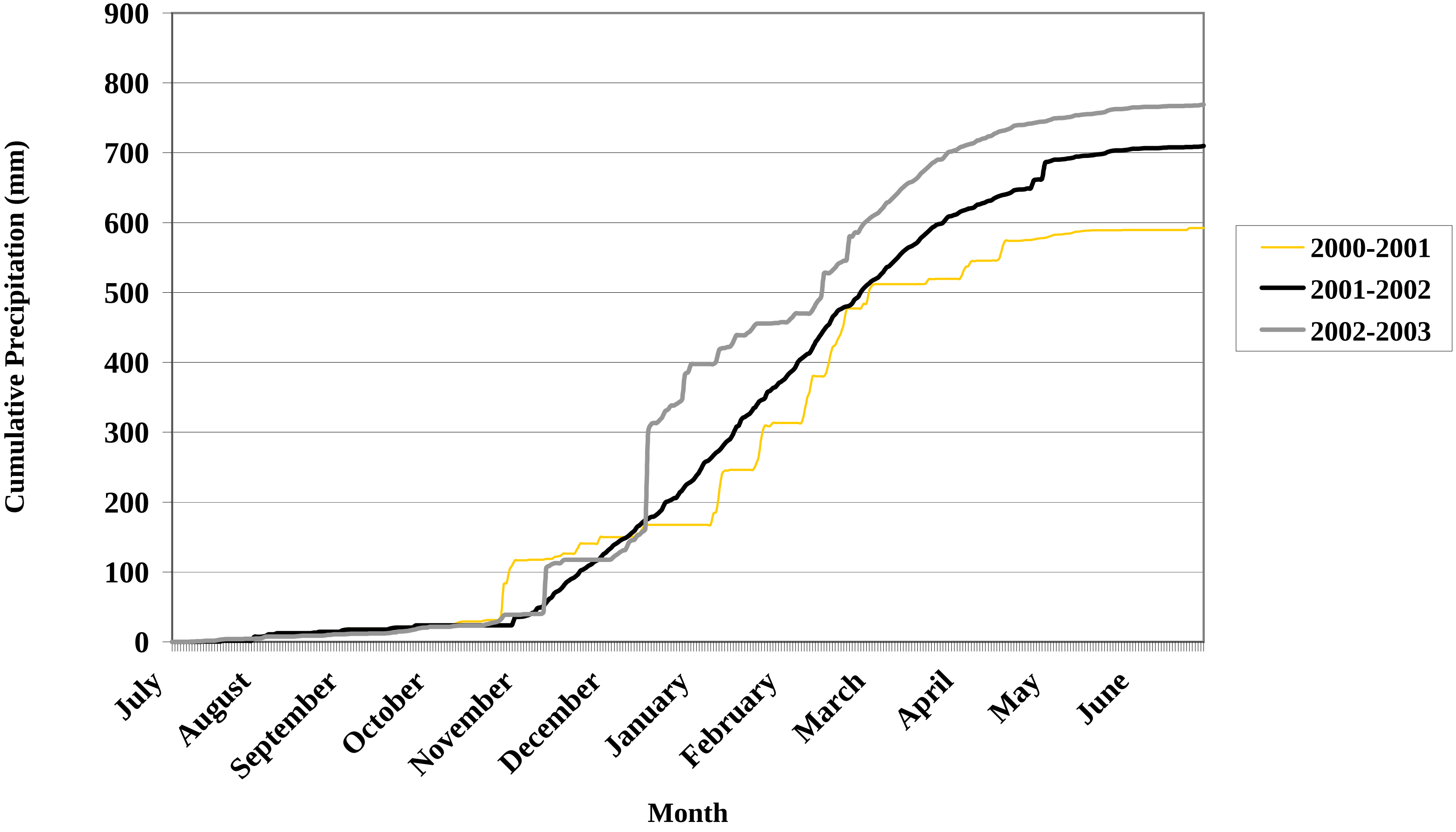


Figure 4.3b. Cumulative Yearly Precipitation for Santa Barbara, California

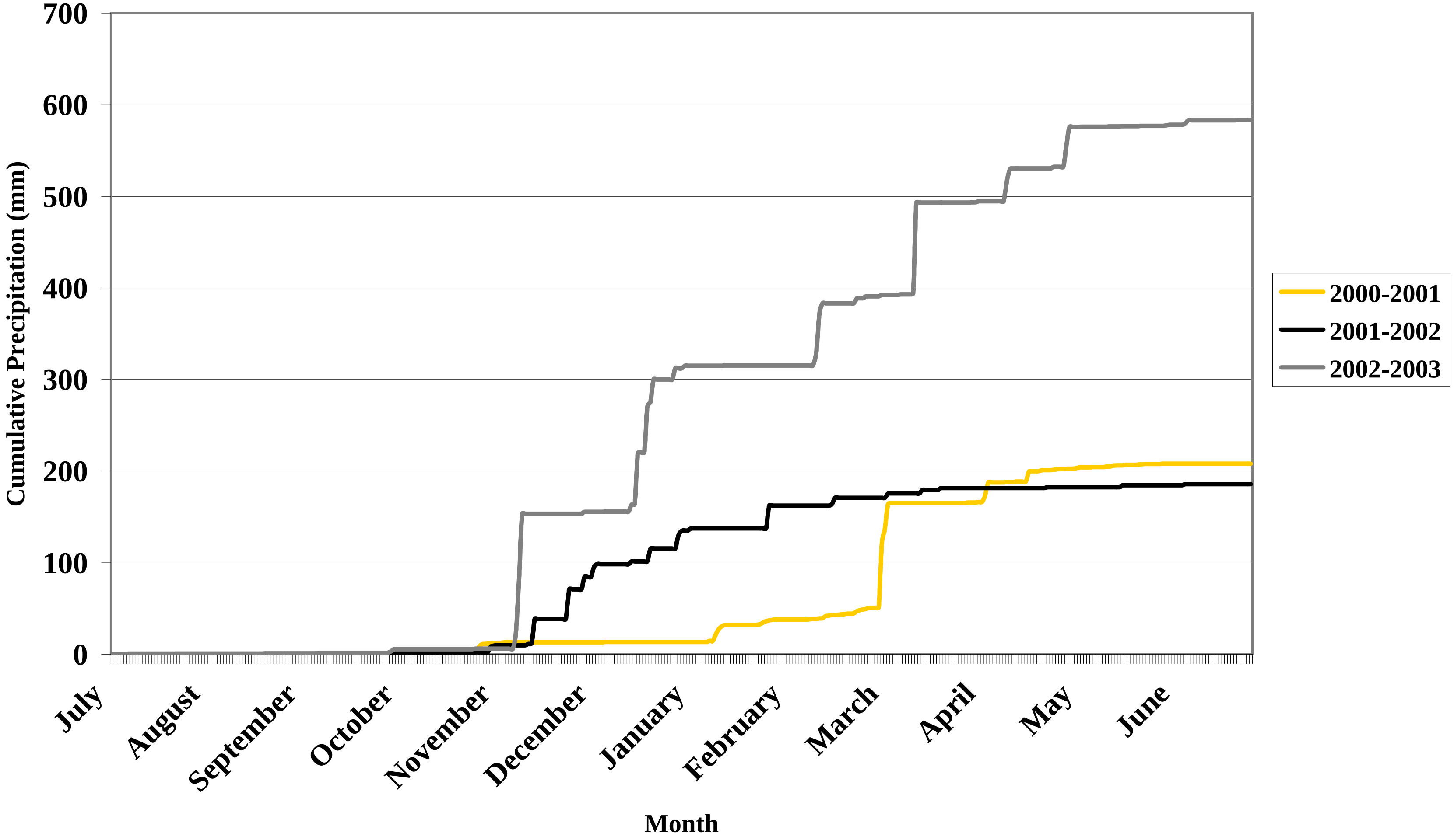
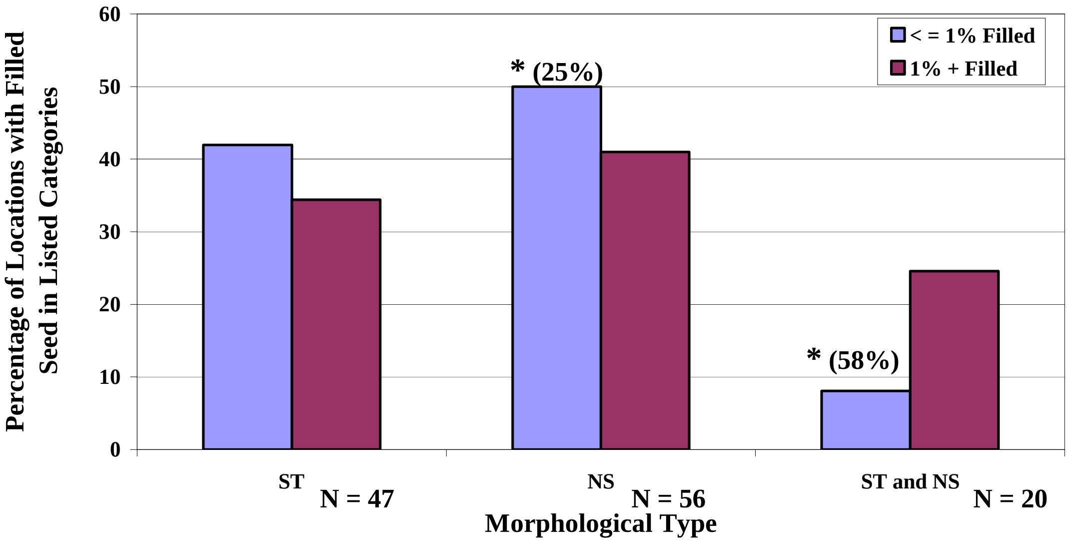


Figure 4.4. Percentage of Filled Seed by Morphological Type for 2001, 2002, and 2003



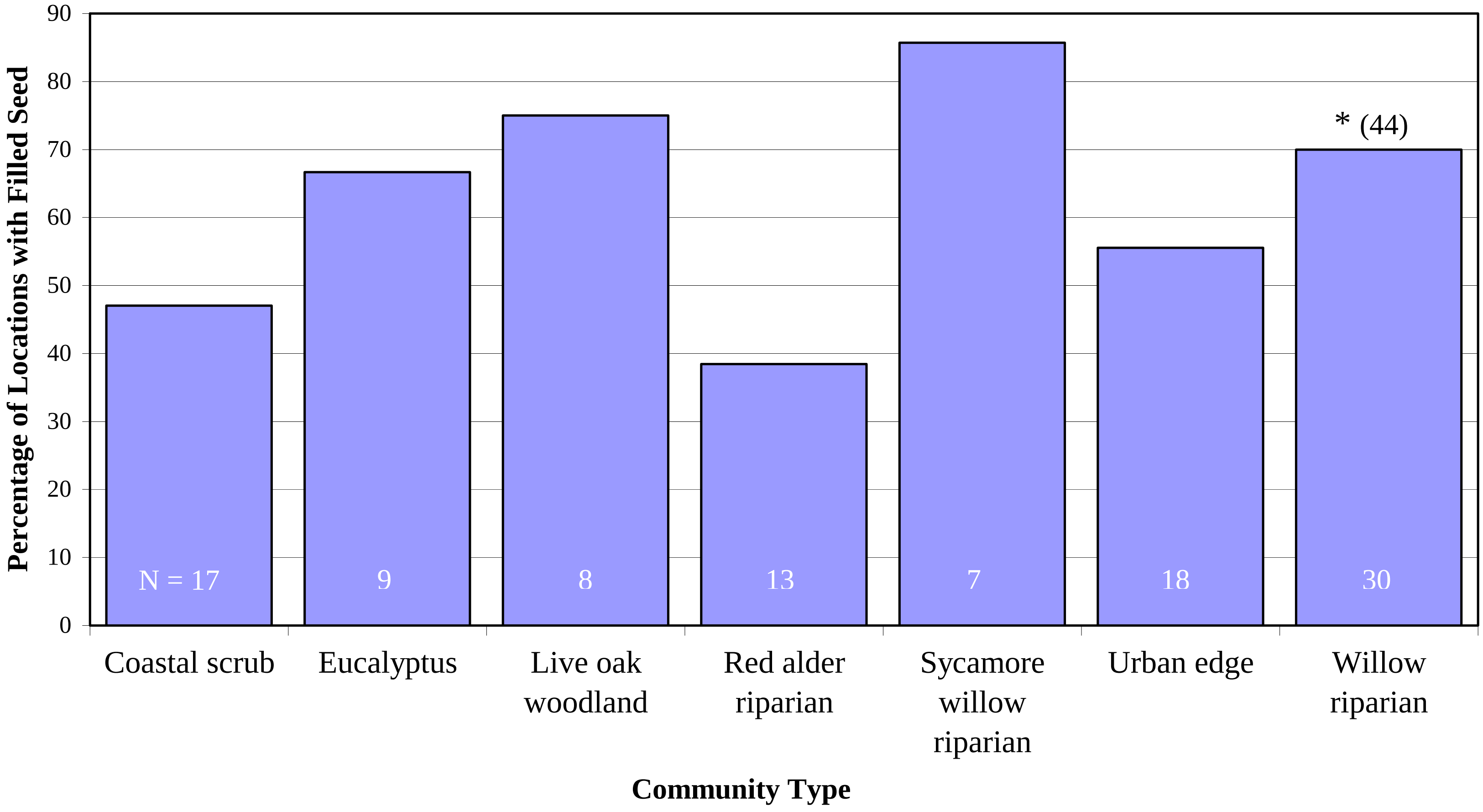
| $X^2$ Contingency Table | | |
|---|---|---|
| | < = 1% Filled | 1% + Filled |
| ST | 1.3763 | 0.0219 |
| NS | 5.1667* | 1.071 |
| BOTH | 11.8763* | 1.3989 |

$X^2$ total = 20.9112

Expected $X^2$ values were 50%< = 1% filled and 50% 1% + filled.

Values with * contribute 15% or greater to the $X^2$ total value.

**Figure 4.5. Filled Seed Production by Community Type in 2001, 2002 and 2003**

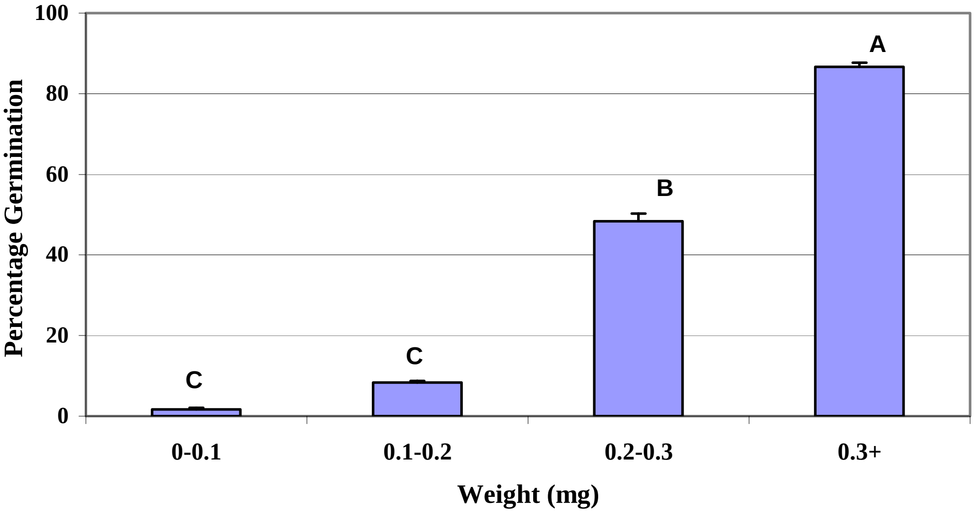


Values with * contribute 15% or greater to the $X^2$ total value.

**Figure 4.6a. Photographs of Cape Ivy Seed Germination in 2001 Study**

**Figure 4.6b. Photograph of Cape Ivy Seeds Germinating in a Petri Dish. Seeds Pictured were Collected in 2003 from Toro Canyon, Santa Barbara, and were Germinated in November, 2004. Photograph by Joe DiTomaso.**

**Figure 4.7. Percentage of Cape Ivy Seed Germination in Four Weight Classes at 20$^{o}$C**



Error bars are Standard Deviation.

Figure 4.8. Viability of Cape Ivy Seed in Three Weight Classes from Three Locations

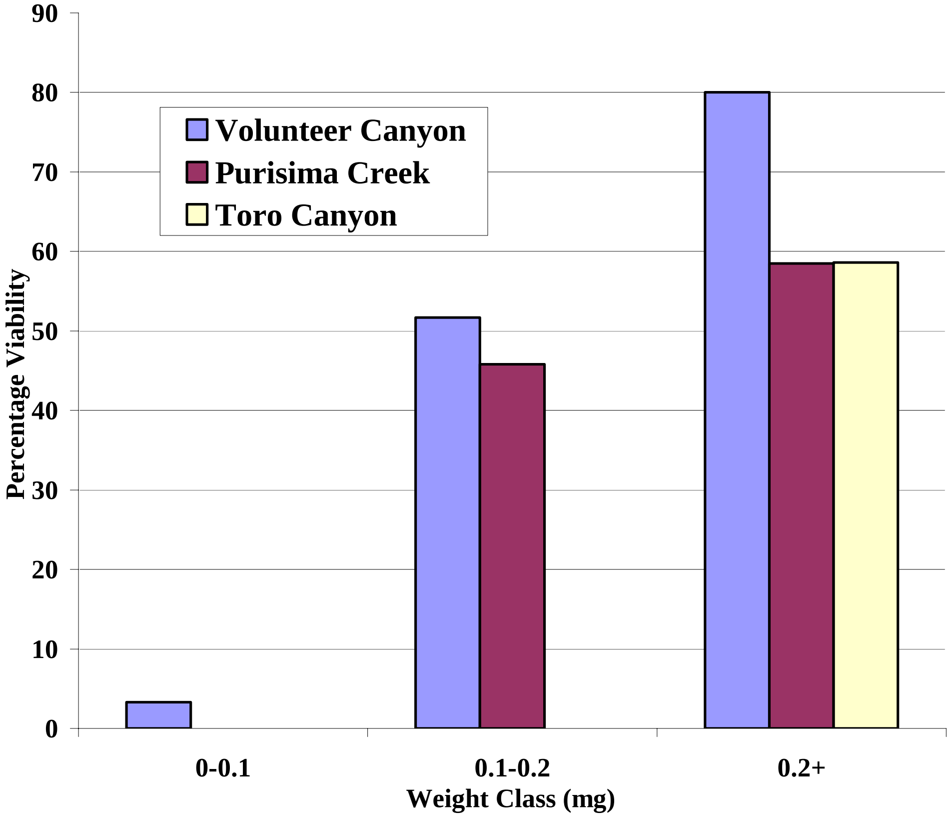
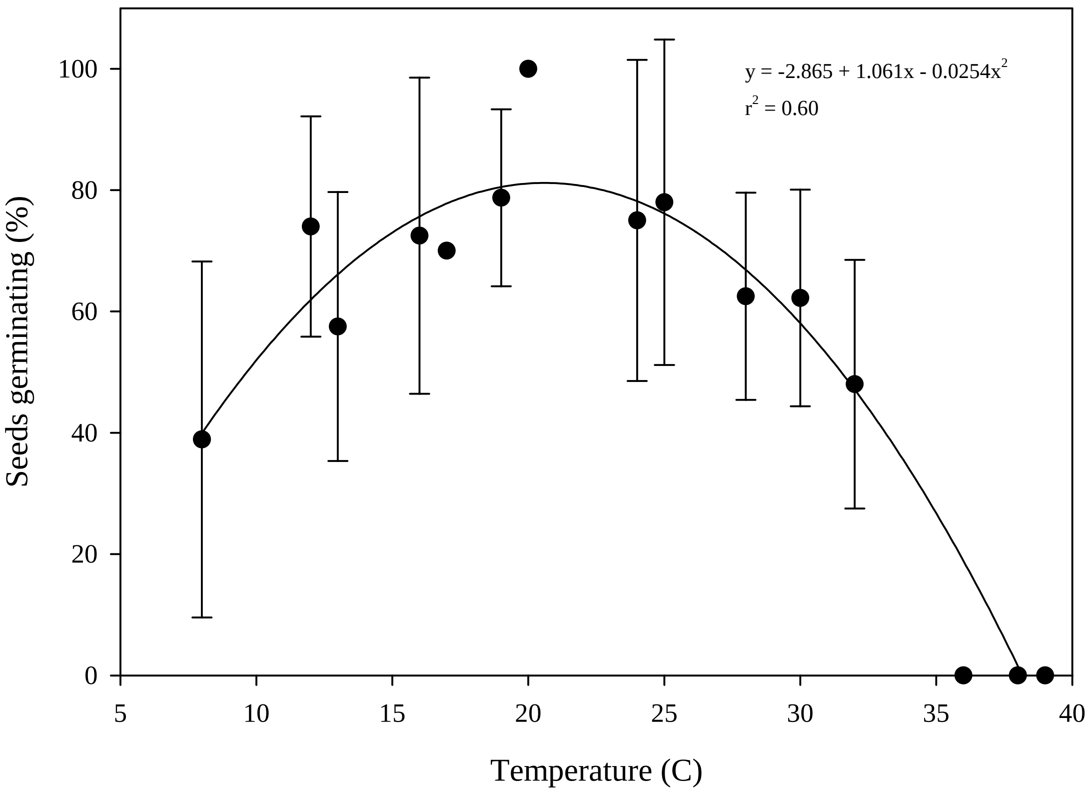


**Figure 4.9. Mean Germination of Cape Ivy Seed at Temperatures from 8 to 39ºC**

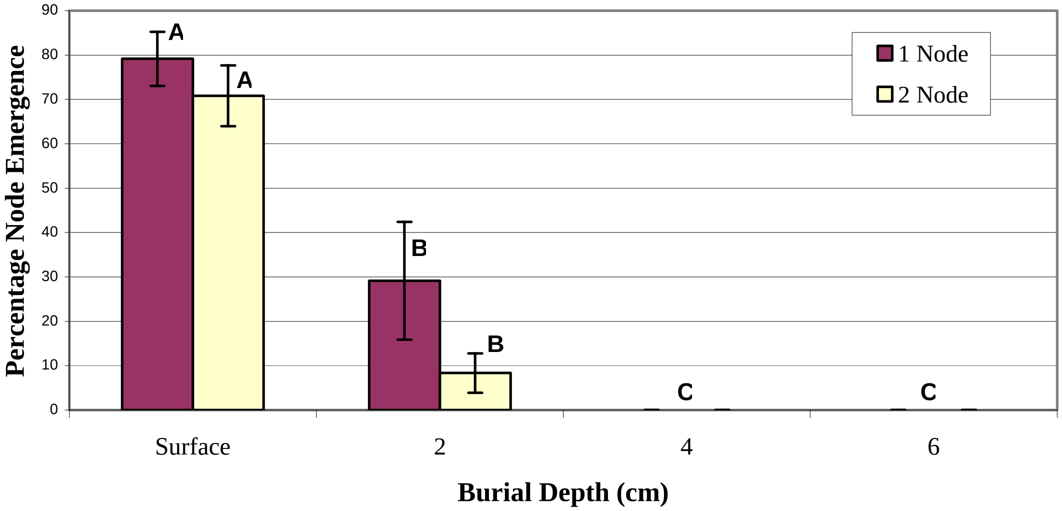


Error bars are Standard Deviation.

**Figure 4.10. Cape Ivy Seed Germination at Different Soil Depths**

Bars are Standard Error.

**Figure 4.11. Cape Ivy One or Two Node Fragment Emergence**



Bars are Standard Error.

# CHAPTER 5

## Overall Conclusions

### INTRODUCTION

When I began this research only a few studies were available on Cape ivy biology. They described the average growth rate of a single population, size of stem pieces required for propagation, drought tolerance, potentially toxic alkaloid production, and the impacts of Cape ivy on plant and insect species richness in infested areas (Stelljes and Seiber 1990, Bossard and Benefield 1995, Catalano et al. 1996, Alvarez 1997, Fisher 1997). After I began this study some additional information became available on the growth and reproductive biology of Cape ivy in South Africa (Rolando 2000).

Now we know that Cape ivy is widely distributed in California and produces viable seed throughout its range. It occurs in a variety of coastal habitats, not just riparian areas. At this point we know there is genetic diversity in growth rate and total biomass production within and between the populations studied. Preliminary data were also collected that indicated diversity of some genetic markers. Over time, populations are expected to spread both vegetatively and through sexually generated wind dispersed seed. Genetic recombination is likely to allow the species to adapt to environmental changes and potentially expand its range. CLIMEX and GARP models were used to estimate the locations of potential spread. In addition to filling in its current distribution along the California coast, Cape ivy’s range could expand into moist, shaded areas of the San Joaquin Valley and the Sierra Nevada foothills.

Some of the potential threats of Cape ivy expansion to native species were quantified by overlaying its distribution with sensitive species location information in the California Natural Diversity Database. Cape ivy was projected to overlap with the known distribution of 17 sensitive species. Some of these sensitive species were plants with restricted distributions (less than 42 occurrences worldwide) and up to 73 percent of their occurrences could be negatively affected by Cape ivy. Cape ivy was also projected to overlap with between 42 and 50% of streams supporting steelhead salmon when current locations were buffered out 500 meters. We do not know, however, whether the proximity of Cape ivy to sensitive species populations actually poses a threat to their continued existence.

## MANAGEMENT

If all populations of Cape ivy were clonal then it would simplify the management of the species. Low genetic diversity would mean less potential for adaptation and subsequent spread in California. Control strategies could be similar for all populations and assumptions could be made that methods developed in one area could be carried over to other areas. However, because viable seed is being produced, and genetic diversity exists between and within some populations, management strategies will probably have to be more diverse in their approaches to Cape ivy control.

One of the first steps in management of a population should be to determine whether viable seed is being produced. Seeds are wind dispersed, so viable seeds could be carried far away from existing infestations. Populations with mixtures of both stipulate and non-stipulate morphological types are the most likely to produce viable

Cape ivy seed, though populations with only one type also produce viable seed. Seed is produced from December through March, and mature seeds are most readily available for collection in February. After drying and separation from the rest of the withered inflorescence, seeds can be either examined under a dissecting microscope or tested directly for viability. Under a microscope, viable seeds appear plump and “filled”, while non-viable seeds are shriveled, dry and break readily when pushed with a fingernail (See Figure 4.1). Viability or germination is also easy to test. Viability can be tested by soaking prepared seeds in a 1% solution of 2,3,5 tri-phenyl tetrazolium chloride, and then dissecting them and checking for staining. Germination can be tested by placing “filled” seed in petri dishes with filter paper and water, or by sprinkling filled seed on the surface of soil in pots and then keeping the soil constantly most. Germination occurs in 1 to 2 weeks.

If the population of interest does not produce viable seed then the methods currently in use at Golden Gate National Recreation Area (GGNRA) would be useful. Their methods include mapping and prioritizing existing infestations, and containment or removal approaches that are based on the sensitivity of habitats infested. Containment is achieved by cutting 1 to 2 meter wide swaths around infested areas, and containment lines are surveyed at regular intervals to make sure infestations are not spreading. All patch removal is done by hand, with all vegetation cleared to at least 0.5 meter above the ground. Frequent monitoring and removal of re-sprouts is essential when using hand removal as plants are brittle and one node fragments are able to form new plants.

When viable seed is being produced in an area, possible spread by wind dispersal must be taken into account. As mentioned above, the managed populations should be mapped and prioritized based on the sensitivity of the community infested and the feasibility of control. The presence of viable seed production in only some of the managed populations would prioritize their removal. Wind dispersed seed production would also rule out control of populations through containment lines.

Control with herbicides may be appropriate for populations with or without viable seeds, but few comprehensive studies are available. A two year control study using herbicide and solarization found that a combination of triclopyr and glyphosate worked best, but no other longer studies are available (Bossard and Benefield 1995, Bossard et al. 2000). In two other herbicide control studies, after a year of repeated treatment the populations were able to rebound to pre-treatment levels (Fagg 1989, de la Torre and Arbesu 1999). More long-term control studies integrating herbicides with other control methods are needed for Cape ivy.

## FUTURE RESEARCH NEEDS

An integrated approach to control of Cape ivy is needed. Some of the pieces of the control puzzle that are still missing include: seed longevity, seedling recruitment, response of seedlings and other demographic stages to competition, and environmental controls of seed production.

Longevity of Cape ivy seed under field conditions is not known. Seeds collected as part of this study were able to germinate after being stored for three years under lab conditions (in paper bags at approximately 21 to 26°C). Land managers need to know whether a long-lived seed bank is present in order to plan how many years of population monitoring is necessary after control programs commence.

Seedling recruitment and its contribution to the genetic structure of Cape ivy populations is also unknown. This is a vitally important area of study because although viable wind dispersed seed is being produced, if it is unable to establish new populations, then current methods developed for managing vegetatively reproducing populations would be sufficient. At this point it is best to assume that seed recruitment plays a role in the population structure of Cape ivy and manage populations accordingly.

Competition may also play an important role in the establishment and expansion of Cape ivy populations. Seedlings or fragments may be able to establish, only to be out-competed by other aggressive native or non-native plants. Also, the seedling or fragment establishment phase may not be the best demographic stage on which to focus control efforts. Recommendations have been made to apply herbicides after the plants have flowered, assuming that they are weakened by the reproductive effort and will be more easily killed (Bossard et al. 2000). Studies investigating this assumption would provide useful information for developing control strategies.

Seed production by Cape ivy may be controlled by climatic or other environmental conditions, and an understanding of those factors could aid in management. Some cyclical behavior of seed production during the years of this study was observed. If the environmental triggers for years of high Cape ivy seed production were known then managers could focus on the control of seed producing populations during those times.

More information could also be collected on the distribution of morphological types and genotypes at a regional or population scale. In conjunction with a molecular analysis of genetic diversity, this type of information could give clues to the distribution of some of the genotypes present and to the history of their introduction. It might even be possible to develop genetic markers that could help identify the South African location where California Cape ivy originated.

Now that scientific information is available on Cape ivy's distribution, genetic diversity and reproductive biology, it can be integrated into management strategies. The weed management community must be informed of the risks posed by viable wind-dispersed seed, eradicate future range expansions, and be ready to educate the public.

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# APPENDIX A

## Molecular Research Summary

## INTRODUCTION

Little is known about how much genetic or phenotypic diversity is present within or among California Cape ivy populations. We were interested in determining whether genetic diversity was present in California Cape ivy for two reasons. If genetic diversity is present between and within populations in California, then the potential for Cape ivy to expand its range in California would be increased. Also, if populations were not genetically uniform clones it could indicate either multiple introductions had occurred or successful genetic recombination through sexual reproduction was occurring. It could also be possible to identify the South African location of California Cape ivy's origin using molecular markers.

## MATERIALS AND METHODS

### Cape Ivy Sample Collection

The locations sampled are listed in Table A-1. Locations are listed by county and include a label used during the experiments to track the DNA source (see abbreviations in Table A-2). Latitude and longitude (in the NAD 83 datum) are included as well as a short description of the location. The samples were collected either from the field or from greenhouse specimens. For field samples, vines from a site were either mixed in a collection bag (bulk samples), or single vines were collected at regular intervals along transects. The type of sample is included in the Notes column of Table A-1. After collection, samples were stored on ice until transfer to a -70ºC freezer. Samples from greenhouse specimens were collected and immediately moved to freezer storage.

### DNA Extraction

DNA was extracted from frozen samples using the CTAB technique (Saghai-Maroof et al. 1984, Doyle and Doyle 1987). The DNA was quantified in a spectrophotometer and the results were used to dilute the samples to the appropriate concentration for the PCR reaction.

### PCR and Electrophoresis

The optimum PCR (polymerase chain reaction) annealing temperature was determined by running a temperature gradient reaction using the MR1Y sample DNA and the C1 and C10 RAPD primers (primer descriptions below). The optimum annealing temperature was found to be 44ºC for RAPDs and 55ºC for ISSRs. The ISSR optimization reaction used MR1Y DNA and UBC primers #801 to 889.

RAPD and ISSR PCR were conducted in an Eppendorf Mastercycler gradient PCR (Westbury, NY) using methods similar to Marsh and Ayres (2002). A list of the RAPD primers used is included in Table A-2. The 200 series numbered RAPD primers were from RAPD Primer Set #3 (University of British Columbia (UBC), http://www.michaelsmith.ubc.ca/services/NAPS/Primer_Sets/). RAPD primers with letters preceding the numbers were from Operon Technologies, Inc., Alameda, CA. Inter-simple sequence repeat (ISSR) primers used were from UBC Primer Set #9 (Microsatellite), from #801 to 889.

PCR products were loaded into 1.5% agarose gels for electrophoresis using methods identical to Marsh and Ayres (1992). After gels were complete, they were stained with ethidium bromide and photographed under UV light. Molecular weights of the visualized bands were estimated by comparing them to a reference ladder run with each gel (Gibco Co., Carlsbad, CA). Bands examined were in the 300 to 1500 bp region, located from the second band of the reference ladder down. Bands for each gel lane were scored as:

0 = No bands
1 = Blurry, 1 band in range, faint, don't use again
2 = Blurrier than category 3, some good bands in range, look at again
3 = Bright bands with blank areas between them, use in further analysis
ST = Streaking, no bands but bright vertical streak

Scores of "0" in Table A-1 were omitted for clarity. The primers which yielded scores of "3" had the clearest bands and could be useful for further investigations.

## RESULTS AND DISCUSSION

A list of the primers used and a score for the bands produced in each gel is in Table A-1. One of the reactions summarized in Table A-1 is pictured in Figure A-1. Four DNA samples were used (CU1, MRIY, LA1, SD1) and the RAPD primers used were 241, 204, 201, 213, 227, 231, 238, 245, 250, A2, A3, A4, A18, B7, C12, D7, D8, and D11. Starting from the top left corner, the ladder is the first lane, followed by the four DNA samples run with primer #241. One interesting observation about this gel is the difference in bands produced for the four DNA samples. Curry, Los Angeles and San Diego are all non-stipulate locations while Marin, in the second place in the DNA order, is the only stipulate sample. There appear to be bands which appear in the non-stipulate plants and not in the stipulate (see primer #204 location).

The best results using ISSR primers were obtained using 55ºC as the annealing temperature. Pictures of the resulting gel, which was run using MR1Y DNA and primers UBC primers #801 to 889 are included in Figure A-2.

Although there were some interesting results obtained in preliminary RAPD reactions (Figure A-1), the results were not replicable over time. DNA samples which gave reliable results over the course of several reactions (MR1Y for example) began to degrade over time and ceased providing consistent results when run with the same primers. There were also undetermined problems with the CTAB DNA extraction technique which would have necessitated re-extraction of all the collected DNA samples.

## LITERATURE CITED

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**Table A-1. Cape Ivy Samples Used for Molecular Analysis**

| County (Label) | Location | Latitude | Longitude | Stipules (ST) or No stipules (NS) | Notes |
|---|---|---|---|---|---|
| Curry (CU1) | Oregon, Section 7 along old state highway | 42.3000 | -124.4075 | NS | Greenhouse specimen |
| Curry (CU2) | Oregon, Pistol River School | 42.2776 | -124.3935 | NS | Greenhouse specimen |
| Del Norte (DN1) | Old State Hwy, south of Orick ranger station | 41.2771 | -124.0871 | NS | Greenhouse specimen |
| Humboldt (HU1) | East of Ferndale along Bluff Rd. | 40.5356 | -124.1599 | NS | Greenhouse specimen |
| Mendocino (MEN1) | North of Ft. Bragg at Rock and Redi Mix | 49.4530 | -123.8009 | NS | Bulk sample |
| Mendocino (MEN2) | Ft. Bragg at Manzanita Rd. south of Pudding Creek crossing | 39.4591 | -123.8056 | ST | Bulk sample |
| Mendocino (MENDTR1) | Schooner Gulch | 38.8678 | -123.6528 | ST | 27m transect, 26 samples |
| Sonoma (SON1) | Sea Ranch, Deer Trail Rd. | 38.7429 | -123.4974 | ST | Bulk sample |
| Sonoma (SON2) | Jenner at gas station | 38.4486 | -123.1140 | NS | Bulk sample |
| Sonoma (SON3) | Bodega Bay – Whale Ship Rd. | 38.3365 | -123.0583 | NS | Bulk sample |
| Sonoma (SON4) | Walker Rd. inland Sonoma County | 38.2822 | -122.7760 | NS | Bulk sample |
| Marin (MAR1Y) | Rodeo Beach Maintenance Shed | 37.8323 | -122.5267 | ST | |
| Marin (MAR2) | Corte Madera, Alto Bowl Open Space, end of Stinson St. | 37.9175 | -122.5192 | NS | Greenhouse specimen |
| San Francisco (SF1) | Presidio, off Battery near west end of Golden Gate bridge | 37.8052 | -122.4761 | ST | Greenhouse specimen |
| Contra Costa (CCA1) | El Cerrito at end of Kings Ct., Hillside Natural Area | 37.9211 | -122.2958 | NS | Greenhouse specimen |
| Contra Costa (CCA2) | Mt. Diablo, North Gate trail off Castle Rock Road along Little Pine Creek | 37.8972 | -121.9952 | NS | Greenhouse specimen |
| Alameda (ALA1) | Albany, 10th St along Cerrito Creek | 37.8834 | -122.2965 | NS | Greenhouse specimen |
| San Mateo (SMT1) | San Bruno Mt., along road to top under *Eucalyptus* | 37.6943 | -122.4372 | NS | Greenhouse specimen |
| San Mateo (SMT2) | Moss Beach along stream with *Salix* | 37.5234 | -122.5144 | ST | Greenhouse specimen |
| San Mateo (SMT3) | San Bruno Mt., closer to bottom | 37.6965 | -122.4507 | ? | Greenhouse specimen |
| Santa Cruz (SC1) | Aptos Creek, Aptos | 36.9816 | -121.9015 | NS | Greenhouse specimen |

**Table A-1. Cape Ivy Samples Used for Molecular Analysis**

| County (Label) | Location | Latitude | Longitude | Stipules (ST) or No stipules (NS) | Notes |
|---|---|---|---|---|---|
| Monterey (MON1) | Pebble Beach, west side of HWY 68 | ? | ? | | Greenhouse specimen |
| San Luis Obispo (SLO1) | Morro Bay *Salicornia* marsh | 35.3466 | -120.8246 | NS | Greenhouse specimen |
| San Luis Obispo (SLO2) | Morro Rock, near parking lot | 35.3704 | -120.8649 | ST | Greenhouse specimen |
| Santa Barbara (SBA1) | UCSB West Campus housing | 34.4175 | -119.8708 | NS | Bulk sample, some seed |
| Santa Barbara (SBA2) | Ortega Ridge Rd. near Jameson | 34.4221 | -119.6113 | ST | Bulk sample |
| Ventura (VEN1) | Foothill west of Victoria Lane crossing | 34.2851 | -119.2165 | NS | Bulk sample, no seed |
| Los Angeles (LA1) | San Dimas Canyon, east side | 34.1659 | -117.7686 | NS | Greenhouse specimen |
| Los Angeles (LA2) | Nichols Canyon Rd. just off Hollywood Blvd | ? | ? | NS | Greenhouse specimen |
| Los Angeles (LA3) | Monrovia City Park, Monrovia Canyon | 34.1736 | -117.9890 | NS | Greenhouse specimen |
| Los Angeles (LA4) | Glendale, at end of Elinita Rd | 34.2068 | -118.2456 | NS | Greenhouse specimen |
| Los Angeles (LA5) | San Dimas Canyon, west side | 34.1659 | -117.7686 | NS | Greenhouse specimen |
| Los Angeles (LA6) | Higuera Creek off main road | ? | ? | NS | Greenhouse specimen |
| Los Angeles (LA7) | Glendale – Elinita Rd. | 34.2068 | -118.2456 | NS | Bulk sample |
| Los Angeles (LA8) | Zuma Beach | 34.0159 | -118.8180 | NS | Bulk sample, seed |
| Los Angeles (LA9) | Rio Honda | 34.0365 | -118.0747 | NS | Bulk sample and seed |
| Los Angeles (LATR1) | San Dimas Canyon | 34.1659 | -117.7686 | NS | 26m transect, ~1m intervals; 2-10, 14, 15-26 |

**Table A-1. Cape Ivy Samples Used for Molecular Analysis**

| County (Label) | Location | Latitude | Longitude | Stipules (ST) or No stipules (NS) | Notes |
|---|---|---|---|---|---|
| Los Angeles (LATR3) | Will Rogers State Historic Park | 34.0509 | -118.5114 | ST/NS | 20m transect, sampled at 1m intervals, many points were ST or NS |
| San Diego (SD1) | Marian Bear State Park | 32.8376 | -117.2265 | NS | Greenhouse specimen |
| San Diego (SD2) | Balboa Park | 32.7450 | -117.1559 | NS | Bulk sample, seed |
| San Diego (SD3) | Marian Bear State Park | 32.8376 | -117.2265 | NS | Bulk sample, seed |
| Los Angeles (LATR2) | San Dimas Canyon | 34.1659 | -117.7686 | NS | 4.4m transect, sub-meter samples |
| Mendocino (MENDTR1) | Schooner Gulch | 38.8678 | -123.6528 | ST | 27 m transect, 26 samples |
| Santa Barbara (SBTR1) | Toro Canyon Rd. | 34.4241 | -119.5753 | ST/NS | 21 m transect, sampled at 1m and sub-meter scales |

## Table A-2. Summary of Cape Ivy RAPD Results

| Date | 1/25/2002 | 3/4/2002 | 3/11/2002 | 3/15/2002 | 4/3/2002 | 4/8/2002 | 5/10/2002 | 7/10/2002 | 7/10/2002 | 7/10/2002 | 7/15/2002 | 7/15/2002 | 7/15/2002 | 7/16/2002 | 7/16/2002 | 7/16/2002 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **DNA source[1]** | MR1Y | MR1Y | MR1Y | CU1, MRIY, LA1, SD1 | CU1, MRIY, LA1, SD1 | CU1, MRIY, LA1, SD1 | MR1Y | CU1 | MR1Y | LA1 | CU1 | MR1Y | LA1 | CU1 | MR1Y | LA1 |
| **RAPD Primer** | | | | | | | | | | | | | | | | |
| 201 | | 1 | | | | | | | | | | | | | | |
| 202 | | 2 | | | | | | | | | | | | | | |
| 203 | 2 | 2 | | | | | | ST | ST | 2 | ST | | | | | |
| 204 | 2 | | | | | 2 | | 2 | ST | ST | 2 | 2 | 2 | | | |
| 205 | | | | | | | | | | | | | | | | |
| 206 | | | | | | | | | | | | | | | | |
| 207 | | | | | | | | | | | | | | | | |
| 208 | 2 | 1 | 3 | 2 | 2 | | 1 | ST | ST | ST | 3 | 3 | 3 | | | |
| 209 | | | | | | | | | | | | | | | | |
| 210 | 2 | | | | | 2 | | 3 | 3 | 3 | | | | | | |
| 211 | 1 | | | | | | | | | | | | | | | |
| 212 | | | | | | | 2 | ST | ST | ST | 2 | 2 | | | | |
| 213 | 3 | 1 | 1 | | | 3 | | | | | | | | | | |
| 214 | | 1 | | | | | | | | | | | | | | |
| 215 | | | | | | | | | | | | | | | | |
| 216 | | | | | | | | | | | | | | | | |
| 217 | | | | | | | | | | | | | | | | |
| 218 | 2 | 1 | | | | | | | | | | | | | | |
| 219 | | | | | | | | | | | | | | | | |
| 220 | 2 | 2 | | | | | | 1 | 1 | | | | | | | |
| 220 | | | 3 | | | | 1 | | | | | | | | | |
| 221 | | | | | | | | | | | | | | | | |
| 222 | 2 | 2 | 3 | 2 | 2 | | 1 | 3 | 3 | | 3 | 3 | 3 | | | |
| 223 | | | | | | | | | | | | | | | | |
| 224 | | | | | | | | | | | | | | | | |
| 225 | | | | | | | | | | | | | | | | |
| 226 | | | | | | | | | | | | | | | | |
| 227 | 2 | 1 | | | | | | | | | | | | | | |
| 228 | 2 | 1 | 3 | 1 | 2 | | 2 | 3 | 3 | 3 | 2 | 2 | 2 | | | |
| 229 | | | | | | | | | | | | | | | | |
| 230 | 2 | 1 | 3 | 1 | 1 | | 1 | 3 | 3 | 3 | | ST | | | | |
| 231 | X | 1 | | | | 1 | | | | | | | | | | |
| 232 | 2 | 2 | 3 | 1 | 1 | | 1 | 3 | 3 | | 1 | | | | | |
| 233 | | | | | | | | | | | | | | | | |
| 234 | | | | | | | | | | | | | | | | |
| 235 | | | | | | | | | | | | | | | | |
| 236 | | | | | | | | | | | | | | | | |
| 237 | 2 | 3 | | 2 | 2 | | 3 | 3 | | 3 | | ST | 2 | | | |
| 238 | 2 | 2 | 3 | | | 1 | 1 | | | ST | 1 | 1 | | | | |
| 239 | | | | | | | 2 | | | | | | | | | |
| 240 | | | | | | | | | | | | | | | | |
| 241 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | ST | 3 | 2 | ST | 2 | | | |

## Table A-2.  Summary of Cape Ivy RAPD Results

| **Date** | 1/25/2002 | 3/4/2002 | 3/11/2002 | 3/15/2002 | 4/3/2002 | 4/8/2002 | 5/10/2002 | 7/10/2002 | 7/10/2002 | 7/10/2002 | 7/15/2002 | 7/15/2002 | 7/15/2002 | 7/16/2002 | 7/16/2002 | 7/16/2002 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **DNA source**[1] | MR1Y | MR1Y | MR1Y | CU1, MRIY, LA1, SD1 | CU1, MRIY, LA1, SD1 | CU1, MRIY, LA1, SD1 | MR1Y | CU1 | MR1Y | LA1 | CU1 | MR1Y | LA1 | CU1 | MR1Y | LA1 |
| **RAPD Primer** | | | | | | | | | | | | | | | | |
| 242 | | 1 | | | | | | | | | | | | | | |
| 243 | 3 | 2 | 3 | 2 | 3 | | 2 | 1 | | 3 | 3 | 3 | | | | |
| 244 | 3 | 3 | 3 | 2 | 2 | | 3 | 3 | | 3 | 2 | 2 | 2 | | | |
| 245 | 2 | 2 | | | | 2 | | 1 | 2 | 3 | 1 | | | | | |
| 246 | | | | | | | | | | | | | | | | |
| 247 | | | | | | | | | | | | | | | | |
| 248 | | | | | | | | | | | | | | | | |
| 249 | | | | | | | 1 | | | | | | | | | |
| 250 | 2 | 1 | | | | 2 | | 3 | | | 1 | | | | | |
| 252 | | | | | | | | | | | | | | | | |
| 253 | | | | | | | | | | | | | | | | |
| 254 | | | | | | | | | | | | | | | | |
| 255 | | | | | | | | | | | | | | | | |
| 256 | | | | | | | | | | | | | | | | |
| 257 | | | | | | | | | | | | | | | | |
| 258 | | | | | | | | | | | | | | | | |
| 259 | | | | | | | | | | | | | | | | |
| 260 | | | | | | | | | | | | | | | | |
| 261 | | | | | | | | | | | | | | | | |
| 263 | | | | | | | | | | | | | | | | |
| 264 | | | | | | | | | | | | | | | | |
| 265 | | | | | | | | | | | | | | | | |
| 266 | | | | | | | 1 | | | | | | | | | |
| 267 | | | | | | | | | | | | | | | | |
| 268 | | | | | | | 3 | 2 | 2 | 2 | | | 1 | | | |
| 269 | | | | | | | 3 | 1 | 1 | 1 | 2 | 2 | 2 | | | |
| 270 | | | | | | | 3 | 3 | | 3 | 2 | | | | | |
| 271 | | | | | | | | | | | | | | | | |
| 272 | | | | | | | 2 | | 1 | 1 | 3 | | 1 | | | |
| 273 | | | | | | | 1 | | | | | | | | | |
| 274 | | | | | | | | | | | | | | | | |
| 275 | | | | | | | 2 | | | 1 | | | | | | |
| 276 | | | | | | | | | | | | | | | | |
| 277 | | | | | | | 2 | 1 | | | 2 | 2 | 2 | | | |
| 278 | | | | | | | | | | | | | | | | |
| 279 | | | | | | | | | | | | | | | | |
| 280 | | | | | | | 1 | | | | | | | | | |
| 281 | | | | | | | | | | | | | | | | |
| 282 | | | | | | | | | | | | | | | | |
| 283 | | | | | | | 3 | | | | | | 2 | | | |
| 284 | | | | | | | 1 | | | | | | | | | |
| 285 | | | | | | | 1 | | | | | | | | | |

## Table A-2. Summary of Cape Ivy RAPD Results

| Date | 1/25/2002 | 3/4/2002 | 3/11/2002 | 3/15/2002 | 4/3/2002 | 4/8/2002 | 5/10/2002 | 7/10/2002 | 7/10/2002 | 7/10/2002 | 7/15/2002 | 7/15/2002 | 7/15/2002 | 7/16/2002 | 7/16/2002 | 7/16/2002 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **DNA source[1]** | MR1Y | MR1Y | MR1Y | CU1, MRIY, LA1, SD1 | CU1, MRIY, LA1, SD1 | CU1, MRIY, LA1, SD1 | MR1Y | CU1 | MR1Y | LA1 | CU1 | MR1Y | LA1 | CU1 | MR1Y | LA1 |
| **RAPD Primer** | | | | | | | | | | | | | | | | |
| 286 | | | | | | | 2 | | | | 2 | | | | | |
| 287 | | | | | | | 1 | | | | | | | | | |
| 288 | | | | | | | | | | | | | | | | |
| 289 | | | | | | | | | | | | | | | | |
| 290 | | | | | | | 1 | | | | | | | | | |
| 291 | | | | | | | | | | | | | | | | |
| 292 | | | | | | | 3 | 2 | 1 | | 3 | 3 | 3 | | | |
| 293 | | | | | | | | | | | | | | | | |
| 294 | | | | | | | | | | | | | | | | |
| 295 | | | | | | | | | | | | | | | | |
| 296 | | | | | | | 2 | | | | | | | 1 | 3 | 3 |
| 297 | | | | | | | | | | | | | | | | |
| 298 | | | | | | | | | | | | | | | | |
| 299 | | | | | | | 1 | | | | | | | | | |
| 300 | | | | | | | | | | | | | | | | |
| 332 | | | 3 | | | | | | | | | | | | | |
| A1 | 1 | | | | | | | | | | | | | | | |
| A2 | 3 | 1 | 1 | | | 3 | | | | | | | | 1 | 1 | 1 |
| A3 | 2 | 1 | | | | 3 | | | | | | | | | | |
| A4 | 2 | 1 | | | | 3 | | | | | | | | | | 1 |
| A5 | | | | | | | | | | | | | | | | |
| A8 | | | | | | | | | | | | | | | | |
| A9 | | | | | | | | | | | | | | | | |
| A10 | | | | | | | 1 | | | | | | | | | |
| A11 | | | | | | | | | | | | | | | | |
| A12 | | | | | | | | | | | | | | | | |
| A13 | 3 | 1 | 3 | | 1 | | 1 | | | | | | | | | 2 |
| A14 | | | | | | | | | | | | | | | | |
| A17 | | | | | | | | | | | | | | | | |
| A18 | 2 | 1 | | | | 2 | | | | | | | | | | |
| B4 | | | | | | | | | | | | | | | | |
| B6 | 1 | | | | | | | | | | | | | | | |
| B7 | 2 | 2 | | | | 3 | | | | | | | | 1 | | 1 |
| B8 | | | | | | | | | | | | | | | | |
| B12 | | | | | | | | | | | | | | | | |
| B15 | | | | | | | | | | | | | | | | |
| B17 | 1 | | | | | | | | | | | | | | | |
| B18 | | | | | | | | | | | | | | | | |
| B19 | | | | | | | | | | | | | | | | |
| B20 | | | | | | | | | | | | | | | | |
| C1 | 1 | 1 | | | | | | | | | | | | | | |
| C2 | 1 | 1 | | | | | | | | | | | | | | |

## Table A-2. Summary of Cape Ivy RAPD Results

| **Date** | 1/25/2002 | 3/4/2002 | 3/11/2002 | 3/15/2002 | 4/3/2002 | 4/8/2002 | 5/10/2002 | 7/10/2002 | 7/10/2002 | 7/10/2002 | 7/15/2002 | 7/15/2002 | 7/15/2002 | 7/16/2002 | 7/16/2002 | 7/16/2002 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **DNA source**[1] | MR1Y | MR1Y | MR1Y | CU1, MRIY, LA1, SD1 | CU1, MRIY, LA1, SD1 | CU1, MRIY, LA1, SD1 | MR1Y | CU1 | MR1Y | LA1 | CU1 | MR1Y | LA1 | CU1 | MR1Y | LA1 |
| **RAPD Primer** | | | | | | | | | | | | | | | | |
| C8 | 1 | 1 | | | | | | | | | | | | | | |
| C10 | 1 | | | | | | | | | | | | | | | |
| C12 | 3 | 2 | 2 | | | 3 | | | | | | | | | | |
| C13 | 3 | 1 | 3 | 1 | | | | | | | | | | | | 1 |
| C14 | | | | | | | | | | | | | | | | |
| C15 | | | | | | | | | | | | | | | | |
| C18 | | | | | | | | | | | | | | | | |
| C20 | | | | | | | | | | | | | | | | |
| D5 | 3 | 2 | 3 | 1 | | | 3 | | | | | | | | | |
| D6 | | | | | | | | | | | | | | | | |
| D7 | 2 | 2 | | | | 2 | | | | | | | | 1 | | |
| D8 | 3 | 2 | 3 | | | 3 | 3 | | | | | | | 3 | 3 | 2 |
| D11 | 3 | | | | | | | | | | | | | | | |
| D12 | | | | | | | | | | | | | | | | |
| D13 | 1 | | | | | | | | | | | | | | | |
| D17 | | | | | | | | | | | | | | | | |
| D18 | 1 | 1 | | | | | | | | | | | | | | |
| D20 | 3 | 1 | 3 | 1 | 2 | | 2 | | | | | | | 3 | 3 | |
| F1 | 2 | | | | | | | | | | | | | | | |
| F2 | | | | | | | | | | | | | | | | |
| F3 | | | | | | | | | | | | | | | | |
| F4 | | | | | | | | | | | | | | | | |
| F5 | | | | | | | | | | | | | | | | |
| F6 | | | | | | | | | | | | | | | | |
| F7 | | | | | | | | | | | | | | | | |
| F8 | | | | | | | | | | | | | | | | |
| F9 | | | | | | | | | | | | | | | | |
| F12 | | | | | | | | | | | | | | | | |
| F13 | | | | | | | | | | | | | | | | |
| F14 | | | | | | | | | | | | | | | | |
| F16 | | | | | | | | | | | | | | | | |
| G2 | | | 1 | | | | | | | | | | | | | |
| G3 | | | 1 | | | | | | | | | | | | | |
| G4 | | | | | | | | | | | | | | | | |
| G5 | | | | | | | | | | | | | | | | |
| G6 | | | | | | | | | | | | | | | | |
| G8 | | | | | | | | | | | | | | | | |
| G9 | | | | | | | | | | | | | | | | |
| G10 | | | | | | | | | | | | | | | | |
| G11 | | | | | | | | | | | | | | | | |
| G12 | | | | | | | | | | | | | | | | |
| G13 | | | 1 | | | | | | | | | | | | | |

## Table A-2. Summary of Cape Ivy RAPD Results

| Date | 1/25/2002 | 3/4/2002 | 3/11/2002 | 3/15/2002 | 4/3/2002 | 4/8/2002 | 5/10/2002 | 7/10/2002 | 7/10/2002 | 7/10/2002 | 7/15/2002 | 7/15/2002 | 7/15/2002 | 7/16/2002 | 7/16/2002 | 7/16/2002 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DNA source[1] | MR1Y | MR1Y | MR1Y | CU1, MRIY, LA1, SD1 | CU1, MRIY, LA1, SD1 | CU1, MRIY, LA1, SD1 | MR1Y | CU1 | MR1Y | LA1 | CU1 | MR1Y | LA1 | CU1 | MR1Y | LA1 |
| RAPD Primer | | | | | | | | | | | | | | | | |
| G14 | | | | | | | | | | | | | | | | |
| G15 | | | | | | | | | | | | | | | | |
| G16 | | | 1 | | | | | | | | | | | | | |
| G17 | | | 2 | | | | | | | | | | | | 3 | 3 |
| G18 | | | | | | | | | | | | | | | | |
| G19 | | | | | | | | | | | | | | | | |
| H1 | | | | | | | | | | | | | | | | |
| H2 | | | | | | | | | | | | | | | | |
| H3 | | | 1 | | | | | | | | | | | | | |
| H4 | | | 1 | | | | | | | | | | | | | |
| H5 | | | 1 | | | | | | | | | | | | | |
| H6 | | | | | | | | | | | | | | | | |
| H7 | | | | | | | | | | | | | | | | |
| H8 | | | | | | | | | | | | | | | | |
| H9 | | | | | | | | | | | | | | | | |
| H10 | | | | | | | | | | | | | | | | |
| H11 | | | | | | | | | | | | | | | | |
| H13 | | | 1 | | | | | | | | | | | | | |
| H14 | | | | | | | | | | | | | | | | |
| H15 | | | | | | | | | | | | | | | | |
| H16 | | | | | | | | | | | | | | | | |
| H17 | | | | | | | | | | | | | | | | |
| H18 | | | 2 | | | | | | | | | | | 2 | 3 | 3 |
| H19 | | | 2 | | | | | | | | | | | 3 | 3 | 3 |
| H20 | | | 2 | | | | | | | | | | | | | |
| X01 | | | | | | | 2 | | | | | | | 3 | 3 | |
| X02 | | | | | | | | | | | | | | | | |
| X03 | | | | | | | 3 | | | | | | | | 2 | 3 |
| X04 | | | | | | | | | | | | | | | | |
| X05 | | | | | | | | | | | | | | | | |
| X06 | | | 1 | | | | | | | | | | | | | |
| X07 | | | 2 | | | | | | | | | | | 1 | 1 | 1 |
| X08 | | | | | | | | | | | | | | | | |
| X09 | | | | | | | | | | | | | | | | |
| X10 | | | | | | | | | | | | | | | | |
| X11 | | | | | | | 3 | | | | | | | | | |
| X12 | | | 1 | | | | | | | | | | | | | |
| X13 | | | 3 | 2 | 1 | | 2 | | | | | | | 3 | 3 | 3 |
| X14 | | | 2 | | | | | | | | | | | 3 | 3 | 3 |
| X15 | | | | | | | | | | | | | | | | |
| X16 | | | | | | | | | | | | | | | | |
| X17 | | | 3 | 1 | 2 | | 2 | | | | | | | 2 | | 2 |

## Table A-2. Summary of Cape Ivy RAPD Results

| **Date** | 1/25/2002 | 3/4/2002 | 3/11/2002 | 3/15/2002 | 4/3/2002 | 4/8/2002 | 5/10/2002 | 7/10/2002 | 7/10/2002 | 7/10/2002 | 7/15/2002 | 7/15/2002 | 7/15/2002 | 7/16/2002 | 7/16/2002 | 7/16/2002 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **DNA source**[1] | MR1Y | MR1Y | MR1Y | CU1, MRIY, LA1, SD1 | CU1, MRIY, LA1, SD1 | CU1, MRIY, LA1, SD1 | MR1Y | CU1 | MR1Y | LA1 | CU1 | MR1Y | LA1 | CU1 | MR1Y | LA1 |
| **RAPD Primer** | | | | | | | | | | | | | | | | |
| X19 | | | 3 | | 1 | | 3 | | | | | | | | | |
| X20 | | | | | | | | | | | | | | | | |

**1. See Table A-1 for DNA source code.**

**Figure A-1. RAPD Gel Run on April 9, 2002, with Four DNA Samples and 18 Primers**

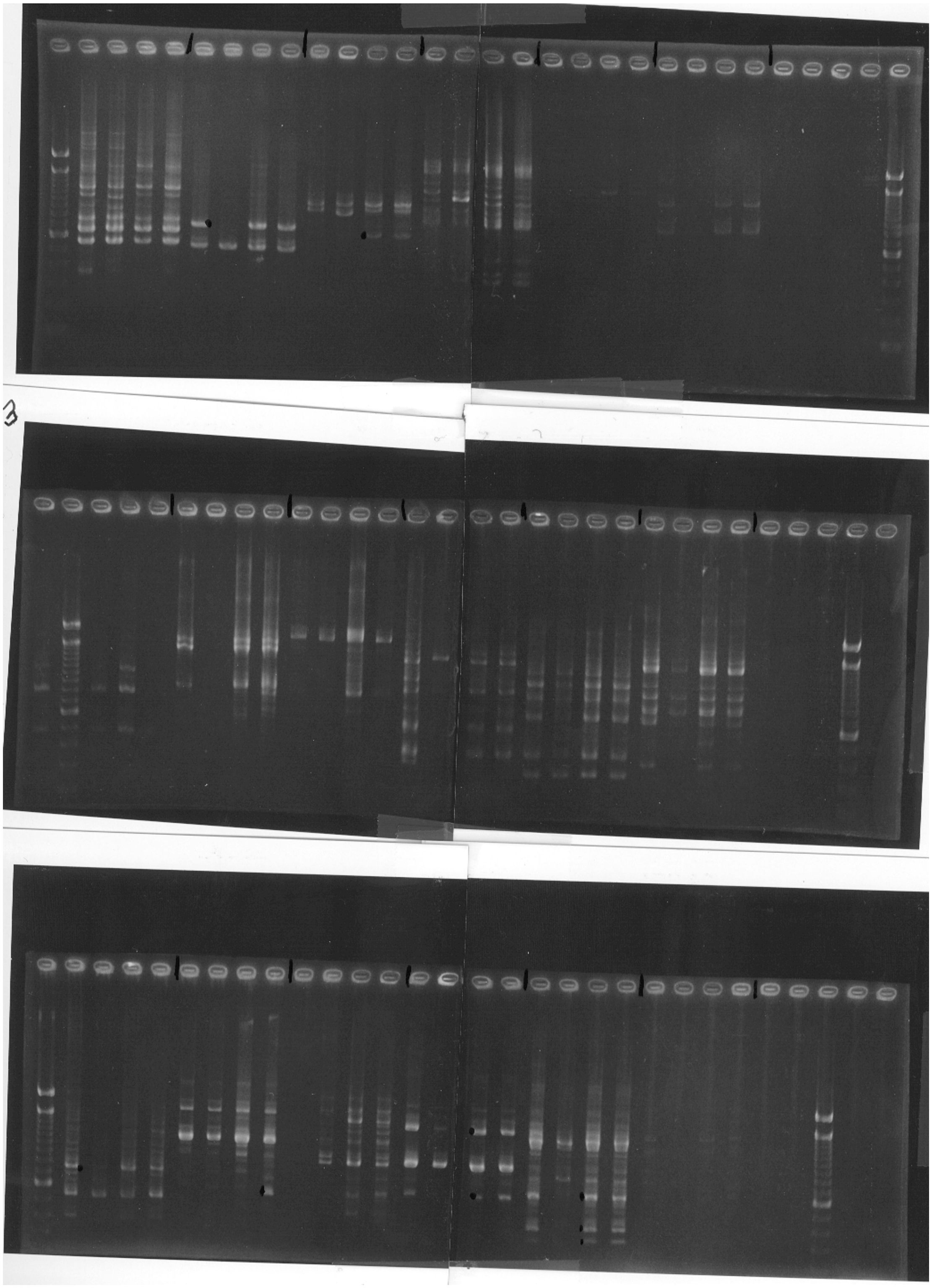
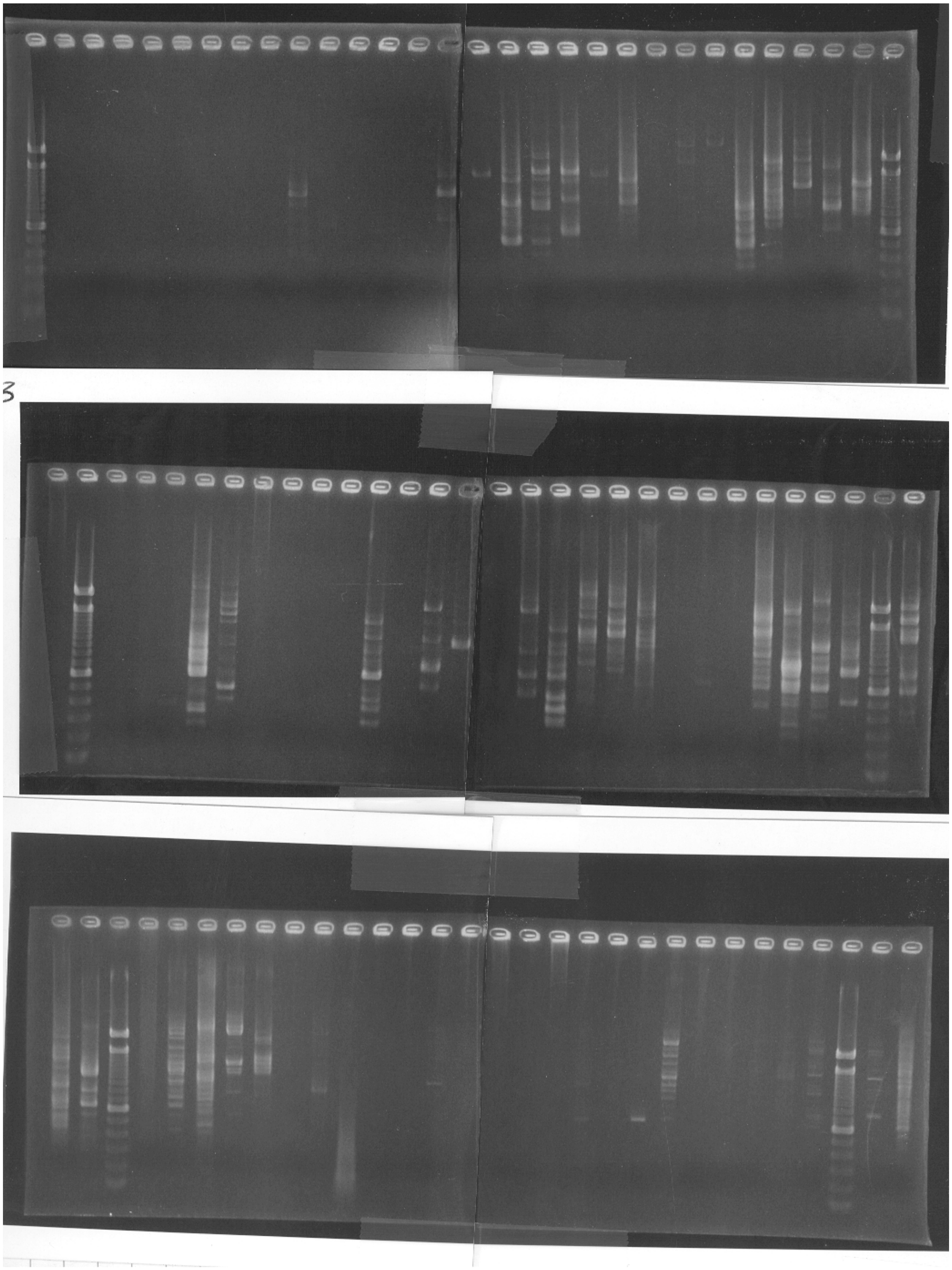


**Figure A-2. ISSR Optimization Gel Run at 55ºC on May 18, 2002, with MR1Y DNA and Primers #801 to 889.**



# APPENDIX B

## Additional Growth Analysis Data

**Table B-1. Full Analysis of Variance for Experiment 1.**

| Source | DF Num | SS | MS Num | F Ratio | Prob > F |
|---|---|---|---|---|---|
| **Log Total Biomass** | | | | | |
| **Population** | **3** | **17** | **5.7** | **8.0** | **0.0015**** |
| **Light percentage[1]** | **2** | **283** | **141.3** | **74.4** | **0.0007***** |
| **Light percentage x Population** | **6** | **5** | **0.9** | **3.6** | **0.0071**** |
| **Genotype nested within Population** | **16** | **12** | **0.8** | **3.0** | **0.0030**** |
| Light percentage x Genotype nested within Population | 32 | 8 | 0.2 | 0.6 | 0.9704 |
| **Initial weight of cutting[2]** | **1** | **6** | **5.9** | **13.8** | **0.0003***** |
| **Relative Growth Rate (Ranks Averaged)** | | | | | |
| **Population** | **3** | **15976** | **5325.3** | **3.7** | **0.0340*** |
| **Light percentage[1]** | **2** | **293595** | **146797.3** | **70.1** | **0.0008***** |
| **Light percentage x Population** | **6** | **19708** | **3284.7** | **9.2** | **< 0.0001***** |
| **Genotype nested within Population** | **16** | **23716** | **1482.2** | **4.0** | **0.0003***** |
| Light percentage x Genotype nested within Population | 32 | 11427 | 357.1 | 0.4 | 0.9982 |
| **Leaf Area (Ranks Averaged) with full sunlight treatment excluded** | | | | | |
| **Population** | **3** | **13643** | **4547.5** | **9.5** | **0.0005***** |
| Light percentage[1] | 1 | 1569 | 1568.5 | 0.6 | 0.5209 |
| Light percentage x Population | 3 | 295 | 98.4 | 0.5 | 0.6588 |
| **Genotype nested within Population** | **16** | **7744** | **484.0** | **2.9** | **0.0190*** |
| Light percentage x Genotype nested within Population | 16 | 2643 | 165.2 | 0.4 | 0.9821 |
| **Leaf Number (Ranks Averaged)** | | | | | |
| **Population** | **3** | **13371** | **4456.9** | **8.0** | **0.0014**** |
| **Light percentage[1]** | **1** | **39610** | **39609.6** | **21.4** | **0.0437*** |
| Light percentage x Population | 3 | 26 | 8.6 | 0.04 | 0.9868 |
| **Genotype nested within Population** | **16** | **9006** | **562.9** | **3.0** | **0.0153*** |
| Light percentage x Genotype nested within Population | 16 | 2946 | 184.1 | 0.4 | 0.9672 |
| **Specific Leaf Area (Ranks Averaged) 100% sunlight treatment excluded** | | | | | |
| Population | 3 | 733 | 244.4 | 1.2 | 0.3448 |
| **Light percentage[1]** | **1** | **19059** | **19059.1** | **34.5** | **0.0190*** |
| Light percentage x Population | 3 | 506 | 168.7 | 1.7 | 0.1967 |
| Genotype nested within Population | 16 | 3370 | 210.7 | 2.2 | 0.0595 |
| Light percentage x Genotype nested within Population | 16 | 1514 | 94.6 | 0.6 | 0.8622 |
| **Initial weight of cutting[2]** | **1** | **677** | **677.2** | **4.3** | **0.0428*** |

**Table B-1. Full Analysis of Variance for Experiment 1.**

| Source | DF Num | SS | MS Num | F Ratio | Prob > F |
|---|---|---|---|---|---|
| **Absolute Growth (Ranks Averaged)** | | | | | |
| **Population** | **3** | **16218** | **5405.9** | **8.5** | **0.0010*** ** |
| **Light percentage[1]** | **1** | **42803** | **42803.3** | **17.2** | **0.0535*** |
| Light percentage x Population | 3 | 314 | 104.7 | 0.5 | 0.7057 |
| **Genotype nested within Population** | **16** | **10294** | **643.3** | **2.9** | **0.0169*** |
| Light percentage x Genotype nested within Population | 16 | 3442 | 215.1 | 0.4 | 0.9664 |
| **Total Length (Ranks Averaged)** | | | | | |
| **Population** | **3** | **19451** | **6483.8** | **11.1** | **0.0002*** ** |
| Light percentage[1] | 1 | 21190 | 21189.5 | 7.8 | 0.1079 |
| Light percentage x Population | 3 | 159 | 53.1 | 0.2 | 0.8950 |
| Genotype nested within Population | 16 | 9419 | 588.7 | 2.2 | 0.0555 |
| Light percentage x Genotype nested within Population | 16 | 4161 | 260.1 | 0.5 | 0.9199 |
| **Number of Internodes (Ranks Averaged)** | | | | | |
| **Population** | **3** | **14348** | **4782.5** | **8.9** | **0.0008*** ** |
| **Light percentage[1]** | **1** | **35495** | **35494.6** | **19.4** | **0.0478*** |
| Light percentage x Population | 3 | 220 | 73.1 | 0.3 | 0.8435 |
| Genotype nested within Population | 16 | 8728 | 545.5 | 2.1 | 0.0766 |
| Light percentage x Genotype nested within Population | 16 | 4206 | 262.9 | 0.6 | 0.8625 |
| **Initial weight of cutting[2]** | **1** | **2159** | **2159** | **5** | **0.0279*** |
| **Length per Day (Ranks Averaged)** | | | | | |
| **Population** | **3** | **21165** | **7054.9** | **11.4** | **0.0002*** ** |
| Light percentage[1] | 1 | 22798 | 22798.3 | 8.9 | 0.0962 |
| Light percentage x Population | 3 | 160 | 53.5 | 0.2 | 0.9066 |
| Genotype nested within Population | 16 | 10011 | 625.7 | 2.2 | 0.0640 |
| Light percentage x Genotype nested within Population | 16 | 4592 | 287.0 | 0.6 | 0.8989 |

1. Light percentage values calculated using separate JMP analysis (see text for description)

* F < 0.05; ** F < 0.01; *** F < 0.001

2. Initial weight of cutting only shown when significant.

### Table B-2. Full Analysis of Variance for Experiment 2.

| Source | DF Num | SS | MS Num | F Ratio | Prob > F |
|---|---|---|---|---|---|
| **Log Total Biomass** | | | | | |
| Population | 2 | 1 | 0.6 | 0.6 | 0.5643 |
| **Light percentage[1]** | **2** | **154** | **76.9** | **103.2** | **0.0003***** |
| Light percentage x Population | 5 | 6.8 | 1.4 | 0.8 | 0.5581 |
| Genotype nested within Population | 15 | 15 | 1 | 1 | 0.8594 |
| Light percentage x Genotype nested within Population | 31 | 53 | 1.7 | 1.4 | 0.1146 |
| **Initial weight of cutting[2]** | **1** | **17** | **17** | **13.6** | **0.0004***** |
| **Relative Growth Rate (Ranks Averaged)** | | | | | |
| Population | 3 | 7340 | 2446.6 | 0.7 | 0.5536 |
| **Light percentage[1]** | **2** | **130241** | **65120.4** | **38.4** | **0.0025**** |
| Light percentage x Population | 6 | 10200 | 1700.1 | 0.6 | 0.7365 |
| Genotype nested within Population | 16 | 55221 | 3451.3 | 1.2 | 0.3186 |
| **Light percentage x Genotype nested within Population** | **32** | **92334** | **2885.5** | **1.8** | **0.0109*** |
| **Initial weight of cutting[2]** | **1** | **7116** | **7115.7** | **4.5** | **0.0360*** |
| **Leaf Area (Ranks Averaged) with full sunlight treatment excluded** | | | | | |
| Population | 3 | 2482 | 827.3 | 0.8 | 0.5037 |
| **Light percentage[1]** | **1** | **23607** | **23607** | **20.7** | **0.0445*** |
| Light percentage x Population | 3 | 4157 | 1385.7 | 1 | 0.4264 |
| Genotype nested within Population | 16 | 16188 | 1011.8 | 1 | 0.7563 |
| Light percentage x Genotype nested within Population | 16 | 23082 | 1442.6 | 1.3 | 0.2461 |
| **Leaf Number (Ranks Averaged)** | | | | | |
| Population | 2 | 181 | 90.5 | 0.1 | 0.9024 |
| **Light percentage[1]** | **2** | **88637** | **44318.5** | **65.7** | **0.0008***** |
| Light percentage x Population | 5 | 5195 | 1039.1 | 0.7 | 0.6006 |
| Genotype nested within Population | 15 | 12673 | 844.9 | 0.6 | 0.8408 |
| Light percentage x Genotype nested within Population | 31 | 44293 | 1428.8 | 1.5 | 0.06717 |
| **Initial weight of cutting[2]** | **1** | **16980** | **16979.6** | **18.1** | **0.0001***** |
| **Specific Leaf Area (Ranks Averaged) 100% sunlight treatment excluded** | | | | | |
| Population | 3 | 8321 | 2773.7 | 3 | 0.0550 |
| **Light percentage[1]** | **1** | **54846** | **54846.5** | **26.1** | **0.0361*** |
| Light percentage x Population | 3 | 2299 | 766.2 | 0.9 | 0.4456 |
| Genotype nested within Population | 16 | 14728 | 920.5 | 1.1 | 0.4139 |

**Table B-2. Full Analysis of Variance for Experiment 2.**

| Source | DF Num | SS | MS Num | F Ratio | Prob > F |
|---|---|---|---|---|---|
| Light percentage x Genotype nested within Population | 16 | 13205 | 825.3 | 1 | 0.4278 |
| **Absolute Growth (Ranks Averaged)** | | | | | |
| Population | 2 | 625 | 312.3 | 0.4 | 0.7031 |
| **Light percentage**$^{1}$ | **2** | **114918** | **57459.1** | **76.1** | **0.0006***** |
| Light percentage x Population | 5 | 5421 | 1084.3 | 0.8 | 0.5457 |
| Genotype nested within Population | 15 | 13280 | 885.3 | 0.7 | 0.7762 |
| Light percentage x Genotype nested within Population | 31 | 41539 | 1340 | 1.6 | 0.0598 |
| **Total Length (Ranks Averaged)** | | | | | |
| Population | 2 | 1349 | 674.3 | 0.8 | 0.4481 |
| **Light percentage**$^{1}$ | **2** | **137417** | **68708.6** | **110.5** | **0.0003***** |
| Light percentage x Population | 5 | 3151 | 630.2 | 0.7 | 0.6585 |
| Genotype nested within Population | 15 | 13072 | 871.5 | 0.9 | 0.5435 |
| Light percentage x Genotype nested within Population | 31 | 30007 | 968 | 1.3 | 0.1580 |
| **Initial weight of cutting**$^{2}$ | **1** | **7722** | **7722.4** | **10.6** | **0.0017**** |
| **Number of Internodes (Ranks Averaged)** | | | | | |
| Population | 2 | 961 | 480.6 | 0.7 | 0.4987 |
| **Light percentage**$^{1}$ | **2** | **96614** | **48307.1** | **74.9** | **0.0006***** |
| Light percentage x Population | 5 | 3911 | 782.2 | 0.89 | 0.5363 |
| Genotype nested within Population | 15 | 9207 | 613.8 | 0.7 | 0.8035 |
| Light percentage x Genotype nested within Population | 31 | 29321 | 945.8 | 1.2 | 0.2683 |
| **Initial weight of cutting2** | **1** | **8498** | **8498.3** | **10.7** | **0.0016**** |
| **Length per Day (Ranks Averaged)** | | | | | |
| Population | 2 | 1285 | 642.6 | 0.8 | 0.4661 |
| **Light percentage**$^{1}$ | **2** | **136136** | **68068** | **118.3** | **0.0003***** |
| Light percentage x Population | 5 | 3158 | 631.6 | 0.7 | 0.6632 |
| Genotype nested within Population | 15 | 13114 | 874.3 | 0.9 | 0.5510 |
| Light percentage x Genotype nested within Population | 31 | 30379 | 980 | 1.3 | 0.1507 |
| **Initial weight of cutting**$^{2}$ | **1** | **7898** | **7898** | **10.8** | **0.0015**** |

1. Light percentage values calculated using separate JMP analysis (see text for description)
* F < 0.05; ** F < 0.01; *** F < 0.001
2. Initial weight of cutting only shown when significant.

**Figure B-1.** ***Plusia biloba*** **Larvae, Pupae and Adults**

***Plusia biloba*** **larvae**

***Plusia biloba*** **pupae**

***Plusia biloba*** **adults**

# APPENDIX C

## Additional Seed Collection Location Data

| Table C-1. Cape Ivy Seed Collection Locations in 2001, 2002 and 2003. | | | | | | | |
|---|---|---|---|---|---|---|---|
| **COUNTY Location** | **Latitude** | **Longitude** | **Collection Date(s)** | **ST/NS** | **Community Types** | **Large Seed and Estimate of % Filled** | **Notes** |
| **CURRY** | | | | | | | |
| North of Pistol River on old highway near Cemetery Rd crossing | 42.2909 | -124.4029 | 2/28/03 | NS | Urban edge | N03 | |
| Pistol River, old school house now a residence | 42.2776 | -124.3935 | 2/15/01;<br>2/28/03 | NS | Urban edge | Y01 (23%)<br>N03 | |
| **HUMBOLDT** | | | | | | | |
| Orick along old State Highway | 41.2771 | -124.0871 | 2/27/03 | NS | Red alder riparian | Y03 (< 1%) | |
| West of Ferndale along Eel River | 40.5356 | -124.1599 | 2/27/03 | NS | Red alder riparian | N03 | |
| McKinleyville, School Rd. | -- | -- | 3/3/01 | UNK | UNK | Y01 (45%) | Collected by Gordon Leppig |
| McKinleyville Central Ave. | -- | -- | 3/3/01 | UNK | UNK | Y01 (1%) | Collected by Gordon Leppig |
| McKinleyville Mad River | -- | -- | 3/3/01 | UNK | UNK | N01 | Collected by Gordon Leppig |
| Shelter Cove, lower Pacific and Neptune | 40.0278 | -124.0743 | 2/27/03 | ST | Urban edge and Red alder riparian | N03 | |
| Shelter Cove, Upper Pacific and Ocean View | 40.0253 | -124.0669 | 2/27/03 | ST | Coastal scrub | N03 | |
| **MENDOCINO** | | | | | | | |
| Westport at north end of town | 39.6467 | -123.7836 | 2/18/01;<br>2/26/03 | ST | Coastal scrub | Y01 (2%) | No seeds observed in 2003 |
| South of Westport, MP76.20 | 39.6221 | -123.7801 | 2/18/01 | ST | Northern coastal scrub | Y01 (2%) | |
| HWY1 MP 75.72 | 39.6159 | -123.7800 | 2/18/01 | ST | Willow riparian | N01 | |
| Pudding Creek Beach Ft. Bragg | 39.4591 | -123.8056 | 2/18/01 | NS | Norhtern dune scrub | N01 | |
| Mendocino near public rest rooms | 39.3047 | -123.7982 | 2/18/01;<br>2/26/03 | ST | Urban edge | N01 | No seeds observed in 2003 |
| Van Damme State Park | 39.2733 | -123.7893 | 2/18/01;<br>2/26/03 | ST/NS | Red alder riparian and coastal scrub | Y01 (1%) | No seeds observed in 2003 |

**Table C-1. Cape Ivy Seed Collection Locations in 2001, 2002 and 2003.**

| COUNTY Location | Latitude | Longitude | Collection Date(s) | ST/NS | Community Types | Large Seed and Estimate of % Filled | Notes |
|---|---|---|---|---|---|---|---|
| Navarro River north of 128 Junction MP 40.67 | 39.1992 | -123.7522 | 2/18/01 | ST | Willow riparian and coastal scrub | Y01 (1%) | |
| North of Machester MP 22.00 | 38.9889 | -123.6835 | 2/18/01 | UNK | Willow riparian | N01 | |
| 11400 S. HWY1 between Elk and Manchester | 39.0738 | -123.6925 | 2/23/02;<br>2/26/03 | ST | Coastal prairie | N02<br>Y03 (< 1%) | |
| HWY 1 north of Elk | 39.1421 | -123.7282 | 2/18/01 | ST | North coast scrub franciscan | N01 | |
| HWY 1 north of Pt. Arena | 38.9309 | -123.7060 | 2/18/01 | ST | Red alder riparian | Y01 (2%) | |
| Pt. Arena MP 15.73 to address 335 HWY1 | 38.9143 | -123.7000 | 2/18/01;<br>2/26/03 | ST | Willow riparian | Y01 (1%) | No seeds observed in 2003 |
| Schooner Gulch | 38.8678 | -123.6528 | 2/19/01;<br>2/25/03 | ST | Red alder riparian | N01 | No seeds observed in 2003 |
| South of Schooner Gulch at 28601 HWY 1 | 38.8671 | -123.6525 | 2/19/01 | ST | North coast bluff scrub | N01 | |
| Gualala at Sedalia Rd | 38.7734 | -123.5339 | 2/19/01;<br>2/25/03 | ST | Redwood | N01<br>N03 | |
| **SONOMA** | | | | | | | |
| Jenner gas station | 38.4486 | -123.1140 | 2/19/01;<br>2/24/02;<br>2/25/03 | NS | Red alder riparian | N01<br>N02 | No seeds observed in 2003 |
| HWY1 MP 34.36 | 38.5250 | -123.2626 | 2/24/02;<br>2/25/03 | NS | Red alder riparian | N02 | No seeds observed in 2003 |
| Sonoma State Beach, Wright’s Beach campground | 38.4006 | -123.0936 | 2/19/01 | NS | Urban edge | Y01 (1%) | |
| Bodega Bay, Whale Ship Rd. | 38.3365 | -123.0583 | 2/19/01;<br>2/21/03 | NS | Willow riparian | Y01 (10%)<br>Y03 (< 1%) | |
| **MARIN** | | | | | | | |
| Marshall | 38.1542 | -122.8898 | 2/20/03 | ST | Urban edge | N03 | |
| HWY1 MP 17.38 north of Bolinas road | 37.9372 | -122.7008 | 2/20/03 | ST | Red alder riparian | N03 | |
| HWY1 MP 14.90 (Volunteer Canyon) | 37.9200 | -122.6698 | 2/20/03 | NS | Willow riparian | Y03 (> 1%)<br>Y04 (> 1%) | 2003-2004 field crossing location |

**Table C-1. Cape Ivy Seed Collection Locations in 2001, 2002 and 2003.**

| COUNTY Location | Latitude | Longitude | Collection Date(s) | ST/NS | Community Types | Large Seed and Estimate of % Filled | Notes |
|---|---|---|---|---|---|---|---|
| Stinson Beach | 37.8967 | -122.6386 | 2/20/03 | ST | Willow riparian | N03 | |
| Muir Beach | 37.8636 | -122.5739 | 2/19/03 | NS | Red alder riparian | Y03 (< 1%) | |
| Rodeo Beach maintenance shed GGNRA | 37.8323 | -122.5267 | 2/15/01;<br>2/18/02;<br>3/16/03 | ST | Willow riparian | Y01 (21%)<br>N02<br>N03 | |
| Rodeo Valley Creek GGNRA | 37.8344 | -122.5404 | 2/15/01 | ST/NS | Central coast arroyo willow riparian forest | Y01 (59%) | |
| **SAN FRANCISCO** | | | | | | | |
| Presidio off Battery | 37.8052 | -122.4761 | 2/15/01;<br>2/18/02;<br>2/19/03 | ST | Coastal scrub and urban edge | Y01 (13%)<br>N02<br>N03 | |
| **ALAMEDA** | | | | | | | |
| Lake Temescal | 37.8350 | -122.5402 | 3/1/01;<br>1/16/02 | UNK | Urban edge | N01<br>Y02 (> 1%) | |
| **SAN MATEO** | | | | | | | |
| San Bruno Mountain | -- | -- | 3/6/01 | UNK | UNK | Y01 (7%) | Collected by Jake Sigg |
| San Bruno Mountain bottom | 37.6965 | -122.4507 | 2/17/01 | NS | Willow riparian | Y01 (32%) | |
| Milagra Ridge GGNRA | 37.6401 | -122.4722 | 2/15/01 | UNK | Northern coastal scrub | N01 | |
| Pacifica, San Pedro Creek | 37.5952 | -122.5043 | 2/19/03 | NS | Willow riparian | Y03 (> 1%) | |
| McNee Ranch Rd. | 37.5538 | -122.5110 | 2/15/01;<br>2/19/03 | ST | Coastal scrub | Y01 (61%) | No seeds observed in 2003 |
| Montara Youth Hostel | 37.5367 | -122.5171 | 2/19/03 | ST | Coastal scrub | N03 | |
| Moss Beach, lower San Vicente Ck | 37.5234 | -122.5144 | 2/19/03 | ST/NS | Willow riparian and coastal scrub | Y03 (> 1%) | |
| Miramar on Lee along Arroyo de en Medio | 37.4944 | -122.4564 | 2/19/03 | ST | Willow riparian and Eucalyptus | N03 | |
| Lobitos Creek at Verde Rd. | 37.3841 | -122.4002 | 2/19/03 | ST | Willow riparian and Eucalyptus | N03 | |
| Half Moon Bay Main Street, Pilarcitos Creek | 37.4664 | -122.4281 | 2/19/03 | ST | Willow riparian | Y03 (< 1%) | |

**Table C-1. Cape Ivy Seed Collection Locations in 2001, 2002 and 2003.**

| COUNTY Location | Latitude | Longitude | Collection Date(s) | ST/NS | Community Types | Large Seed and Estimate of % Filled | Notes |
|---|---|---|---|---|---|---|---|
| Purisima Creek Rd west of Verde crossing | 37.4043 | -122.4143 | 2/19/03;<br>1/26/04 | ST | Willow riparian and coastal scrub | Y03 (> 1%)<br>Y04 (> 1%) | Used for temperature gradient study |
| Leon Creek off Higgins/Purisima Rd | 37.4524 | -122.4163 | 2/19/03 | ST | Willow riparian | N03 | |
| Tunitas Creek Rd | 37.3622 | -122.3899 | 2/19/03 | ST | Red alder riparian | Y03 (> 1%) | |
| San Gregorio | 37.3261 | -122.3857 | 2/19/03 | ST/NS | Willow riparian | Y03 (> 1%) | Yes for ST and NS flowers |
| Pescadero, Stage Rd and North Hollow | 37.2550 | -122.3818 | 2/19/03 | ST | Willow riparian | Y03 (> 1%) | |
| San Vicente Creek off Etheldore | 37.5223 | -122.5051 | 2/19/03 | ST/NS | Willow riparian and Eucalyptus | Y03 (< 1%) | ST yes and NS no large seeds |
| Gazos Creek off HWY1 | 37.1674 | -122.3580 | 2/18/03 | ST/NS | Willow riparian | N03 | |
| **SANTA CRUZ** | | | | | | | |
| Big Creek, PM 35.49 on HWY1 | 37.0869 | -122.2700 | 2/18/03 | ST | Willow riparian | N03 | |
| Davenport, Coast Rd. | 37.0111 | -122.1915 | 2/18/03 | ST/NS | Urban edge | N03 | |
| HWY1 and Laguna Rd, MP25 | 36.9869 | -122.1500 | 2/18/03 | ST | Coastal scrub and willow scrub | Y03 (> 1%) | |
| Santa Cruz, Western Ave. near Monarch | 36.9700 | -122.0576 | 2/18/03 | NS | Urban edge | N03 | |
| La Selva Beach, San Andreas Rd./Seascape intersection | 36.9301 | -122.8558 | 2/16/01 | NS | Urban edge | N01 | |
| La Selva Beach San Andreas Rd./Oceanview intersection | 36.9507 | -122.8630 | 2/17/01 | NS | Arroyo willow riparian | Y01 (3%) | |
| Sunset Beach | 36.8968 | -121.8364 | 2/16/01 | NS | Eucalyptus and coatal scrub | Y01 (9%) | |
| Sunset Beach access road outside park | 36.8985 | -121.8330 | 2/16/01 | NS | Urban edge | N01 | |
| Watsonville Slough | 36.8880 | -121.8040 | 2/16/01;<br>2/13/03 | ST | Willow riparian | Y01 (36%)<br>Y03 (> 1%) | |
| Pajaro River | 36.8810 | -121.7914 | 2/16/01 | ST | North coast black cottonwood riparian | Y01 (65%) | |

**Table C-1. Cape Ivy Seed Collection Locations in 2001, 2002 and 2003.**

| COUNTY Location | Latitude | Longitude | Collection Date(s) | ST/NS | Community Types | Large Seed and Estimate of % Filled | Notes |
|---|---|---|---|---|---|---|---|
| **MONTEREY** | | | | | | | |
| Elkhorn Slough near Moss Landing powerplant | 36.8086 | -121.7823 | 2/17/01 | ST | Urban edge | Y01 (81%) | |
| Prunedale South Rd | 36.7880 | -121.6695 | 2/13/03 | NS | Willow riparian | N03 | |
| Prunedale Crazy Horse Canyon Rd. | 36.8125 | -121.6237 | 2/17/01;<br>2/13/03 | ST/NS | Live oak woodland | Y01 (37%)<br>N03 | |
| San Juan Grade Rd, east of Prunedale | 36.8036 | -121.5798 | 2/13/03 | NS | Live oak woodland | Y03 (> 1%) | |
| San Jose Ck, HWY1 | 36.5233 | -121.9250 | 2/16/01;<br>2/13/03 | ST | Willow riparian and urban edge | Y01 (69%) | No seeds observed in 2003 |
| Gibson Creek, HWY1 | 36.5073 | -121.9350 | 2/16/01;<br>2/13/03 | ST | Urban edge and coastal scrub | Y01 (53%) | No seeds observed in 2003 |
| **SAN LUIS OBISPO** | | | | | | | |
| San Simeon Creek | 35.5994 | -121.1173 | 2/12/03 | ST | Willow riparian | Y03 (> 1%) | |
| Cambria business park, Burton off HWY1, follow down hill and take right | 35.5646 | -121.0788 | 2/12/03 | ST/NS | Sycamore willow riparian | Y03 (> 1%) | |
| Cayucos under HWY1 bridge | 35.4532 | -120.9056 | 2/12/03 | NS | Willow riparian | Y03 (> 1%) | |
| Toro Creek Rd. east of HWY1, south of Cayucos | 35.4166 | -120.8676 | 2/12/03 | ST/NS | Willow and black cottonwood riparian with Eucalyptus | Y03 (> 1%) | |
| Morro Bay State Park in salt marsh off South Bay Rd. | 35.3466 | -120.8246 | 2/11/03 | NS | Salt marsh | Y03 (< 1%) | |
| Montana de Oro | 35.2881 | -120.8781 | 2/11/03 | NS | Eucalyptus and willows | N03 | |
| Cal Poly San Luis Obispo | 35.3011 | -120.6696 | 2/12/03 | NS | Bay oak woodland and willow riparian | Y03 (< 1%) | |
| San Luis Obispo, intersection of High St and Higurea | 35.2724 | -120.6698 | 3/21/01;<br>2/12/03 | NS | Willow riparian | Y01 (45%)<br>Y03 (< 1%) | |
| Oceano | 35.1100 | -120.6241 | 2/11/03 | NS | Willow riparian | Y03 (> 1%) | |

| Table C-1. Cape Ivy Seed Collection Locations in 2001, 2002 and 2003. | | | | | | | |
|---|---|---|---|---|---|---|---|
| **COUNTY Location** | **Latitude** | **Longitude** | **Collection Date(s)** | **ST/NS** | **Community Types** | **Large Seed and Estimate of % Filled** | **Notes** |
| Avila, on Avila Rd. across from hot springs spa | 35.1869 | -120.7120 | 2/11/03 | ST | Sycamore willow riparian | Y03 (< 1%) | |
| Oso Flaco Lake | 35.0314 | -120.6198 | 2/11/03 | ST | Willow riparian | Y03 (> 1%) | |
| Chorro Flats in Morro Bay State Park | -- | -- | 2/17/01 | UNK | UNK | Y01 (63%) | Collected by Dave Chipping |
| **SANTA BARBARA** | | | | | | | |
| Orcutt | 34.8661 | -120.4528 | 2/11/03 | NS | Willow riparian | Y03 (< 1%) | |
| Lompoc River Park | 34.6509 | -120.4339 | 2/10/03 | NS | Willow riparian | Y03 (< 1%) | |
| UC Santa Barbara west campus housing | 34.4175 | -119.8708 | 2/7/02 | NS | Urban edge | Y02 (< 1%) | |
| Santa Barbara off Ortega Ridge Rd. | 34.4221 | -119.6113 | 2/7/02;<br>2/10/03 | ST | Urban edge | Y02 (> 1%) | No seeds observed in 2003, population partially controlled |
| Toro Canyon Rd. at horse trail | 34.4241 | -119.5753 | 2/7/02;<br>4/21/02;<br>2/10/03 | ST/NS | Live oak woodland | Y02 (> 1%)<br>Y03 (> 1%) | |
| Toro Canyon Creek at 101 frontage intersection | 34.4161 | -119.5756 | 2/10/03 | ST/NS | Sycamore willow riparian | Y03 (> 1%) | Copious seed production, used for seed germination and viability tests |
| Carpenteria Creek off Arbol Verde St. | 34.3932 | -119.5114 | 2/10/03 | ST/NS | Sycamore willow riparian | Y03 (> 1%) | |
| **LOS ANGELES** | | | | | | | |
| Leo Carrillo State Park | 34.0479 | -118.9335 | 2/6/02;<br>2/8/01 | NS | Sycamore riparian woodland | Y01 (27%) | Exirpated 2002 |
| Zuma Beach | 34.0159 | -118.8180 | 2/8/01;<br>2/6/02;<br>2/9/03 | NS | Willow riparian | Y01 (34%)<br>Y02 (< 1%)<br>Y03 (< 1%) | |
| Pacific Palisades | 34.0528 | -118.5526 | 2/8/01;<br>4/21/02;<br>2/9/03 | ST/NS | Live oak woodland | Y01 (53%)<br>Y02 (> 1%)<br>Y03 (> 1%) | |

**Table C-1. Cape Ivy Seed Collection Locations in 2001, 2002 and 2003.**

| COUNTY Location | Latitude | Longitude | Collection Date(s) | ST/NS | Community Types | Large Seed and Estimate of % Filled | Notes |
|---|---|---|---|---|---|---|---|
| Temescal Canyon | 34.0511 | -118.5285 | 2/8/01;<br>2/6/03 | NS | Sycamore willow riparian | Y01 (58%)<br>Y03 (> 1%) | |
| Will Rogers State Park | 34.0509 | -118.5114 | 2/8/01;<br>2/6/02;<br>2/6/03 | ST/NS | Scrub and Eucalyptus | Y01 (74%)<br>Y02 (> 1%) | Population eradicated, no seed production in 2003 |
| San Dimas | 34.1659 | -117.7686 | 2/7/01;<br>2/5/02;<br>2/6/03 | NS | Red alder riparian | Y01 (31%)<br>Y02 (> 1%) | Extirpated in 2003 by fire and erosion after flooding |
| Monrovia Canyon Park | 34.1736 | -117.9890 | 2/7/01;<br>2/6/03 | NS | Red alder riparian | Y01 (53%)<br>Y03 (< 1%) | |
| Glendale Elinita Rd. | 34.2068 | -118.2456 | 2/7/01;<br>2/6/02;<br>2/6/03 | NS | Live oak woodland | Y01 (37%)<br>Y02 (< 1%)<br>Y03 (> 1%) | |
| Rio Honda | 34.0365 | -118.0747 | 2/8/02 | NS | Oak woodland | N02 | |
| Palos Verdes, 3625 Palos Verdes Rd. North | 33.8015 | -118.3681 | 2/7/03 | NS | Urban edge | N03 | |
| **SAN DIEGO** | | | | | | | |
| Bonsall Preserve | 33.2998 | -117.2265 | 2/01;<br>2/8/02;<br>2/8/03 | NS | Willow riparian and Eucalyptus | Y01 (58%)<br>Y02 (> 1%)<br>Y03 (> 1%) | Population treated with herbicide in 2002 or 2003, seeds collected from small living remnants |
| Fallbrook, Heyneman Hollow | 33.3724 | -117.2071 | 2/8/03 | NS | Live oak woodland and Sycamore riparian | N03 | |
| Leucadia | 33.0670 | -117.2978 | 2/8/03 | NS | Urban edge | N03 | |
| Marian Bear County Park | 32.8376 | -117.2265 | 2/10/02;<br>2/9/03 | NS | Live oak woodland | Y02 (< 1%) | No seeds observed in 2003 |
| Balboa Park | 32.7450 | -117.1559 | 2/10/02 | NS | Urban edge, Eucalyptus | Y02 (> 1%) | |