

Soil nutrients trump intraspecific effects on understory plant communities

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Abstract Understanding the links between intraspecific genetic variation and patterns of diversity in associated communities has been the primary focus of community genetics or ‘genes-to-ecosystem’ research in ecology. While other ecological factors, such as the abiotic environment, have well-documented influences on communities, the relative contributions of genetic variation versus the environment to species interactions remains poorly explored. In this study, we use a common garden experiment to study a coastal dune plant community dominated by the shrub, *Baccharis pilularis*, which displays a morphological dimorphism in plant architecture. We found the differences in the understory plant community between erect and prostrate morphs of *Baccharis* to be statistically significant, but small relative to the impacts of nutrient additions (NPK and C additions), for the richness, cover, and biomass of the understory plant community. There were no significant interactions between *Baccharis* morphology and nutrient-addition treatments, suggesting the influence

of nutrient addition was consistent between erect and prostrate morphs. Moreover, we found no difference in overall plant community composition between *Baccharis* morphs, while NPK additions led to shifts in understory community composition compared to unfertilized shrubs. In sum, our results indicate that nutrients are the more important factor governing understory plant community structure in a coastal dunes ecosystem followed by intraspecific variation in dominant shrub architecture. Our results address a growing call to understand the extended consequences of intraspecific variation across heterogeneous environments in terrestrial ecosystems.

Keywords Architecture · *Baccharis pilularis* · Dunes ecosystem · Genotype-environment interactions · Plant community

Introduction

Communities are often dominated by a few species and the presence and abundance of these dominants can influence the diversity and composition of the subdominant community (Smith et al. 2004; Souza et al. 2011). Among dominant species, there can be variation in interactions with their subdominant counterparts, with competitive ability and resistance to species invasion depending on the identity of a given dominant (Knight et al. 2008). Similarly, genetic variation within dominant species can also have important consequences for other plant species (Booth and Grime 2003; Crutsinger et al. 2006, 2010). Indeed, a growing amount of research over the past decade has sought to understand the links between genetic variation at the population level and patterns of diversity in associated communities (Whitham et al. 2006). This research area, often

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referred to as community genetics or ‘genes-to-ecosystem’ ecology, has typically focused on ecological consequences of genetic variation within plant species (Hughes et al. 2008; Hersch-Green et al. 2011). For example, Vellend et al. (2010) showed that different genotypes of Kentucky bluegrass varied in their resistance to dandelion invasion. Similarly, variation in understory plant composition has been shown to be associated with a hybrid zone of overstory *Populus angustifolia* and *Populus fremontii* trees (Adams et al. 2011; Lamit et al. 2011). The main take-home message of the majority of these studies is that intraspecific variation matters for communities. An important next step in this research approach is asking, relative to what? (Hughes et al. 2008; Hersch-Green et al. 2011).

There are numerous other ecological factors, such as the abiotic environment, that have long been known to have strong influences on community assembly. Within plant communities, soil nutrient availability is one important factor that can limit productivity and govern community composition (Pierik et al. 2011). For example, many dune ecosystems are characterized by sandy and fast-draining soils, thereby creating a nutrient-poor environment (Maun 2009). This limitation in soil nutrients can, in turn, influence the abundance of competitive dominant species in sand dunes, as well as have direct impacts on the overall diversity of the plant community (Barbour et al. 1973; Lichter 1998). To date, there has been very little work comparing relative contributions of intraspecific variation versus nutrient availability for species interactions in local plant communities (Johnson et al. 2008).

In this study, we use a common garden experiment to study a coastal dune plant community dominated by a shrub, *Baccharis pilularis*, that displays a intraspecific dimorphism in plant architecture. We focus on plant architecture because it has been shown to be particularly important for shaping the understory abiotic conditions (Classen et al. 2007; Crutsinger et al. 2010). Specifically, we ask the following question: What is the relative importance of the intraspecific variation in *Baccharis* architecture versus soil nutrient availability for the richness, community composition, and productivity of the subdominant plant community?

Materials and methods

Study system

Baccharis pilularis De Candolle (Asteraceae, coyote bush) is a dominant, dioecious shrub growing along the coast of California. Two distinct architectural forms co-occur: an erect morph (ca. 1–4 m tall, sometimes classified as a distinct subspecies *B. pilularis* subsp. *consanguinea*) and a

prostrate morph (ca. 0.1–0.2 m tall, *B. pilularis* subsp. *pilularis*; Baldwin et al. 2012). The two architectural morphs differ in many traits relevant to interactions with other plant species, including height, branch length and number, and leaf size (Rudgers and Whitney 2006). Our prior work in this system has shown that this architectural dimorphism can influence abiotic conditions, with the understory of erect morphs having higher light availability, warmer soil surface temperatures, and a shallower litter layer compared to prostrate plants (Crutsinger et al. 2010). Corresponding with these differences, erect morphs had higher understory plant species richness and abundance compared to prostrate morphs (Crutsinger et al. 2010). The architectural dimorphism in *B. pilularis* has a strong genetic basis. Clones of the two forms planted in a common garden have retained architectural differences for over a decade (Crutsinger et al. 2010) and the progeny of single architectural parents segregated into both erect and prostrate offspring (Thompson et al. 1995; J. A. Rudgers, unpublished data). Moreover, the prostrate morph of *B. pilularis* is widely used as a groundcover in landscaping and retains its short stature across diverse environments (Ehler 1982). Though there is strong evidence for a genetic basis to differences in plant architecture, we acknowledge though that we did not compare individual genotypes or calculate heritability values in this study. Hereafter, we refer to these differences as ‘intraspecific variation’ or ‘morphological variation’ within *B. pilularis*, but we still discuss our results in the context of other studies interested in intraspecific genetic variation.

We conducted this study in the coastal sand dunes at the University of California-Davis Bodega Marine Reserve (BMR) in Bodega Bay, California (38°19′N, 123°04′W). The two architectural morphs of *B. pilularis* (hereafter referred to as simply ‘*Baccharis*’) account for similar percentage cover of the dunes at BMR (prostrate = 13 % cover, erect = 16 % cover). Like most dune ecosystems, the dunes at BMR are characterized as being very nutrient limited (Barbour et al. 1973). Taken together, the architectural dimorphism within co-occurring *Baccharis* shrubs and nutrient limitation in the BMR soil made it an ideal system to compare the community consequences of intraspecific variation versus soil nutrient availability.

Common garden experiment

In 1998, one of us (J. A. R.) established a common garden experiment at BMR to control for effects of environmental variation on the upright and prostrate architectures of *Baccharis*. The common garden occupied a 60-m × 60-m area, originally consisting of 250 plants (125 erect, 125 prostrate) in 1-m² plots spaced 3 m apart and arranged along fifteen 60-m transects. Plants were grown from cuttings of locally growing adult *Baccharis* plants of both genders of

the two morphs from randomly chosen locations throughout the 147-ha BMR reserve. Cuttings were started in the greenhouse prior to planting the garden, and each individual was assigned at random to plot locations within the common garden [for further details on the common garden see Rudgers and Whitney (2006)]. Plots were hand-weeded for the first year and then understory plant species have been allowed to colonize from 1999 until the present.

In March 2010, of the original plants, ~130 had survived in the common garden. There was no significant difference in percent mortality between morphs (erect = 44 %, prostrate = 56 %; $\chi^2 = 1.312$, $df = 1$, $P = 0.252$). For this study, we randomly chose 65 individuals, 32 erect morphs and 35 prostrate to be used in a soil nutrient manipulation. These shrubs were approximately evenly split between male and female plants (erect *male* = 18, *female* = 13; prostrate *male* = 17, *female* = 19). We did not include gender as a factor in this study, as our prior work showed minimal influence of gender on understory plants (Crutsinger et al. 2010). Nutrient-addition treatments included: (1) additions of a slow-release NPK fertilizer (14:14:14 Apex Nursery Fertilizer, Simplot, Lathrop, CA) at 20 g/m² or ~3 μg N, P, K per gram soil; (2) additions of C applied as sucrose at a rate of 150 g C/m² beginning in March and repeated every 60 days; and (3) an un-amended control. Application of sucrose, which is 46 % C in a molecular form readily available to microbes, results in immobilization of plant-available N in the soil. Addition rates are consistent with other studies investigating controls of N and C on plant population and community dynamics (e.g., McLendon and Redente 1992; Sanders et al. 2007).

Preliminary soil analysis showed that our nutrient additions were within the range experienced by the plant community in the dunes. We collected soil samples from beneath prostrate ($n = 9$) and erect ($n = 9$) shrubs in the common garden by first scraping away the litter layer and then using 1.5 \times 10-cm soil core. Soil samples were ground to a fine powder by hand using a mortar and pestle. Sub-samples of each material type were then analyzed for total C and N in a soil elemental analyzer (NC 2500; Carlo-Erba, Milan) at the University of California, Berkeley, using acetanilide (10.36 % N and 71.09 % C) as a reference standard. Soils of these dunes were almost entirely sand with very low concentrations of nutrients (mean N = 0.08 %; mean C = 1.1 %; mean C:N = 12.29). We observed no differences in either initial soil C ($t = -0.25$, $P = 0.798$) or N ($t = -0.08$, $P = 0.930$) content, or the C:N ratio ($t = 0.207$, $df = 16$, $P = 0.838$), between the two *Baccharis* morphs. However, soil N varied 6.4-fold among all our samples, or between 3.0 and 19.2 μg N/g dry soil, which is consistent with natural variation reported by other studies at BMR. For example, Alpert and Maron (2000) observed variation of

11.7–20.1 μg N/g dry soil in the grasslands immediately adjacent to our common garden. We estimate that our fertilization treatments increased N availability by ~25 %, based on the average of the natural variation (11.1 μg N/g dry soil) observed in our preliminary soil analyses, with a potential range of 15–200 %.

In spring of 2011, fourteen months after beginning the nutrient-addition experiment and at the peak of growing season, we sampled the richness, cover, and biomass of all understory plant species, including native and exotic species, under each *Baccharis* shrub. To do this, we randomly placed a 15 \times 15-cm quadrat under each bush and visually estimated the cover of each plant species. We then harvested the aboveground biomass of each species individually within the quadrat. Plants were oven-dried at 60 °C for 72 h and weighed to the nearest 0.01 g.

Data analysis

The *Baccharis* shrubs used in this study were a subset (those that were alive) of the original *Baccharis* plants randomly distributed in the common garden. To account for any potential loss of random placement because of mortality or the influence of spatial effects, we initially used spatial location (transect) within the common garden as a factor in our statistical analyses. However, spatial location was not significant in any of our models and so, for clarity, was dropped from the analyses. We first used a multivariate ANOVA that tested the independent factors of *Baccharis* architecture and nutrient addition on all understory plant variables (richness, cover, and biomass combined). We followed up these analyses with separate full-factorial ANOVA models to examine the effects of *Baccharis* architecture and nutrient addition, as well as the potential interactions between the two, on each variable. We also correlated understory plant richness, cover, and biomass with *Baccharis* height as a continuous variable. Next, we calculated standard effect sizes as an estimate of the relative importance of *Baccharis* genetic variation versus soil nutrient additions. Effect size is a general term for the parameter used to measure the effect of a treatment or a variable within each study. This was done by taking the difference between the mean values of the two groups divided by the total SD. For *Baccharis* morphological variation, we used the differences between erect and prostrate morphs. For the nutrient-addition treatment, we used the difference between NPK addition and sugar additions (i.e., reduction in N availability) to estimate the overall effect size, as these represented the highest and lowest levels of available N. Cohen (1988) suggests a rule of thumb for characterizing effect sizes: a ‘small’ effect = 0.10, a ‘medium’ effect = 0.30, and a ‘large’ effect = 0.50.

We used separate analysis of similarity (ANOSIM) tests to examine whether plant community composition based on Bray-Curtis dissimilarity (using relative biomass) differed between *Baccharis* architecture and nutrient-addition treatments. ANOSIM is analogous to an ANOVA on community dissimilarity values. The generated R statistic is a relative measure of separation between groups. A value of 0 indicates there is complete overlap in the community composition between groups, while a value of 1 indicates that there is no overlap (Clarke and Gorley 2006). We visualized these results using non-parametric multidimensional scaling analysis on Bray-Curtis dissimilarity values in PRIMER version 6 (Clarke and Gorley 2006) using 100 restarts.

Lastly, we used separate ANOVA models to examine the relative effects of *Baccharis* architecture and nutrient addition on the cover and biomass of the seven most abundant understory species (see Appendix A for the individual species' details). For all significant analyses, we used Tukey post hoc tests to compare levels within factors. In all analyses, cover estimates were log transformed prior to analysis to improve normality.

Results

In total, we observed 21 understory species in the common garden (11 native, ten exotic) (Appendix A). We found that *Baccharis* architecture ($F_{1,61} = 3.865$, $P = 0.05$) and nutrients ($F_{2,69} = 24.407$, $P < 0.0001$) had significant effects on the overall plant community responses, but there was no interaction between *Baccharis* architecture and nutrients ($F_{2,61} = 0.316$, $P = 0.72$), indicating that the effects of nutrients did not depend on the identity of a particular *Baccharis* morph.

Baccharis intraspecific variation

When comparing the two *Baccharis* architectures (erect versus prostrate morphs), we found no difference in total

understory plant species richness (Table 1) and a marginal difference ($P = 0.077$) in total cover, with erect morphs having ~30 % higher cover compared to prostrate morphs (Table 1; Fig. 1a, b). We observed positive correlations between plant species richness ($r = 0.28$, $P = 0.02$) and cover ($r = 0.31$, $P = 0.009$) with the height of *Baccharis* shrubs. Understory biomass was 66 % greater under erect morphs (Table 1; Fig. 1c), with a positive (though marginally significant) correlation with plant height ($r = 0.22$, $P = 0.07$). Standard effect sizes for differences in *Baccharis* architecture ranged from 0.21–0.33 (Table 1). We found no difference in overall community composition between morphs (global $r = 0.01$, $P = 0.19$). Of the seven most abundant understory species, only two species varied between the two *Baccharis* architectural morphs. *Ammophila arenaria* and *Festuca microstachys* cover (marginally significant) were higher under erect morphs compared to prostrate morphs (Table 2). In addition, *A. arenaria* biomass was 2.1 times higher beneath erect morphs (Table 2).

Nutrient additions

In contrast to *Baccharis* architecture, we found much stronger effects of nutrient addition on the understory plant community. NPK and control shrubs had 2.2 and 1.9 times more plant species, respectively, than C-added shrubs (Table 1; Fig. 1d). There was no difference between NPK and control treatments, indicating that C addition had a negative impact on understory richness. NPK shrubs had over 2.4 times the total plant cover of control shrubs and 4.2 times that of C-added shrubs (Table 1; Fig. 1e). NPK shrubs had over 4.3 and 6.2 times the understory plant biomass, respectively, compared to control and C-added shrubs (Table 1; Fig. 1f). Standard effect sizes for differences in nutrient treatments ranged from 1.06 to 1.51 (Table 1). Overall composition of the understory plant community also differed across the nutrient manipulation (global $r = 0.06$, $P = 0.01$). The main difference was between the NPK and control shrubs (global $r = 0.123$, $P = 0.005$), and

Table 1 Results from ANOVA examining effects of *Baccharis pilularis* intraspecific variation (*morph*), soil nutrient manipulation (*nutrients*), and their interaction on total richness, cover (%), and biomass (g) of all understory plants in a decade-old common garden

Variable	Source	df	MS	F	P	Standard effect size
Total richness	Morph	1, 61	3.50	0.97	0.32	0.21
	Nutrients	2, 61	29.14	8.07	0.001	1.06
	Morph × nutrients	2, 61	4.67	1.29	0.28	
Total cover (%)	Morph	1, 61	2,017.44	3.22	0.08	0.29
	Nutrients	2, 61	13,778.05	21.98	>0.0001	1.51
	Morph × nutrients	2, 61	148.20	0.23	0.79	
Total biomass (g)	Morph	1, 61	96.17	3.73	0.05	0.33
	Nutrients	2, 61	433.79	16.86	>0.0001	1.27
	Morph × nutrients	2, 61	22.80	0.88	0.41	

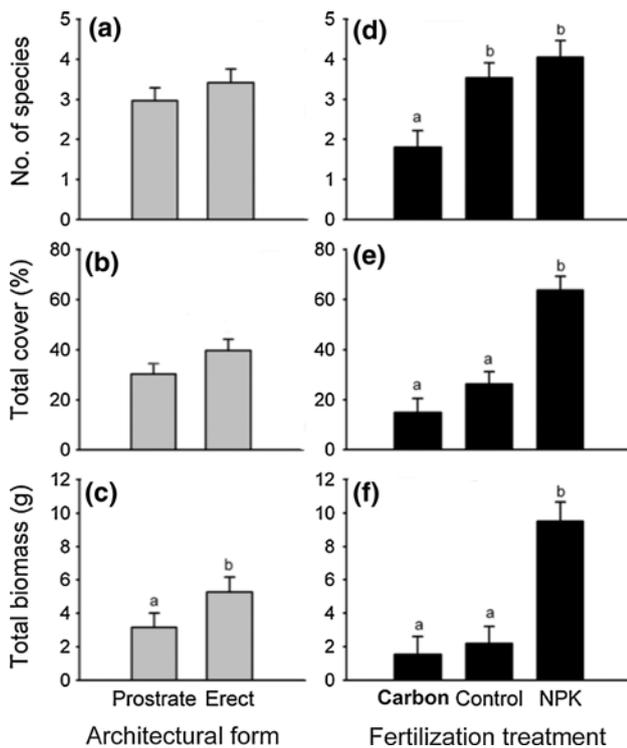


Fig. 1 Effects of morphological variation within *Baccharis pilularis*, and fertilization treatment (C addition, control, and NPK addition) on **a, d** understory plant richness, **b, e** percent cover, and **c, f** total above-ground biomass in a common garden experiment in a coastal dunes ecosystem. Bars are means (+SEM); pairwise differences ($P < 0.05$) are indicated by lowercase letters

was driven primarily by differences in relative biomass of individual species (Fig. 2).

Of the seven most abundant understory species, only *A. arenaria*, *F. microstachys*, *Pterostegia drymarioides*, and *Rumex acetosella* responded significantly positively to NPK additions, with the cover and biomass of all four species ranging from 1.5 to more than 24 times greater under NPK-added shrubs compared to C-added and control shrubs (Table 2).

Discussion

In coastal dune ecosystems, shrubs can act as important ecosystem engineers by altering the environment beneath their canopies and, in turn, shaping the subdominant plant community (Cushman et al. 2010). In this common garden experiment, we observed considerable intraspecific variation in this engineering capability, with differences in cover and biomass of understory plant species between erect and prostrate morphs of *Baccharis*, and a positive association between understory plants and *Baccharis* height. In our prior work, an increase in height combined with a decrease

in canopy density resulted in more light available to understory plants under erect morphs (Crutsinger et al. 2010). In a similar study, but in a system with more continuous trait variation, variation in the stem density among genotypes of a dominant perennial forb, *Solidago altissima*, determined colonization dynamics of sub-dominant plant species (Crutsinger et al. 2006, 2010). This research, along with work in other systems (Michalet et al. 2011), posits that researchers interested in the role of dominant species for the assembly of plant communities should consider the effects of intraspecific variation within dominants to improve predictive power.

Our results were mostly consistent with prior research of understory plants at this site (Crutsinger et al. 2010) and all results were similar in the direction of response. Previously, we observed that erect *Baccharis* morphs showed higher understory richness compared to prostrate morphs, though the magnitude of this difference was only a single species on average. In this study, we found no significant variation in understory richness between morphs. Differences in richness results could be explained by both seasonal differences in the study or by reduced power from our smaller sample size in this study. We actually found much greater differences in *A. arenaria* biomass in this study compared to our previous work (210 % higher beneath erect morphs versus 48 % higher in 2008). As *A. arenaria* spreads clonally through rhizomes, increased differences could be because of disproportionate spread over time of new rhizomes under erect morphs compared to prostrate morphs.

The effect of plant morphological variation, though present, was small relative to the impacts of nutrient addition of the dune soils, particularly considering the time course of the treatments (1 year for nutrient amendments vs. 13 years of accumulated morphological effects). In our preliminary soil analyses, we observed considerable variation in soil N content in the dunes and it is possible our nutrient additions extended beyond the natural range of N availability typically observed for understory plants. In which case, perhaps it is not too surprising that nutrient effects were greater than those of the different *Baccharis* morphs. In all cases, the standard effect sizes of nutrient addition were higher than the differences between *Baccharis* morphs (Table 1). For example, we found no effect of *Baccharis* architecture on understory richness, whereas C additions, which can limit N availability in soils (Alpert and Maron 2000), reduced the number of species by half compared to control and NPK-added shrubs. Similarly, NPK addition resulted in a several-fold increase in understory plant cover and biomass, while cover and biomass varied by only 30 and 66 % between morphs. To date, there has been very little research on relative effects of intraspecific variation versus the environment for plant communities. Johnson et al. (2008) conducted a greenhouse experiment comparing competitive effects of

Table 2 Results from ANOVA examining the effects of *B. pilularis* intraspecific variation in architecture (*morph*), soil nutrient treatment (*nutrients*), and their interaction on the cover and biomass of individual species

Variable	Source	df	MS	F	P
<i>Ammophila</i> cover	Morph	1	740.22	5.20	0.02
	Nutrients	2	621.23	4.36	0.01
	Morph × nutrients	2	258.40	1.81	0.17
<i>Ammophila</i> biomass	Morph	1	95.81	5.72	0.01
	Nutrients	2	69.01	4.12	0.02
	Morph × nutrients	2	44.06	2.63	0.08
<i>Pterostegia</i> cover	Morph	1	138.44	0.60	0.43
	Nutrients	2	558.89	2.45	0.09
	Morph × nutrients	2	88.99	0.39	0.67
<i>Pterostegia</i> biomass	Morph	1	0.01	0.04	0.83
	Nutrients	2	2.15	5.30	0.007
	Morph × nutrients	2	0.08	0.21	0.80
<i>Festuca microstachys</i> cover	Morph	1	64.23	3.25	0.07
	Nutrients	2	22.73	1.15	0.32
	Morph × nutrients	2	22.87	1.15	0.32
<i>Festuca microstachys</i> biomass	Morph	1	1.53	1.83	0.18
	Nutrients	2	0.76	0.91	0.40
	Morph × nutrients	2	0.01	0.01	0.98
<i>Festuca myuros</i> cover	Morph	1	94.41	0.25	0.61
	Nutrients	2	2,887.32	7.64	0.001
	Morph × nutrients	2	14.62	0.03	0.96
<i>Festuca myuros</i> biomass	Morph	1	1.76	0.32	0.56
	Nutrients	2	37.85	7.06	0.001
	Morph × nutrients	2	2.60	0.48	0.61
<i>Acmispon</i> cover	Morph	1	114.94	1.32	0.25
	Nutrients	2	121.42	1.40	0.25
	Morph × nutrients	2	119.95	1.38	0.25
<i>Acmispon</i> biomass	Morph	1	0.53	2.04	0.15
	Nutrients	2	0.57	2.19	0.11
	Morph × nutrients	2	0.56	2.15	0.12
<i>Cirsium</i> cover	Morph	1	5.05	1.54	0.21
	Nutrients	2	4.93	1.50	0.23
	Morph × nutrients	2	4.93	1.50	0.23
<i>Cirsium</i> biomass	Morph	1	1.98	1.54	0.21
	Nutrients	2	1.88	1.47	0.23
	Morph × nutrients	2	1.88	1.47	0.23
<i>Rumex</i> cover	Morph	1	1.36	0.03	0.85
	Nutrients	2	110.76	2.63	0.08
	Morph × nutrients	2	1.06	0.02	0.97
<i>Rumex</i> biomass	Morph	1	0.93	0.173	0.67
	Nutrients	2	34.67	6.419	0.003
	Morph × nutrients	2	1.63	0.303	0.73

Species are listed in order of abundance in the common garden: *Ammophila arenaria*, *Pterostegia drymarioides*, *Festuca microstachys*, *Festuca myuros*, *Acmispon heermannii*, *Cirsium quercetorum* and *Rumex acetosella*

different *Oenothera biennis* (common evening primrose) genotypes on *Bromus inermis* (smooth brome) grown under two nutrient regimes. As with our results, they found that *Oenothera* varied genetically in its competitive interactions with *Bromus*, but that soil fertility had a much stronger effect on the performance of *Bromus*.

While studies on the responses of plant communities are rare, there has been some research comparing plant intraspecific variation versus the environment for higher trophic levels, notably for arthropod populations and communities (Tack and Roslin 2011). Indeed, the trend seems to hold that environmental factors, such as soil nutrients,

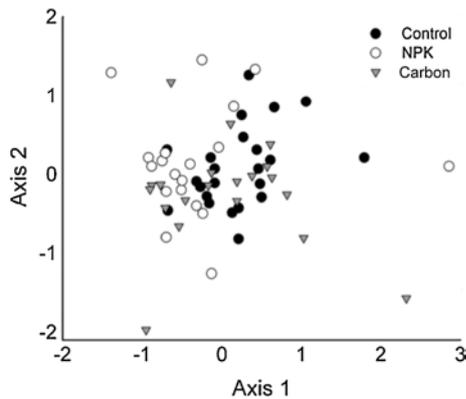


Fig. 2 Non-metric multidimensional scaling ordination of similarity in understory plant community composition in three fertilization treatments based on Bray-Curtis similarities for a sand dune community dominated by *Baccharis pilularis* shrubs. Treatments included NPK addition (white circles), sugar (C) additions (gray triangles), and controls (black circles)

soil moisture, and site locality, tend to have stronger effects than intraspecific variation. For example, Maddox and Cappuccino (1986) showed genetic variation within *Solidago altissima* (goldenrod) plants in resistance to aphid herbivory was greatest under drought conditions in a watering experiment. Johnson and Agrawal (2005) found that larger-scale habitat differences had a stronger influence on arthropod communities than variation among *Oenothera biennis* genotypes. Yet, there are certainly exceptions where the direct effects of plant genotype are stronger, or significant genotype by environment interactions occur suggesting that the two factors can depend on one another (Donaldson and Lindroth 2007). Furthermore, the relative importance of genetic variation versus the environment might vary when common gardens are replicated at different sites (Tack and Roslin 2011).

The overarching goal of our study was to compare the relative importance of *Baccharis* architecture versus soil nutrient additions, and not to evaluate the exact degree to which plant communities are limited by soil nutrients or which individual nutrients (N, P, or K) are particularly important in the dunes at BMR. In parallel with other dune ecosystems (Maun 2009), we found that plants growing in the dunes at BMR are nutrient limited, evidenced by a several-fold increase in both plant cover and biomass. Nutrient addition was a benefit to individual exotic species. Of the seven most abundant species, four responded to NPK, of which three were exotic. European dune grass (*A. arenaria*) is the most dominant exotic species that occurs throughout the dunes at BMR and made up the bulk of the biomass in our samples. *A. arenaria* biomass increased by four-fold with NPK additions compared to controls. Our results complement previous work on plant communities in the

grasslands adjacent to the dunes at BMR where increases in soil nutrient availability have been shown to promote the abundance of invasive plant species (Maron and Connors 1996). However, we did not observe a reduction in exotic biomass with C addition or facilitation of native plant species, both of which have been seen in other studies (Alpert and Maron 2000; Blumenthal et al. 2003). Alpert and Maron (2000) used sawdust as a readily available form of C for soil microbes, applied in different quantities and different intervals compared to our study using sugar.

Taken together, our results indicate that nutrients are the more important factor governing the coastal dunes community relative to intraspecific variation within a dominant shrub. What is clear from this work, and the work of others (Johnson et al. 2008), is that more studies are needed before any general consensus can be agreed on about the relative strengths and interactions between intraspecific variation and the environment in regards to how communities are structured and ecosystems function. Moreover, the study of environmental factors need not just be limited to abiotic conditions, as there are numerous biotic influences (Hughes et al. 2010) that can also influence the ecological consequences of intraspecific variation.

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