Jed R. Redwine and C. Pascale William Florida International University - Miami, FL

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# Leaf thickness and canopy region accounts for carbon, nitrogen, and carbon stable isotope contents in two co-occurring species of subtropical hardwood trees

## Introduction

Recent syntheses of a large number of independently collected datasets confirm the globally significant relationship between leaf thickness and longevity across species, habitats, landscapes, and biomes (Wright et al. 2004). My study seeks to connect these large scale phenomena to a physiological basis in a community of subtropical trees native to south Florida.

## Method

- I chose 3individuals of *Canella winterana* (L.) Gaertn. and *Zanthoxylum fagara* (L.) Sarg.
- These species have contrasting roles in succession.
- Trees were located along a randomly chosen transect and all trees were part of a phenological monitoring project for the last 3 years.
- To ensure coverage of the entire scale of variability I selected and clipped a branches from the lower, middle, and upper canopy of each individual tree sensu Suomela and Ayers (1994).
- I randomly selected 10 leaves from each branch for morphological, and nutrient analysis.
- Because isotopic analysis is more expensive, we obtained isotopic results for only 5 of the 10 leaves from each canopy location.

## Analysis

Data were analyzed using the GLM procedure in SAS. Two nested MANCOVA tests were utilized to test the species and individual canopy location as sources of variance in concert with leaf thickness and area/mass ratio as covariates possible covariates of four response variables:

molar Carbon content per unit area
molar Nitrogen content per unit area
$\delta^{13}$Carbon content
$\delta^{15}$ Nitrogen content

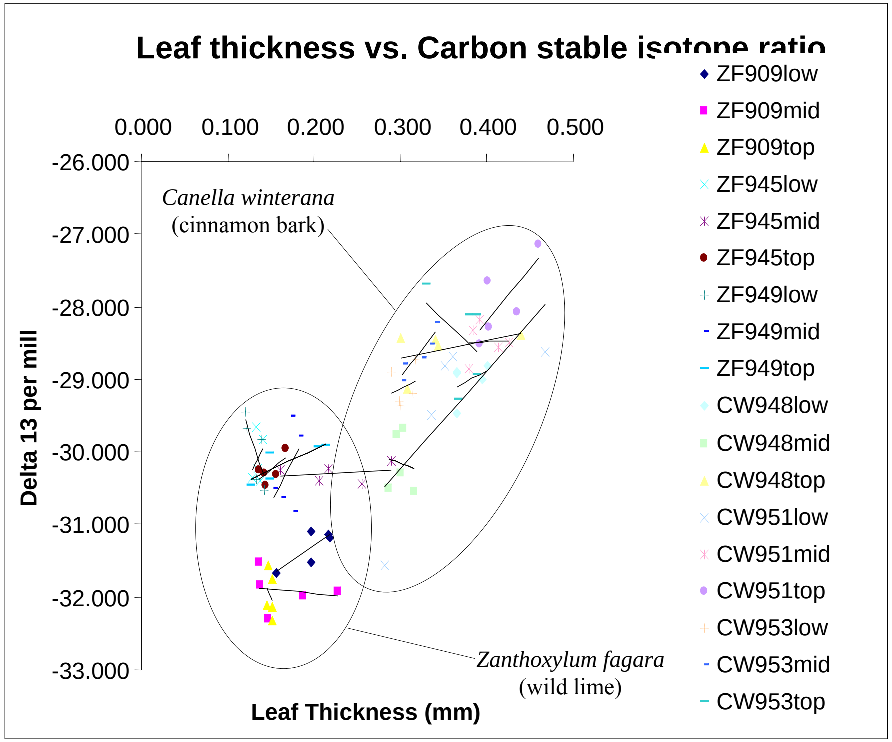


Figure 1. A plot of the data indicates that the global relationship between thickness and per mil $\delta^{13}$C content holds both across species and within individual branches.

## Results

| Source | mole C per cm$^2$ | mole N per cm$^2$ | $\delta^{13}$ C | $\delta^{15}$ N |
|---|---|---|---|---|
| Species | **< 0.0001** | **< 0.0001** | **< 0.0001** | **< 0.0001** |
| Tree (canopy location) | **< 0.0001** | **< 0.0001** | **< 0.0001** | **< 0.0001** |
| leaf thickness (mm) | **< 0.0001** | **< 0.0001** | **0.0009** | **0.0134** |
| leaf area/mass ratio | **< 0.0001** | **0.0303** | 0.4542 | 0.5116 |
| Full model | **< 0.0001 / 0.97** | **< 0.0001 / 0.85** | **< 0.0001 / 0.903** | **< 0.0001 / 0.89** |

Table 1. Indicates the p-values and $R^2$ depicting the contribution of four sampling sources: species, the sampling location nested within sampled individual, and covariates leaf thickness and leaf area to mass ratio in explaining the variability of the four selected response variables: molar carbon and nitrogen contents, and the relative composition of stable and light isotopes of carbon and nitrogen. The final row indicates the significance (p-value) and precision ($R^2$) of the full nested model. Significant p-values are indicated in bold.

## Discussion

- Leaf morphology and nutritional contents are now hypothesized to be globally constrained features of angiosperms thought to be fundamental components of leaf economy. Our macronutrient results support this idea.
- Nitrogen isotope patterns are not well understood, but our sampling scheme was successful in explaining the variability of these patterns.
- Carbon isotopic contents of plant tissues are created by the selectivity of carbon fixing enzymes (notably Rubisco and PEP carboxylase) which are profoundly different in their ability to discriminate against heavy isotopes of carbon, with Rubisco ~ -29 per mil and PEP carboxylase ~ -1.1 per mil (Raven and Farquar et al 1990).
- The direction and pattern (see Figure 1) of our results may suggest that changes in leaf thickness directly modulate the role of PEP carboxylase in fixing carbon among leaves contained in this sample.
- In light of recent findings by Hibberd and Quick (2004) of the activity of PEP carboxylase in leaves, stems, and petioles of celery and tobacco, this result may support to the developing theory (Raven 2004) that shifts in morphology are fundamental in shifting the relative roles of these ubiquitous carbon-fixing enzymes. in all angiosperms.

Hibberd, J.M. and W.P. Quick. 2004. Characteristics of C4 photosynthesis in stems and petioles of C3 flowering plants ature **415**: 451-454. Raven, J.A. 2002. Evolutionary options. Nature **415**: 375-376.
Raven, J.A. and G.C. Farquhar. 1990. The influence of N metabolism and organic acid synthesis on the natural abundance of isotopes of carbon in plants. New Phytiologist **116**: 505-529.
Suomela J. and Ayers, M.P. 1994. Within-tree and among-tree variation in leaf characterisitics of mountain birch and its implications for herbivory. Oikos **70**:212-222.
Wright, I.J. et al. 2004. The worldwide leaf economics spectrum. Nature **428**:821-827.

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