TESTING SUBSPECIES LIMITS IN *MONARDELLA VILLOSA*

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ABSTRACT

Testing Subspecies limits in *Monardella villosa*

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Several subspecies of *Monardella villosa* (California Coyote Mint) have been distinguished on the basis of leaf thickness, shape, and trichome characteristics, yet many intermediates are known. We investigated morphological differences in natural populations of two subspecies (*M. v.* subsp. *villosa* and *M. v.* subsp. *franciscana*) in the Scott Creek watershed, north of Davenport, in Santa Cruz County, CA. *Monardella villosa* subsp. *franciscana* grows in coastal scrub in gulches and ocean terraces whereas subsp. *villosa* grows at more protected inland sites. Morphological difference between subspecies may be adaptations to these different habitats. I grew plants in a common garden at Cal Poly, San Luis Obispo to determine if the morphological differences were genetically based. I also conducted a reciprocal transplant of the two subspecies between inland and coastal populations to determine if they are locally adapted.

The morphological differences (leaf hair density and length as well as leaf base angle) between subspecies were maintained in the common garden, yet no patterns of local adaptation were observed in germination or survival of the subspecies in reciprocal transplants in the first year. However, *Monardella* is a perennial plant and fitness differences may exist in later life stages that I have not yet measured.

Keywords: Reciprocal transplant, *Monardella*, Speciation, Morphology

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Chapter 1

INTRODUCTION

The foundation of taxonomy, a science concerned with description, identification, nomenclature and classification, is in the patterns of similarities and differences. The acorns of an oak, the legume of a pea, the fragrance of a mint and the cone of a conifer help us group together large number of species based on shared characteristics, or synapomorphies. There are groups, however, in which morphology is difficult to interpret. This can be due to a lack of morphological variation, highly variable morphology within species, or convergence on similar morphologies. Groups of organisms that cannot be easily classified based on their morphology have been problematic for taxonomist to assign names based on their evolutionary relationship.

The genus *Monardella* Benth. is diverse and widespread in California, with over 30 species and 50 taxa recognized (Elvin and Sanders, 2009). Diverse morphology within and between taxa combined with a wide range of climate and soil habitats make this group taxonomically difficult (Sanders et al., 2012). The generally terminal clustered cyme (glomerule), made of flowers with 5 lobed corollas, 4 stamens and subtended by a whorl of bracts distinguish *Monardella* from other Genera in Lamiaceae. Plant pubescence, habit, bract morphology and annual vs. perennial life cycles all help distinguish species within *Monardella*. The highly variable morphology for each of these characters has resulted in taxonomic uncertainty often with many synonyms for one taxon. The difficulty in interpreting the morphology of *Monardella* could be because the

genus is a recent radiation in California. Preliminary genetic analyses on *Monardella* have revealed little variation in inter-transcribed spacer (ITS) sequences, estimated to be less than 5 mya (Prince, 2009).

Monardella villosa Benth. is one of the variable species in the genus, with subspecies: *franciscana*, *obispoensis* and *villosa* currently recognized (Sanders et al., 2012). The subspecies have been recognized based on differences in pubescence characteristics and leaf shape. Two subspecies, *Monardella villosa* subsp. *franciscana* (Elmer) Jokerst and *M. v.* subsp. *villosa* grow closely together in the coastal ranges from Monterrey to Mendocino county, CA. *Monardella v. f.* usually grows in terraces and gulches adjacent to the coast, whereas subsp. *villosa* typically grows at more inland sites. *Monardella villosa* subsp. *franciscana* has thick triangular leaves that are often wooly pubescent abaxially, which distinguishes it from subsp. *villosa* which has thinner leaves with an obtuse leaf base angle (Sanders et al., 2012).

In this study I investigated the genetic basis of phenotypic variation between subsp. *villosa* and *franciscana* in California. I conducted a greenhouse common garden and a field reciprocal transplant experiment to test whether the morphological differences are genetically based and adaptive in their local habitats. Phenotypic measurements were made on wild and greenhouse grown plants to test for morphological plasticity. Germination and survival were measured for 16 months in a reciprocal transplant to test for any adaptive divergences between populations.

I hypothesize that the differences in morphological characters recognized in *Monardella villosa* are genetically based, and adaptive to their niche environments. If these two subspecies have different morphologies due to selection in different but

adjacent habitats, I have the opportunity to study how early divergence might ultimately lead to speciation. I set up a reciprocal transplant to study this adaptive hypothesis.

The basis for determining local adaptation of intraspecific taxa is accomplished by comparing fitness measures of local and immigrant genotypes in each other's habitat. Local adaptation can be quantified by comparing the germination, survival, flowering and seed set along with other ecological interactions, such as herbivory and pollinator visitation, in a reciprocal transplant. Strict local adaptation can be determined if the local form does better relative to the immigrant in both experimental sites. A lesser degree of local adaptation is measured if taxa do better in their local habitat relative to the away habitat, but not better in their local habitat relative to the foreign plants (reviewed in Sobel et al., 2010).

MATERIALS AND METHODS

Study Species

Monardella villosa (Lamiaceae) was described by George Bentham (1844) based on a collection from Bodegas, CA. The current taxonomic treatment recognizes 3 subspecies found in western California from Santa Barbara County to Oregon (Sanders et al., 2012). The species is a subshrub, perennial, with glomerule inflorescences that flower from late spring to early summer. *Monardella villosa* subsp. *villosa*, subsp. *franciscana*, and subsp. *obispoensis* differ in leaf shape and pubescence characteristics. Subspecies *franciscana* has a more triangular leaf shape, truncate leaf base, and typically more abaxially woolly-pubescent leaf surface than subsp. *villosa* (Jokerst, 1992) (Figure 2). *Monardella villosa* subsp. *obispoensis* is distinguished from the other two by the abundant branched trichomes on the abaxial leaf surface. *Monardella villosa* subsp. *villosa* has the largest

range distributed from the Klamath range in northern California throughout the inner and outer coast ranges to Santa Barbara County. Subspecies *franciscana* occurs from the north coast through the central coast regions near the ocean. Finally, subspecies *obispoensis* occurs in the central coast region (Sanders et al., 2012). These regions follow the region designations of the Jepson Manual (Baldwin et al., 2012)

Study Site

Swanton Pacific Ranch, approximately fourteen miles north of Santa Cruz along Highway 1, encompasses 3200 acres donated to Cal Poly in 1993 by Al Smith (Dietterick, 2011). The ranch property contains over 12% of California's native and introduced flora, including many rare and endangered taxa (West, 2013). The ranch is also diverse geologically with more than 26 soil map units (Staff, 2013). Scotts Creek and its tributaries flow through the ranch property creating many riparian and wetland areas. The ranch has evergreen forests of Douglas fir, coast redwood, California nutmeg, and Monterey pine; mixed evergreen forest with Shreve oak, coast live oak, Tan-bark oak, California Buckeye, and California Bay. The ranch also contains grasslands, coastal scrub, and chaparral and spans elevationally from sea level to over 1,000 feet. Both subsp. *villosa* and *franciscana* occur on Swanton Pacific Ranch (Figure 1).

Figure 1: Map of common garden locations used in the reciprocal transplant and populations used in the experiments.

Greenhouse and Field Measurements

Seeds were collected by Mr. Jim West in the summer of 2011 from locations on and around Swanton Pacific Ranch property. Twenty-five separate seed collection represent the 17 populations. Seed collection locations, dates, and site descriptions are in appendix A.

Seeds used in the greenhouse common garden were stratified in moist petri dishes in a 2 degree celsius refrigerator and planted in a 1:1:1 peat, perlite and sand mix in 4” pots at Cal Poly’s plant conservatory greenhouse. I watered plants for 10 minutes four times a week, and reduced to three times per week upon germination. I separated the seedlings into individual 4” pots before they reached 2.5 inches, and watering was further reduced to twice a week to keep plants alive.

The plants grown in the greenhouse were used for two purposes. First I measured leaf pubescence and leaf base angle of each population using two mature expanded leaves from separate nodes of three different plants. I used the remaining plants grown in the greenhouse for a second reciprocal transplant on Swanton Pacific Ranch for future experimentation (Data not shown here).

I also measured leaf shape and pubescence from native populations on Swanton Pacific Ranch and compared them with the greenhouse grown plants to determine the genetic basis and plasticity of traits. I chose plants from all populations of the original seed collection on January 12th, 2013 for the field morphological measures. One branch from each individual in a population was collected. I randomly chose three branches per population and measured leaf base angle, trichome density and hair length on two mature leaves from two separate nodes per branch. After I made morphological measurements on

the wild specimens I pressed and accessioned the plants into the Hoover Herbarium (OBI) on the Cal Poly campus (Appendix C).

I measured leaf base angle by the angle between the petiole and leaf base (Figure 2). I measured leaf hair density, on both adaxial and abaxial surfaces, by taking a leaf punch, counting the trichomes and dividing the total number by the area of 28.27mm². Leaf hair length was recorded by measuring three trichomes found on expanded leaf tissue of each sample and recording the average. Elevational data and distance from shore measurements were made using Google Earth.

Figure 2: A & B): Images of the leaf surfaces of *Monardella villosa* subsp. *villosa* and *Monardella villosa* subsp. *franciscana*. C): Leaf base angle. D): pubescence characteristics of both subspecies adaxial and abaxial side.

Reciprocal Transplant Measurements

I chose the plots for the reciprocal transplant to represent suitable habitat for *Monardella* and installed them near natural populations. The plots found at the inland site represent common habitat for subsp. *villosa* are found along RW Pozzi Ranch Road on Swanton Ranch. These inland plots are numbered one through four and can be found on the west facing slope located on the east side of Pozzi Road. Plots one and two occur on an exposed slope near the forest margin in a sunny location approximately 10 meters from each other. Plots three and four are approximately 200 meters north along Pozzi Road on a slope near a forest margin in a much more shaded area. I numbered the coastal plots representing common subsp. *franciscana* habitat five through eight located in Big Willow gulch on the western terraces of Swanton Pacific Ranch approximately two kilometers west from the inland plots. The plots are on the north facing slope of Big willow Gulch spaced approximately ten meters from each other (Appendix B).

The same seed collections used in the greenhouse common garden were also used in the reciprocal transplant study at Swanton Pacific Ranch. I glued forty individual seeds from each seed source collection to toothpicks using Elmer's wood glue. I spray painted the toothpicks different color combinations to distinguish each plant family for census observations. I designed the plots using a random number generator with 5 seeds per seed source collection (1000 total) assigned to each of eight plots, four inland and four coastal (Figure 1). Rebar, chicken wire and light gauge wire were used to build cages to discourage herbivory by deer, cattle or other small mammals. I also drove T-posts around the coastal plots to deter cattle from trampling each plot.

The seeds in the reciprocal transplant were planted in November of 2011. The

location of each seed was assigned randomly and resulted in a 12 x 11 grid that was .75 meter wide and 1 m long. I censused the seeds every 1-2 months to determine germination and survival success until March 1, 2013. The use of marked toothpicks greatly increased the accuracy of census dates, as the colors were used to double check the identity of each maternal family. On the last census date I marked the remaining plants with a permanent metal scratch label for ease of future work.

Soil Determination

The USDA's Natural Resources Conservation Service has conducted numerous soil surveys throughout the country and makes these data available at no cost to the public. Soils data for all of Santa Cruz County were imported to the map document and polygons were created based on the various soil types listed in the attribute table. As with slope and aspect, the intersect tool was used on the population's coordinate layer to determine which soil type each population had present at its site.

To determine the soils that each subspecies was associated with I collected coordinate information using a Garmin GPS unit of populations of *Monardella* throughout Swanton Pacific Ranch. Coordinates were imported into ArcMap 10.1 as a separate layer. A digital elevation model (DEM) was obtained from Cal Poly's data services (G drive) and imported to the map document. The DEM had an accuracy of 1m2. The aspect tool was used to create a layer of 9 different polygon types representing the following aspects: flat, N, NE, E, SE, S, SW, W, and NW. The slope tool was also applied to create a layer containing 14 different polygon types representing the following slopes: 0, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, and 65 degrees. The intersect tool was then used on the coordinate layer to determine which polygon type in both the aspect

and slope layers that each populations point fell within. From this I found corresponding aspect, slope data and soil type for each population in our study area.

Statistical Analysis

To determine the environmental and genetic influences on traits I compared morphological measurements between field collected and greenhouse grown specimens (Appendix D). I compared the trait values of greenhouse and field measurements using a one way comparison of means in JMP (JMP, Ver 10.0 SAS Institute Inc., Cary, North Carolina, USA). This generated T-values to determine significance of difference between means and were graphed in JMP.

I analyzed the reciprocal transplant data in excel and JMP. The percentage alive for each census date value was calculated as the number germinated and alive in the transplant divided by the total number of seeds planted for each population. Survival was calculated by taking the number alive per population and dividing it by the total number of seeds that germinated. I then compared these by using a one way comparison of means to determine significance using a student's t-test.

I double checked the subspecies circumscription of populations using a discriminant analysis using the leaf base angle, pubescence density and trichome length of each population on JMP (Appendix G). The results all agreed except for population 15, so I chose the circumscription result using the greenhouse data.

RESULTS

I found that across all traits measured in the greenhouse and field collected specimens, the significant differences found in the field between subspecies remained significantly different in the greenhouse (Figure 3). *Monardella villosa* subsp.

franciscana has longer trichomes on the adaxial and abaxial leaf surface, has a greater trichome density on the abaxial leaf surface, and has a more truncate leaf base angle than subsp. *villosa*. There is no difference in hair density on the adaxial leaf surface between the subspecies in the field, but in the greenhouse subsp. *franciscana* had significantly higher adaxial hair density than subsp. *villosa* (Figure 3).

There is a significant ($P < .05$) difference between the subspecies distance from the ocean. On average, subsp. *franciscana* grew closer to the shoreline than subsp. *villosa*. *Monardella v. v.* had a significantly larger angle between the petiole and leaf base than *M. v. f.*, and this difference was maintained in the greenhouse. Leaf hair length is significantly longer on the adaxial and abaxial surface of subsp. *franciscana* ($P < .0001$), and the greenhouse and wild measurements remained unchanged within both subspecies. Leaf hair density on the adaxial surface between subspecies in the field were not significantly different, however, in the greenhouse, subsp. *franciscana* had a much higher leaf hair density than the field measurements while subsp. *villosa* remained the same. Leaf hair density on the abaxial surface of subsp. *franciscana* was higher ($P < .0001$) in field and greenhouse measurements. The plants grown in the greenhouse had much higher leaf hair density than in the wild ($P < .0001$) (Figure 3).

Figure 3: Greenhouse vs. field characteristics based on subspecies delineation.

A) Distance from ocean. B) Leaf base angle. C) Adaxial leaf hair length. D) Abaxial leaf hair length. E) Adaxial leaf hair density. F) Abaxial leaf hair density

Survival, Germination and Subspecies

There was no difference in germination and survival between subspecies in the reciprocal transplant at any census collection at either location (Appendix E). The population means were measured as a percent alive of total seeds planted. Germination peaked in February and March of 2012 at both sites, while the most dramatic seedling mortality occurred from June through September of 2012 (Figure 4).

Difference in germination of subspecies between locations was significant for both subsp. *villosa* and subsp. *franciscana*. Germination was significantly higher at the coastal site ($P < .0014$). Survival at the inland site was significantly higher than at the coastal location for both subspecies ($P < .05$) (Figure 5). This indicate a harsher environment for young plants immediately adjacent the ocean.

Figure 4: Percent germinated and alive by subspecies at different time points during the reciprocal transplant

Figure 5: A) Germination and B) survival of *Monardella villosa* at inland and coastal plot locations

DISCUSSION

This study has shown that populations of *Monardella villosa*, hypothesized to represent two subspecies in the Santa Cruz area, have genetically based differences for leaf hair length, abaxial trichome density and leaf base angle. This shows that populations on Swanton Pacific Ranch have genetic differences that determine distinct morphologies of the two subspecies. However, these characters do not appear to be adaptive in the different environments for germination or early life survival. The successful establishment of subspecies in both their ‘home’ and ‘away’ environments means that no barriers have evolved to block either subspecies from germinating or surviving the first year and a half of their life in habitats where the other subspecies occur. Therefore, the distribution of the two subspecies cannot be explained by what I measured. Results of the reciprocal transplant indicated that both subspecies of *M. v.* survived better at inland sites, suggesting a harsher habitat at the immediate coastal habitats.

Morphological Plasticity in Wild and Greenhouse Plants

Genetically based variations in leaf characters could mean there is an adaptive divergence (Housman et al., 2002). I found that differences in morphologies measured on field collected plants remained unchanged when plants were grown in a common garden except adaxial trichome density. This suggests that most of the phenotypic variation between populations on Swanton Pacific Ranch are genetically based, whereas trichome density is environmentally plastic (Figure 3). Leaf trichome density and length have been shown to affect transpiration rate and gas exchange across diverse lineages of plants (Brewer et al., 1991).

Brewer et al. (1991; 1997) have shown that leaf pubescence density can affect the

frequency and duration of water on leaf surfaces (leaf wetness). Increased leaf wetness has been shown to negatively affect plants by decreasing photosynthetic rate (Ishibashi and Terashima, 2006), increasing disease susceptibility (Doss et al., 1987; Hartman et al., 1999), and decreasing growth rate (Tullus et al., 2012). The hairier subspecies *franciscana* typically found near the coast could be an adaptive divergence in response to the coastal fog influence. The longer and more dense trichomes of subsp. *franciscana* could hold the water droplets further away from the leaf surface, allowing for gas exchange to occur through stomata, and increase transpiration. The hairs may also function in UV protection (Choinski and Wise, 1999) and/or creating a boundary layer decreasing the rate of water loss (Ehleringer and Mooney, 1978).

Leaf trichome production may also have associated costs (Mauricio, 1998). In a study of *Arabidopsis kamchatica* in Alaska the more glabrous populations produced significantly more fruit than the pubescent populations, showing a selection for glabrousness (Steets et al., 2010). The reduced trichome density and length may benefit subsp. *villosa* in a similar fashion. Adaxial leaf hair density was not significantly different in field collected specimens, but subsp. *franciscana* had significantly higher trichome density in greenhouse grown specimens (Figure 3). This shows that adaxial leaf hair density may be more plastic than other features. Leaf hair density has been implicated in several adaptive studies (Björkman et al., 2008; Steets et al., 2010), and the environmental plasticity may allow this early to mid successional species a higher survival rate in the heterogenous environments it is found in.

Reciprocal Transplant Discussion

Local adaptation was not detected in my reciprocal transplant study of *M. v.* Germination and survival did not differ between subspecies at the coastal or inland plots. The morphological differences found to be genetically based, did not correlate with a higher germination or survival for either subspecies. However, these measurements are only part of the plants life cycle, and local adaptation may be measured in another life stage. The question remains, why are there different forms of *M. v.* on Swanton Pacific Ranch? And why do they occur where they do? If there is no selection keeping the subspecies distinct, why isn't the homogenizing effect of gene flow creating a more morphologically similar set of populations?

The percentage of plants that germinated at the coast was higher, perhaps due to the increased moisture brought in by the maritime fog. The inland plants tended to survive better, likely due to the more loamy soils at inland sites relative to the sandier bonnydoon soils of the coastal site (Appendix F). The harsher, windier conditions of the coast may also have played a role in the reduced survival of plants in the common gardens. This pattern of higher seedling mortality at the coast may play more of a role in local adaptation in later life stages by affecting the flowering and seed success of each subspecies.

The distributional pattern of *M. v.* may have alternate explanations. The prevailing winds on Swanton Pacific Ranch from the Northwest may allow seeds of *M. v. f.* to move inland, while blocking *M. v. v.* from migrating to the immediate coastal environments. The calyx of *M. v.* is persistent in fruit, and become dried, scarious and reflexed which I speculate may function in wind dispersal of seed in this species. The distribution of these

subspecies may also be based on a historical or novel selection pressures such as extinct herbivores or recently introduced pests (Eastman et al., 2009).

While local adaptation hypotheses are commonly used to explain distributional patterns, studies showing strict local adaptation are not found a majority of the time (Leimu and Fischer, 2008). Local adaptation can be hindered by gene flow. If new suites of genes enter a population that are undergoing selection, the result can be a loss of specialization at the genetic and phenotypic levels (Kawecki and Ebert, 2004; reviewed in McKay et al., 2005). Because of the close proximity of these subspecies on Swanton Pacific Ranch gene flow is likely to occur and introgression a possibility.

Potential Future Studies

Two reciprocal transplants are now in place on Swanton Pacific Ranch, and future students will have the opportunities to study other potential selection pressures keeping subsp. *villosa* and subsp. *franciscana* apart. These pressures may include survival, pollinator bias, flowering success, hybrid viability, and seed set. There is a difference in odor between the two subspecies that warrants further investigation. Several undergraduates have committed to continue observation and data collection of the reciprocal transplant plots.

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APPENDICES

- A. Seed collection location data
- B. Locations of plots used in experiment
- C. List of accessioned plants in Hoover Herbarium (OBI)
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APPENDIX A

Seed collection location

Family #	Population	Species	Date	GPS	Elv. (M)	Description
1	4	M.v.f	10/17/11	37°03'56.36"N/122°15'08.90"W	271	China ladder Gulch (WF)
2	3	M.v.f	9/27/11	37°04'14.10"N/122°15'19.27"W	308	Big Willow gulch (WF)
3	4	M.v.f	10/17/11	37°03'56.36"N/122°15'08.90"W	271	China ladder Gulch (WF)
4	17	M.v.	10/5/11	37°04'41.94"N/122°15'00.09"W	339	Scotts Creek (EF) Buckeye ridge
5	14	M.v.	10/11/11	37°05'09.54"N/122°14'47.95"W	299	Scotts Creek /Schoolhouse ridge complex
5	14	M.v.	10/11/11	37°05'01.42"N/122°14'46.38"W	197	Scotts Creek /Schoolhouse ridge complex
6	8	M.v.v.	10/15/11	37°05'14.65"N/122°14'54.81"W	148	Scotts Creek Ws/Wf RB over purdy rd by slid
7	6	M.v.f.	9/27/11	37°02'32.48"N/122°13'19.78"W	70	Scotts creek/ WF brushy slope near casa ver
8	13	M.v.	9/24/11	37°05'44.55"N/122°14'12.98"W	770	Scotts creek/EF slope near seymore field
9	8	M.v.v.	9/24/11	37°05'13.78"N/122°14'55.44"W	148	Scotts Creek/Purdy rd, near slide
10	13	M.v.	9/24/11	37°05'41.88"N/122°14'17.51"W	933	Scotts Creek/Top of seymore hill/SF
11	15	M.v.	9/23/11	37°05'08.32"N/122°14'26.65"W	499	Scotts Creek/Schoolhouse ridge/Mill crk side

12	3	M.v.f	9/21/11	37°04'13.87"N/122°15'21.31"W	274	WF slope of Big willow gulch
13	12	M.v.	9/24/11	37°05'49.77"N/122°14'52.00"W	406	Scotts creek/s-facing roadbank
14	10	M.v.v	9/27/11	37°03'52.45"N/122°13'39.60"W	75	Scotts creek/WF brush slope
15	11	M.v.v.	10/13/11	37°02'57.21"N/122°12'51.76"W	439	Scotts creek/SF rdbank near NF of Q. creek
16	5	M.v.f	9/28/11	37°03'16.30"N/122°14'29.72"W	236	WF slope above lower prairie gulch
17	17	M.v.	10/4/11	37°04'44.90"N/122°14'58.41"W	322	Scotts creek/SEF edge of buckeye grove ridg
17	17	M.v.	10/4/11	37°04'44.41"N/122°15'00.43"W	338	Same as above
18	1	M.v.f.	9/30/11	37°05'12.57"N/122°15'56.16"W	261	WF oak woodland above Las trancas arroyo
19	16	M.v.	10/11/11	37°05'09.54"N/122°14'47.95"W*	299	See 5
19	16	M.v.	10/11/11	37°05'01.42"N/122°14'46.38"W*	197	see 5
20	7	M.v.v	10/15/11	37°06'41.73"N/122°15'33.20"W	944	Scotts creek/SF upper laird gulch
21	1	M.v.f.	9/30/11	37°05'12.57"N/122°15'56.16"W	261	WF oak woodland above Las trancas arroyo
22	2	M.v.f.	9/30/11	37°05'00.21"N/122°15'51.24"W	292	SF hillside, coastal scrub above washout turr
23	3	M.v.f.	9/2/11	37°04'13.99"N/122°15'19.59"W	305	WF slope above Lower big willow gulch
24	3	M.v.f	9/2/11	37°04'13.99"N/122°15'19.59"W*	305	WF slope above Lower big willow gulch
25	9	M.v.v	9/10/11	37°04'46.18N/122°14'46.08W	112	Scotts creek/rdbank above swanton rd
26		M.v.v.	3/4/12	37°05'11.76"N/122°14'50.38"W	367	Scotts Creek/WF ridge overlooking squirell fl road

Appendix B

Locations of plots used in experiment

Plot	Latitude	Longitude
		-
1	37.08529551	122.2470895
		-
2	37.08534403	122.2471552
		-
3	37.08655564	122.2487863
		-
4	37.08667139	122.2487782
		-
5	37.08667139	122.2487782
		-
6	37.07057627	122.2555322
		-
7	37.07056984	122.2554384
		-
8	37.07064032	122.2554059

Appendix C

List of accessioned plants in Hoover Herbarium (OBI)

Family #	Population #	Accession number (OBI)
5	14	77164
6+9	8	77165
10	13	77166
7	6	77167
8	13	77168
15	11	77169
4	17	77170
11	15	77171
25	9	77172
22	2	77173
2,12,23,24	3	77174
17	17	77175
1+3	4	77176
13	12	77177
16	5	77178
18+21	1	77179
19	16	77180

Appendix D

Population mean morphology measures

From	Pop	n	pop mean hr len top	pop mean LBA	pop mean hr len bot	pop mean den top	pop mean den bot	pop mean distance
F	1	6	1	89.83333333	1.166666667	7.310458672	7.062846363	468
F	2	6	0.333333333	90	0.583333333	5.65970994	5.223440632	408
F	3	6	1.333333333	90	1.333333333	7.39889164	7.180756986	328.8333333
F	4	6	1.416666667	90	1.458333333	8.182997288	7.841056479	289
F	5	6	1.125	92.5	1.125	5.615493456	5.305978069	290
F	6	6	1	90	0.916666667	5.022992572	5.836575876	744
F	8	6	0.5	90	0.333333333	9.031953779	5.777620564	1743
F	9	6	0.5	117.5	0.291666667	5.223440632	3.932319302	1478
F	11	6	0.708333333	96.66666667	0.75	5.305978069	4.174036081	1731
F	12	6	0.791666667	94.16666667	0.541666667	4.067916519	3.478363401	2428
F	13	12	0.875	87.91666667	0.854166667	8.126989742	8.701804033	3111
F	14	6	0.5	90	0.25	11.908973	5.742247377	1828
F	15	6	0.52	86.66666667	0.39	6.211531659	5.779978776	2264
F	16	6	0.75	90	0.583333333	6.473293244	5.689187596	1742
F	17	12	0.616666667	100.1666667	0.479166667	6.673741304	4.987619385	1165.5
G	1	5	0.62	91.5	0.64	7.385921472	11.27697206	468
G	2	3	0.333333333	93	0.433333333	13.25315411	18.51196793	408
G	3	8	0.857142857	92.61904762	1.021428571	10.22285108	11.46091263	318.75
G	4	4	1.333333333	99.48384615	1.083333333	6.437920057	6.060606061	289
G	5	1	2	91	1	8.48956491	21.22391227	290
G	6	2	1.125	92	0.9375	6.720905554	11.28404669	744
G	7	3	0.383333333	93	0.266666667	7.145383799	10.28180639	2556

G	8	5	0.357	103.8125	0.3125	5.376724443	6.685532367	1759.2
G	9	3	0.3	100	0.2	11.86180875	11.93255512	1478
G	10	2	0.5	95	0.5	4.598514326	5.836575876	1953
G	11	2	0.4	105	1	3.5726919	3.961796958	1731
G	12	2	0.4	92	0.4	3.148213654	5.235231694	2428
G	13	4	0.9	91.5	0.7125	8.896356562	9.603820304	3111
G	14	3	0.291666667	94.04761905	0.341666667	4.339110954	3.843886334	1828
G	15	2	0.5	95	0.5	6.048814998	7.251503361	2264
G	16	3	0.433333333	85	0.4	12.09763	19.95047754	1742
G	17	6	0.616666667	105.1707317	0.433333333	7.593444169	6.496875369	1165.5

Appendix E

Reciprocal transplant data

Region	assigned ssp.	N Rows	Mean(Percent	Mean(Percent	Mean(Percent	Mean(Percent	Mean(Percent	Mean(Percent	Mean(Percent	Mean(Percent	Mean(Percent
C	M.v.f.	32	0	36.25	39.0625	35.78125	33.75	28.28125	19.84375	19.84375	10.15625
C	M.v.v.	36	0	42.222222	43.611111	37.222222	34.444444	25	15.277778	15.277778	8.611111
I	M.v.f.	32	1.09375	25.4769737	26.8914474	25.9457237	22.6644737	20.0082237	15.3207237	14.6957237	14.8519737
I	M.v.v.	36	3.611111	23.611111	22.5308642	21.558642	16.666667	15.555556	11.111111	11.111111	9.722222

Appendix F

Soil Data Table

Population	ObjectID	Name	Slope (Degrees)	Aspect	Soil Code	Soil Type	Elevation (feet)	X	Y
8	1	M.v.f.	15	SE	146	Isos Loam	651.345337	-122.236	37.0975
	2	M.v.f.	30	SE	118	Complex	652.975525	-122.236	37.09705
	3	M.v.f.	35	E	118	Complex	767.29425	-122.237	37.09574
	5	M.v.f.	15	SE	146	Isos Loam	501.28064	-122.235	37.09313
	6	M.v.f.	15	E	113	r Complex	445.096924	-122.235	37.09171
	7	M.v.f.	10	S	146	Isos Loam	438.826233	-122.235	37.09136
	8	M.v.f.	45	E	113	r Complex	874.739624	-122.237	37.09459
	9	M.v.f.	Unknown	Unknown	118	Complex	Unknown	-122.265	37.08691
	10	M.v.f.	Unknown	Unknown	118	Complex	Unknown	-122.265	37.08613
	11	M.v.v.	Unknown	Unknown	118	Complex	Unknown	-122.266	37.08598
18 & 21	12	M.v.f.	20	SW	106	amy Sand	440.747711	-122.261	37.08315
	13	M.v.f.	Unknown	Unknown	118	Complex	Unknown	-122.266	37.08683
	14	M.v.f.	Unknown	Unknown	169	Clay Loam	Unknown	-122.264	37.08339
	15	M.v.f.	5	E	113	r Complex	323.478394	-122.25	37.07832
	16	M.v.v.	25	E	113	r Complex	303.321045	-122.25	37.07914
	17	M.v.v.	0	SW	171	quel Loam	104.414894	-122.246	37.07949
	18	M.v.f.	5	NW	169	Clay Loam	199.97699	-122.246	37.08373
	19	M.v.v.	15	SE	118	Complex	313.495636	-122.247	37.08598
	20	M.v.v.	55	W	171	quel Loam	158.072327	-122.249	37.08716
	21	M.v.v.	50	NW	169	Clay Loam	176.016617	-122.249	37.0874
23 & 24	22	M.v.v.	0	SW	168	Clay Loam	522.583191	-122.241	37.08564
	23	M.v.v.	25	S	113	r Complex	422.261383	-122.248	37.09716
	24	M.v.f.	25	SW	142	Complex	958.438232	-122.238	37.09497
	25	M.v.v.	20	E	153	Complex	950.373474	-122.259	37.11159
	26	M.v.f.	20	NW	118	Complex	294.297913	-122.256	37.07052
	27	M.v.f.	20	NW	118	Complex	328.540039	-122.255	37.07055
	28	M.v.f.	40	NW	118	Complex	333.385742	-122.255	37.07058
	29	M.v.f.	35	NW	118	Complex	290.181976	-122.252	37.06566
	30	M.v.f.	35	NW	118	Complex	258.864471	-122.242	37.05453
	31	M.v.v.	0	N	170	quel Loam	64.500107	-122.228	37.06457
1 & 3	32	M.v.v.	35	SE	169	Clay Loam	411.850555	-122.214	37.04923
	33	M.v.f.	50	NW	169	Clay Loam	60.124996	-122.222	37.04236

Appendix G

Discriminant analysis data