Differences in Leaf Mechanical Properties among Species of Chaparral Shrubs Suggest Leaf-Level Niche Segregation

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Abstract

Niche theory has a widespread acceptance among zoologists; however, among botanists, it is controversial because of the simplistic resources utilized by plants. Niche segregation implies resource partitioning.[1] Leaves regulate three major plant resources: light capture, carbon uptake, and water usage. At the leaf level, evidence of resource partitioning may exist among species with differential leaf morphology. One such example prevails in the co-occurring sumac (family Anacardiaceae): lemonade berry (Rhus integrifolia) has thick, leathery leaves with little folding; laurel sumac (Malosma laurina), has thin leaves with dramatic folding; and sugar bush (Rhus ovata), has intermediate leaf thickness and folding.[2] We hypothesized that differences in leaf mechanical strength correspond to differences in resource partitioning and morphology. To test this hypothesis, we measured leaf mechanical properties at a common site, where all three species co-occur, using a mechanical testing machine (Instron). The properties measured were: 1) tensile strain at leaf break, 2) tensile stress at leaf break, and 3) Young's Modulus, which measures leaf stiffness. Laurel sumac was found to exhibit significantly greater tensile strain at leaf break than sugar bush, which was significantly greater than lemonade berry ($P < 0.5$, $n = 10$, one-way ANOVA). Laurel sumac also experienced significantly greater tensile stress at leaf break than sugar bush or lemonade berry. Furthermore, lemonade berry had significantly higher Young's Modulus than both sugar bush and laurel sumac. These observed differences in leaf mechanical traits among species suggest differences in resource utilization capacities by leaves under mechanical stress such as high winds, herbivory, salinity, or drought. This may represent a leaf-level niche segregation (a niche axis), which facilitates the coexistence of these three, closely related species, at coastal sites. However, the leaves of laurel sumac and sugar bush may be better adapted to the inland sites where lemonade berry is not found.[3]

Introduction

This study compares the differences in tensile properties between *Rhus integrifolia* (lemonade berry), *Malosma laurina* (laurel sumac), and *Rhus ovata* (sugar bush), three closely related and co-occurring chaparral species of the *Anacardiaceae* family. The plants are similar in appearance, all growing to heights of 4.5 m (15 ft), with dense fruit clusters at the ends of their branches.[2] A major difference between the three species is in their distribution. Lemonade berry exists predominately at low altitude, coastal areas. Contrastingly, the laurel sumac and sugar bush are found further inland; however, sugar bush habituates on both the hillsides as well as the adjacent valleys, which are subject to very low, night temperatures (<0ºC), whereas laurel sumac is found exclusively on the warmer mountain tops.[3] Also, there are significant differences between the leaf morphology of the species. Lemonade berry has thick, oblong-shaped, leathery leaves with relatively little folding. Laurel sumac has thinner leaves with a dramatic fold along the mid-vein and an abrupt sharp tip. Sugar bush has spade-shaped leaves of intermediate thickness, with slighter folding, and a glossy appearance.[2]

Mechanical strength is a physiological component that affects the survival and distribution of plants, and is thus an important parameter in plant ecology. At the leaf level, an increase in mechanical strength is often associated with a subsequent increase in protection against herbivory. The structural composition of a leaf, a determinant of morphology and mechanical strength, can be telling of its utilization of resources, since leaves regulate the three major resources of the plant via stomatal control: the light capture, the carbon uptake, and water usage.[1] We hypothesized that differences in leaf mechanical strength of the three species correspond to differences in leaf morphology and thus resource utilization.

Materials and Methods

Samples were taken from ten adult plants for each of the three co-occurring chaparral species (lemonade berry, laurel sumac, and sugar bush) found along the Dana Martel trail located on the Pepperdine University campus in Malibu, California. It was presumed that all of the specimens were under similar environmental conditions because of this proximity. This assumption eliminates the presence of environmental differences that would affect tensile strength; for example, varying environmental conditionals illicit differential water usage, and studies have shown that water loss correlates with tensile strength.[4] Also, the selected plants were spaced large enough apart to avoid the inclusion of a hybrid in the study.

A standardized method of leaf selection was used so the leaves were presumably mature and close in age. The following leaf measurements were made using a vernier caliper: total blade length, width, thickness, and average clamped blade length. These values were input into the Instron program, which was specially designed to calculate and the total transverse area of the leaves. To measure the leaf biomechanical properties, the leaf samples were centered laterally and fastened into the clamps of the Instron (at a standard setting of 12mm between the clamps). Between trials, only one set of clamps were adjusted (the other served as a reference point).

When each trial began, a constant rate of force was applied to the leaf up to the "break point", in which the leaf tissue was compromised, usually tearing along the mid-vein or another adjacent, parallel trajectory. The Young's Modulus and other values were then calculated for each trial (with the break point set manually) and graphs were produced by the Instron program. Data were analyzed with an ANOVA and Fisher's PLSD tests to compare the leaf mechanical strength of the three species.

Figure 1. Instron mechanical testing machine

Figure 2. Laurel sumac

Figure 3. Sugar bush

Figure 4. Lemonade berry

Photo credit (fig. 2-4): Dennis Ancinec

Data and Results

Taxon	Transverse Area (mm^2)	Young's Automatic Modulus (N/mm^2)	Tensile Stress at Break (N/mm^2)	Tensile Strain at Break (mm/mm)
Rhus integrifolia (lemonade berry)	26.741 ± 2.259	22.128 ± 11.044	1.208 ± 0.342	0.095 ± 0.022
Malosma laurina (laurel sumac)	20.455 ± 3.418	13.027 ± 4.049	1.613 ± 0.353	0.162 ± 0.016
Rhus ovata (sugar bush)	31.940 ± 4.123	11.463 ± 4.785	1.165 ± 0.464	0.136 ± 0.019

***Table 1*. Leaf tensile properties** (ANOVA values; $n = 10$ leaves/species; significance defined as $p < 0.05$)
The transverse area was normalized for this study.; even though significance was seen for this measurement ($p < 0.0001$) it did not effect the other values. Young's Modulus was calculated to determine the resistance of the system to an externally applied force, defined simply by the initial slope of the stress/strain curve, and found to be significantly different for the three species ($p = 0.0062$). In addition, the tensile stress at break is a measure of the maximum force/transverse area experienced by the leaf at the break point, and significance was seen ($p = 0.0300$). Last, the tensile strain at break is a measure of the amount of tissue "stretching", defined by the difference in initial leaf width, and the width at the break point. Significance was found for this measurement ($p < 0.0001$).

Summary of Statistical Significance from Fisher's PLSD:

- Transverse Area: **R.o. > R.i. > M.l.**
- Young's Automatic Modulus: **R.i. > R.o. = M.l.**
- Tensile Stress at Break: **M.l. > R.o. = R.i.**
- Tensile Strain at Break: **M.l. > R.o. > R.I.**

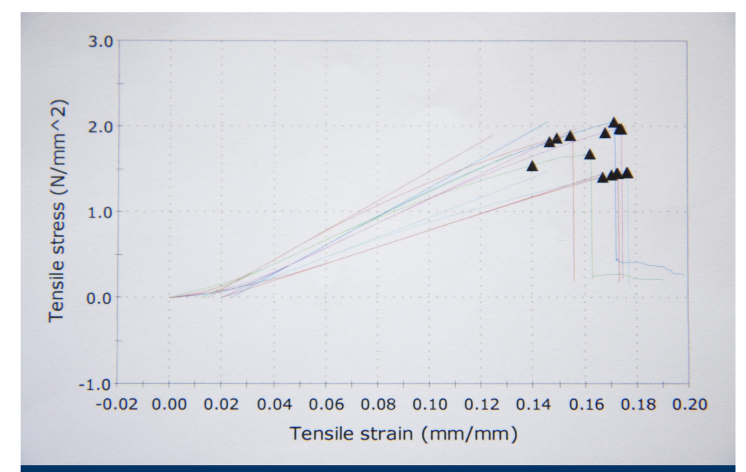

Figure 5. Stress vs. strain curve (laurel sumac)

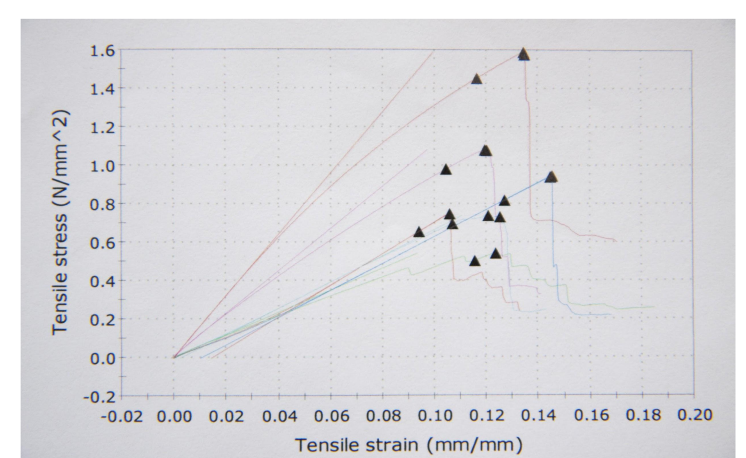

Figure 6. Stress vs. strain curve (sugar bush)

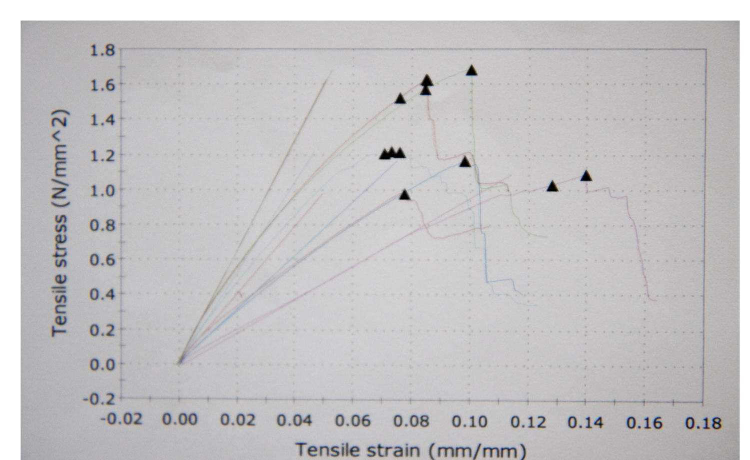

Figure 7. Stress vs. strain curve (lemonade berry)

Conclusions

1) **Hypothesis supported: the three species of the *Anacardiaceae* family exhibit different biomechanical properties.**

2) **Laurel sumac endures the greatest stress before failure; however, it accomplishes this by a greater level of leaf stretching, effectively compromising its leaves' architecture in a stress response.**

3) **Lemonade berry displays the most leaf "stiffness" as defined by Young's Modulus.**

4) **This represents differential utilization of resources at the leaf-level, a niche axis about which species segregation can occur.**

References

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"Our life is an apprenticeship to the truth that around every circle another can be drawn; that there is no end in nature, but every end is a beginning, and under every deep a lower deep opens." -Ralph Waldo Emerson, 1841