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Stress tolerance: Understanding morphological plant trade-offs in serpentine soil

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ABSTRACT

Habitat specialization in abiotically stressful environments establishes refugia for native plant species. In California, serpentine habitats support plant communities adapted to high-stress environments. Serpentinite is a heavy-metal substrate that proves too toxic for many plants but provides a crucial competitive-free refuge for California's native species. The unique plant communities found on serpentine soil pose an opportunity to study the ecological specialization of serpentine tolerators, plants that survive on and off serpentine. To understand the effects of soil type on tolerator trade-offs, we conducted an observational study at McLaughlin Natural Reserve, a protected site for native serpentine tolerators. In this study, we asked if morphological adaptations observed across two serpentine tolerator species and between a specialist and avoider pair differ across soil types. We particularly examined the effects of species, serpentine soil, and their interaction on yerba santa (*Eriodictyon californicum*), toyon (*Heteromeles arbutifolia)*, and two species of Arctostaphylos- common manzanita (*Arctostaphylos manzanita*) and white-leaf manzanita (*Arctostaphylos viscida*). Our results showed slight differences in intraspecific functional traits in tolerators' on serpentine and non-serpentine soil. These findings contradicted previous studies that tolerators on serpentine generally trade competitive abilities in favor of abiotic stress-tolerant adaptations. However, there were significant interspecific trait differences, suggesting that the adaptations to edaphic factors result in various reproductive, drought-tolerant, and fire-based strategies.

Keywords: serpentine, endemic, tolerator, serpentine syndrome, morphological trade-offs

INTRODUCTION

Abiotic stressors such as temperature, drought, and salinity can negatively impact plant survival, yet some species capitalize on intolerable environments. Edaphic stress enables plants to adapt to harsh environments like high-elevation alpines, low-rain deserts, hypoxic vernal pools, and heavy-metal soils. Habitat specialization in abiotically stressful environments establishes shelter for native plant species. Local adaptation is how plant populations become better suited to their environments through fitness tradeoffs. In California, serpentine habitats support a plethora of endemic plants that have adapted to these high-stress environments. Therefore, it is important to focus on understanding the mechanisms that maintain these edaphic systems, since approximately fifteen percent of threatened or endangered taxa in California show some degree of association with stressful substrates (Safford et al. 2005).

Serpentine soil is made from serpentinite rock; it has high magnesium and iron levels and lacks essential nutrients like calcium, sodium, and potassium (Rajakaruna 2011). Water deficiency has also been shown to be another added stress factor in many serpentine habitats (Proctor and Woodell 1975). The biogeochemical composition of serpentinite is responsible for the limited community diversity coined as “serpentine syndrome” (Brooks 1977), where serpentine communities have unusually poor plant productivity, high endemism, and vegetation types distinctive from neighboring habitats (Whittaker 1954). Certain studies even suggest that lower calcium levels in serpentine soil lead to higher plant infection rates (Springer 2006). Moreover, necrosis is a common response of resistant plants to fungal infection, where dark brown or red spots on the leaves can indicate nutrients (zinc) deficiency or pathogenic stress (Heath 1984).

Although only one percent (or 2860 km^2) of the land area in California contains serpentine soil, it provides habitat for about ten percent of California’s endemic flora (Kruckeberg 1986). To survive in serpentine habitats, plant species adopt one of three strategies: endemism to serpentine soil, avoidance of inhabitable serpentine, or tolerance of both non-serpentine and heavy-metal serpentine soils. (Palm and Volkenburgh 2014). Serpentine tolerators are typically endemic plants that can survive on both serpentine and non-serpentine substrates (Anacker 2011). The functional traits allowing that variation in habitat selection include reduced leaf size, reduced stature, increased tolerance to drought, more developed root systems, and earlier-flowering phenology (Brady 2005; Westoby et al. 2002). Serpentine tolerators also invest large amounts of energy into anti-herbivory defense (Clarkson and Hanson 1980). Fitness trade-offs on serpentine are not overall beneficial. In fact, tolerators have lower survival rates compared to their non-serpentine counterparts (Rajakaruna and Harrison 2011). High selective pressures affecting these stress-tolerant plants cause slower growth rates and render them incapable of competing on non-serpentine soils (Grime 2006).

In this study, we explore the intraspecific and interspecific variation of functional traits in serpentine tolerator species. Specifically, we looked at two serpentine tolerators toyon (*Heteromeles arbutifolia*) and yerba santa (*Eriodictyon californicum*), one specialist white-leaf manzanita (*Arctostaphylos viscida*), and one avoider common manzanita (*Arctostaphylos manzanita*). We asked how does serpentine affect the morphology of tolerant species? Previous studies suggest that tolerant species are limited to serpentine soils due to increased competition within non-serpentine environments (Kruckeberg 1954). Due to trade-offs that favor resource accumulation over growth, we hypothesize leaves will be smaller and thicker on serpentine soil with more drought-tolerant textures present (Springer et al. 2006; Westoby et al. 2002). We also hypothesize tolerators on serpentine will have shorter heights and smaller leaf sizes than non-serpentine individuals since prior studies have demonstrated that serpentine species have slower growth rates and lower plasticity from reduced essential nutrients (Aerts and Chapin, 2000). Additionally, we believe that disease indicators like necrosis will be more prevalent in serpentine soil because high calcium soil concentration increases susceptibility to fungal infection. Since non-serpentine communities are more dense and susceptible to fire, herbivory and necrosis will be more common on non-serpentine while fruiting and flowering will be more common on serpentine soil.

METHODS

2.1 2.1 Study System and Site

To understand the effects of soil type on morphology, we conducted an observational study at McLaughlin Natural Reserve in Lake County, California. One-third of the reserve has serpentine soil that supports endemics. We targeted chaparral habitats since they embody a high degree of biodiversity and house year-round woody species. Because our study focused on serpentine's impact on morphological trade-offs, we targeted sites with tolerator species present. We compared one non-serpentine chaparral and two serpentine chaparral sites with similar slopes and aspects. Grizzly Peak (38°87175 N, -122°44956 S) is a mountainside on McLaughlin's northeastern boundary that houses both serpentine chaparral and basalt chaparral on its south-facing slopes. For our second serpentine chaparral site, we surveyed a south-facing slope two miles southeast of Grizzly Peak (38°85855 N, -122°39420 S). Both communities burned in the August 2015 Jerusalem fire and have achieved steady recoveries over five and a half years.

2.2 Study Organisms

Yerba santa is a perennial evergreen shrub endemic to California. Its slender dark green leaves are often coated in waxy resin to reduce water loss (Hanes 1974). Like toyons and manzanitas, yerba santa's evergreen leaves allow these shrubs to maximize winter rains for photosynthesis (Hanes 1974). The tough, leathery leaves have a fuzzy underside and the shrub flowers from May to July. Seeds germinate following a fire and adult yerba santas can resprout from their rhizomes after a disturbance (Howard 1992). Yerba santa's shallow root system has main roots at the top with multi-branching horizontal rhizomes to capitalize nutrient uptake in summer droughts.

Toyon is a perennial evergreen shrub endemic to California chaparral. Its spiky leaves help minimize transpiration and defend against herbivory (Stranger 2000), while their leathery texture provides more fire resistance than most native textures. Toyon is an obligate resprouter; it depends on resprouting from deep underground roots for regeneration (Hanes 1974). Although generally fire-resistant, toyon regrows quickly following disturbance. Toyon has a deep and wide root system with surface feeder roots to reach both surface-level and ground-water (Hanes 1974). Mature toyon flowers in early summer, while berries ripen in fall and perish in winter.

We also studied two species of *Arctostaphylos;* common manzanita is a serpentine avoider while white-leaf manzanita is a serpentine specializer. Although separate species, we believe that they exemplify serpentine's evolutionary influence in species divergence within the genus. Manzanitas are shade-intolerant, meaning they typically grow tall and shade other species to dominate light uptake (Howard 1992). Both manzanitas are evergreen shrubs native to California chaparral and have non-wilting, slightly fuzzy leaves for water conservation (Hanes 1974). While white-leaf manzanitas have pale green leaves, common manzanitas have shiny green leaves. Their reduced leaves limit photosynthetic capacity but grow vertically to reduce heat load and transpiration (Hanes 1974). Its lateral shallow roots capitalize rain as a main water source. Both common and white-leaf manzanitas are obligate seeders and require fire for germination; adults cannot resprout after fires and rely on a soil seed bank to regenerate. While obligate resprouters (like toyon and yerba santa) avoid drought by having deeper roots (Bell et al., 1996), obligate seeders (like manzanita) have shallow roots but a low leaf size to limit surface area exposed to water loss (Anacker et al. 2011). Like toyons and yerba santas, manzanitas are susceptible to necrosis- the irreversible death of living tissue. Manzanitas bloom from February to April while fruits develop starting late spring and ripen in early summer.

2.3 Data Collection

Over four consecutive days in February, we measured the above-ground morphological traits of the four tolerators. We measured age, height, base circumference, average leaf length of 3 leaves, average leaf thickness of 5 leaves, leaf texture, signs of herbivory, and presence of necrosis. We categorized plants as adult or juvenile based on the presence of berries on toyons and the presence of flowers on yerba santa. Toyon leaf textures were categorized as waxy or dry and brittle, manzanita leaves as matte or fuzzy, and yerba santa leaves as smooth or leathery. We noted the presence of herbivory by brown holes, beetles, or ripped edges on leaves. We noted the presence of necrosis by red spots on manzanitas and brown spots on toyons and yerba santas. Although common and white leaf manzanitas bloom in winter and early spring, we did not observe berries or flowers. Therefore, we measured reproductive maturity by height and classified adults as taller than 1 meter. For all individuals, we measured height from the ground to the tallest point and measured circumference around the base or thickest branch. To ensure the independence of samples, we selected plants at least three meters apart.

2.4 Data Analysis

To examine the effect of serpentine soil on plant morphological traits, we used JMP Student Edition v14 for all statistical analyses. We performed two-way ANOVA and Tukey HSD post-hoc tests to compare the effect of soil type on circumference, height, leaf length, and leaf thickness. Additionally, we ran chi-squared tests to identify patterns of herbivory, age, leaf texture, necrosis, and flowering between serpentine and non-serpentine.

RESULTS

We sampled 306 plants in total. We measured 105 yerba santa (48 serpentine, 57 non-serpentine), 101 toyon (46 serpentine, 55 non-serpentine), and 100 manzanita (46 serpentine, 54 non-serpentine). There was no direct effect of leaf length on both toyon and yerba santa. Common manzanitas on non-serpentine had longer leaves than white-leaf manzanitas on serpentine soil (Fig. 1, Table 1). In general, all our plant species displayed thicker leaves on non-serpentine soil than serpentine soil (Fig. 2, Table 1).

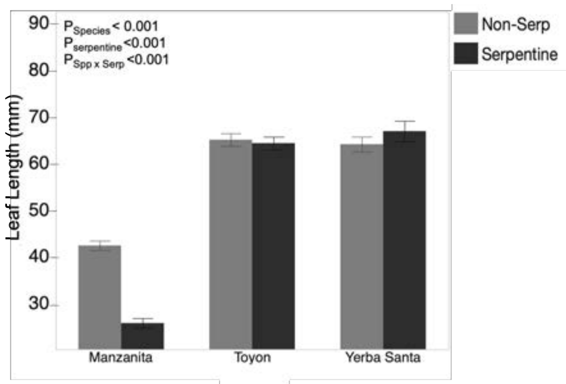

Figure 1. The effects of species, serpentine and their interaction on leaf length for toyon *(Heteromeles arbutifol*ia), yerba santa (*Eriodictyon californicum)* and two species of *Arctostaphylos*- common manzanita (*Arctostaphylos manzanita*) on non-serpentine and white-leaf manzanita (*Arctostaphylos viscida*) on serpentine. There was no direct effect of leaf length on toyon or yerba santa. There was a significant effect of leaf length between common manzanita and white-leaf manzanita. Error bars represent ± 1 S.E.

Table 1. ANOVA statistics summarizing the effects of species, serpentine soil and their interaction on plant morphology. The plant species included were toyon (*Heteromeles arbutifolia),* yerba santa (*Eriodictyon californicum)* and two species of *Arctostaphylos*- common manzanita (*Arctostaphylos manzanita)* and white-leaf manzanita (*Arctostaphylos viscida).* Asterisks represent p-values of significant importance (**p< 0.001, *p< 0.01).

	Height		Circumference		Leaf Length		Leaf Thickness	
Effect	df	*F*	df	*F*	df	*F*	df	*F*
Species	2	16.970**	2	290.722	2	2.183**	2	57.571**
Serpentine	1	0.002	1	16.078	1	3.857**	1	12.025*
Species x Serpentine	2	4.832*	2	24.346*	2	8.505**	2	0.976

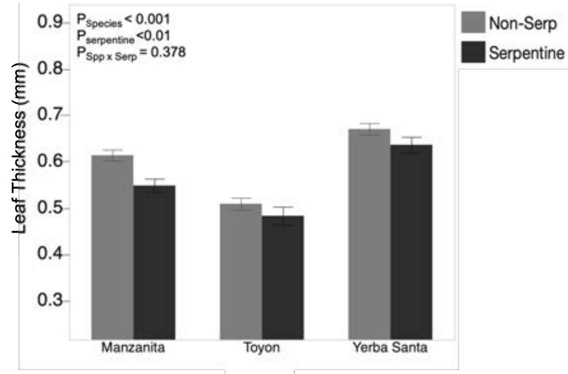

Figure 2. The effects of species, serpentine and their interaction on leaf thickness for toyon *(Heteromeles arbutifolia*), yerba santa (*Eriodictyon californicum)* and two species of *Arctostaphylos*- common manzanita (*Arctostaphylos manzanita*) and white-leaf manzanita (*Arctostaphylos viscida).* Toyon and yerba santa had thinner leaves on serpentine than off serpentine. White-leaf manzanita had thinner leaves than common manzanita. Error bars represent ± 1 S.E.

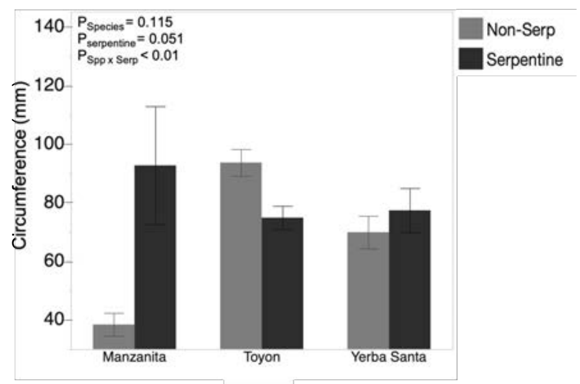

Figure 3. The effects of species, serpentine and their interaction on circumference for toyon *(Heteromeles arbutifol*ia), yerba santa (*Eriodictyon californicum)* and two species of *Arctostaphylos*- common manzanita (*Arctostaphylos manzanita*) and white-leaf manzanita (*Arctostaphylos viscida*). Toyon had smaller basal radii on serpentine soil. Yerba santa had smaller basal radii off serpentine soil. Common manzanita had smaller basal radii than white-leaf manzanita. Error bars represent ± 1 S.E.

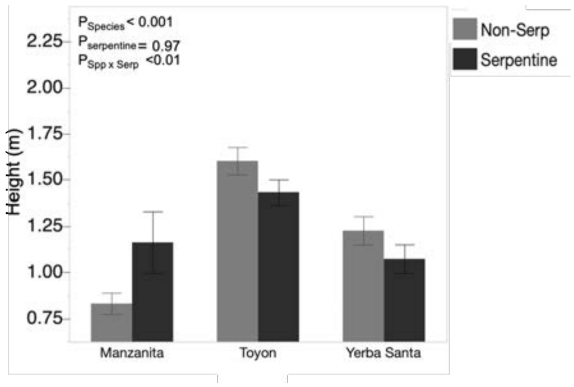

Figure 4. The effects of species, serpentine and their interaction on height for toyon *(Heteromeles arbutifolia*), yerba santa (*Eriodictyon californicum)* and two species of *Arctostaphylos*- common manzanita (*Arctostaphylos manzanita*) and white-leaf manzanita (*Arctostaphylos viscida).* Toyon and yerba santa were shorter on serpentine than off serpentine. Common manzanita was shorter than white-leaf manzanita. Error bars represent ± 1 S.E.

There was no direct effect of serpentine on circumference on either species, except again for the interaction between serpentine soils and species (Fig. 3, Table 1). White-leaf manzanita bases on serpentine were thicker than common manzanitas on non-serpentine soils. Yerba santa bases were thicker on serpentine while toyon bases were thicker off serpentine (Fig. 3, Table 1).

Overall, toyon was the tallest species followed by yerba santa and then manzanitas (Fig. 4, Table 1). Although there was no direct effect on plant height, there was a significant interaction between serpentine soils and species such that manzanitas in serpentine grew taller while toyon and yerba santa grew shorter (Figure 4, Table 1). On average, white-leaf manzanitas had the greatest height difference. On serpentine, they were 0.33 meters taller than common manzanita on non-serpentine.

With regards to leaf texture, yerba santa waxiness and dry brittleness did not differ depending on soil type (N=105 X^2=0.748 P=0.387) and toyon leaves were leathery and matte regardless of soil type. Manzanita texture differed based on soil type- (N= 100, X^2= 5.513, P=0.019). We found common manzanita leaves were 20% fuzzier on non-serpentine soil than white-leaf manzanita on serpentine soil. Toyon necrosis was 22% more prevalent on non-serpentine than serpentine (N= 101, X^2= 6.419, P= 0.011). In contrast, white-leaf manzanita necrosis was 26% more present on serpentine than in common manzanita on non-serpentine (N= 100, X^2= 5.633, P= 0.018). Yerba santa necrosis was not statistically more prevalent on non-serpentine than serpentine (N= 105, X^2= 1.251, P= 0.263).

Soil type did not have an effect on yerba santa flowering (N= 105, X^2= 1.827, P= 0.177) or toyon fruiting (N= 101, X^2= 2.953, P= 0.229). Overall, soil type did not determine the presence of herbivory in yerba santa (N= 105, X^2= 2.041, P= 0.153), toyon (N= 101, X^2= 0.198, P= 0.656), or manzanita (N= 100, X^2= 0.624, P= 0.43). Furthermore, tolerator ages did not differ between serpentine and non-serpentine soil (manzanita: N= 100, X^2= 1.962, P= 0.161; yerba santa: N= 105, X^2= 1.827, P= 0.177; toyon: N= 101, X^2= 1.183, P= 0.277).

DISCUSSION

Overall, we found that compared to tolerators on non-serpentine, yerba santas and toyons on serpentine had a shorter stature and slightly thinner leaves. However, leaf length did not statistically differ on and off serpentine and plant circumference did not depend on serpentine soil. Between the specialist and avoider manzanita species, the white-leaf manzanitas were taller than common manzanitas with a wider radius, but had shorter and slightly smaller leaves.

Regarding the considerable variation between the common and white-leaf manzanita, there are no studies on the morphological comparisons between the two species. Therefore, we believe that it is a safe assumption to first attribute morphological differences to genetic differences rather than edaphic factors. However, it would be interesting to conduct further research on what leads these two very similar species to specialize to grow in two very different habitats.

As expected, the tolerators toyon and yerba santa tended to be shorter on serpentine. This matches previous research that shows many serpentine flora exhibit "stunted" growth on poor soil conditions to allow for better water retention (Whittaker et al. 1954). The lack of macronutrients found on serpentine soil may cause this height variation between tolerators. When comparing the specialist and avoider manzanitas, white-leaf manzanitas were considerably taller than common manzanitas. This height variation is unexpected because white-leafs grow shorter at 1 to 4 meters whereas common manzanitas are typically taller at 1.8 to 3.66m (Howard 1992). Since white-leaf's larger height on serpentine is not attributed to genetic differences, we can consider edaphic factors as a strong contributor.

The longer leaf lengths on serpentine may demonstrate the effects of soil fertility on tolerator growth rates. This contradicts previous research that observed a physiological trade-off in serpentine tolerators that favors drought tolerance over photosynthetic uptake at the seedling stage (Anacker et al. 2011). Regardless of serpentine strategy, all target species had thinner leaves on serpentine than non-serpentine. This leaf reduction is in line with multiple studies suggesting that plants growing in stressful habitats tend to have thicker leaves to maximize productivity without having to sacrifice efficient water use (Yun and Taylor 1986). Our tolerator species may have developed similar adaptations to compensate for the lack of water retention on serpentine soil.

Since the presence of toyon berries and yerba santa flowers did not differ on and off serpentine, there is no evidence of a phenology shift or earlier maturation due to soil stress. Serpentine toyons had less evidence of necrosis than their non-serpentine counterparts, suggesting the fungi is less prevalent on serpentine or serpentine toyons are less vulnerable to infection. This contradicts previous research that suggests serpentine soil's low calcium concentration increases the tolerator's susceptibility to pathogens (Springer et al. 2006). Although we did not observe variations in flowering or fruiting between soil types, there could be distinct differences after longer post-fire periods or during the spring flowering season.

The lack of cohesive morphological differences across our plant species may be due to loose boundaries between serpentine and non-serpentine soil types. Serpentine areas typically do not occur in isolated patches with clear boundaries, but rather are intermeshed among other soil types. Perhaps surveys done on sites with more distinct soil boundaries may demonstrate a clear pattern in morphological trait adaptations.

Furthermore, reduced heights on serpentine may be credited to fire and trade-offs disfavoring growth. Fire affects serpentine and non-serpentine communities differently, so five and a half years after the 2015 Jerusalem fire may not have been enough time to re-establish similar communities or be at an age to see drastic contrasts. Fire has shown to be less frequent and severe on serpentine because the lower fertility of serpentine soil leads to more open vegetation and less competition. Serpentine soil's abiotic stressors uphold lower biomass accumulation, less fuel storage, and a discontinuous canopy cover (Safford and Harrison 2004). Previous studies observed that soil fertility, plant cover, biomass, and fire severity were higher on sandstone than serpentine soil, but the time since the last fire and uneven fire severity were higher on serpentine soil (Safford and Harrison 2004). As a result, fire has a longer-lasting effect on non-serpentine community height (Anacker et al. 2011). However, we observed tolerators on serpentine were shorter than those on non-serpentine, indicating a slower recovery. Despite being more affected by fire, tolerators on non-serpentine soils possess morphological traits that favor growth and biotic competitive abilities over nutrient uptake and abiotic tolerance. Endemic shrub species on serpentine chaparral tend to burn unevenly and less severely, but recover slower than those on burned non-serpentine chaparral (Safford and Harrison 2004). The Jerusalem fire may have had longer-lasting effects on serpentine, such as replacing obligate resprouter or seeder adults in the non-serpentine community with juveniles. Once again, tolerators on serpentine display morphological trade-offs that favor drought tolerance over photosynthetic capacity. Our results suggest that fire has less evident but longer lasting effects on serpentine tolerators.

For future research, it would be informative to perform a greenhouse experiment to compare common and white leaf manzanita growth in both serpentine and non-serpentine soils. This experiment would prove that any differences in functional traits would be directly caused by soil type rather than distinct species adaptations. Conducting long-term monitoring of these manzanita species, paired with genetic analysis, could also illustrate if species isolated on serpentine demonstrate ecotypic differentiation overtime. Ecotypes have been hypothesized to be the first steps toward sympatric speciation. Adaptive genetic differentiation and phenotypic plasticity can increase the fitness of plant lineages in high-stress environments (Baythavong and Stanton 2010). Therefore, monitoring the level of gene flow within our toyon and yerba santa communities would pose an opportunity to observe ecological speciation in the serpentine system.

Abiotically stressful environments like serpentine create an essential refuge for native plant species, so it is important to understand how serpentine's stressful abiotic factors shape the community. Despite losing traits that reduce competitive and reproductive ability, morphological trade-offs are essential for a tolerator's survival in contrasting environments.

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