CHANGES IN LEAF LITTER ACROSS AGES OF *HYERONIMA ALCHORNEOIDES* TREES

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Abstract: A leaf can be an asset or a cost to its parent plant, depending on how much energy it produces and consumes. When leaves are no longer beneficial, a tree can drop them in the form of leaf litter. At La Selva, Costa Rica, I examined the leaf litter of young *Hyeronima alchorneoides* trees located in three adjacent monoculture plots planted in 1991, 2001, and 2004. I found evidence for changes in leaf lifespan with tree age. This may support the idea that inter-leaf competition and the permanence of fixed carbon change as *H. alchorneoides* trees age.

Key Words: canopy cover, canopy volume, photosynthesis, respiration

INTRODUCTION

A leaf can be an asset or a cost to a plant, depending on how much energy it produces or consumes. As trees increase in height and grow new leaves high in their canopies, old leaves that are lower in their canopies may become shaded and respire in excess of their photosynthetic contribution. Such leaves that become a net cost to their parent tree are often dropped in the form of leaf litter. Thus, the rate of leaf litter fall may serve as an indicator of inter-leaf competition within trees.

The rate of leaf litter fall from a tree may also serve as an indicator of leaf lifespan. Assuming that the lifespan of leaves is equal across trees with different numbers of leaves, then the number of leaves falling from the tree per unit time should be in proportion to the number of leaves on the tree. If the ratio of the number of leaves falling per unit time to the number of leaves on a tree is not equal across ages, then the lifespan of leaves on a tree may be changing as a tree ages.

I collected data on how leaf litter changes with tree age in monocultures of *Hyeronima alchorneoides*, a tropical, non-deciduous tree. Such changes in leaf litter may be insightful in understanding how inter-leaf competition and leaf lifespan change with tree age.

These relationships may also illuminate how the dynamics of carbon storage change with tree age. The carbon that is fixed by trees with short leaf lifespans may be cycled back into the atmosphere more rapidly, through leaf decomposition, than carbon that is fixed by trees with long leaf lifespans. This suggests that trees which allocate fixed carbon to long-lifespan leaves may serve as longer-term carbon sink than trees that allocate fixed carbon to short-lifespan leaves. Understanding these potential changes in the dynamics of carbon storage across tree ages is an important goal for *H. alchorneoides*, since it is a candidate for reforestation and silviculture in Central America (Jimenez 2002).

METHODS

I studied *H. alchorneoides* in an experimental monoculture plantation located at the confluence of the Puerto Viejo and

Sarapiqui Rivers at La Selva Biological Station, Costa Rica. The monoculture was composed of three adjacent similarly sized plots of *H. alchorneoides*. One plot was planted in 1991, a second in 2001, and a third in 2004 (Haggar 1997). The density of the monoculture was constant across tree ages, with one tree planted approximately every 3 m. In each plot, I randomly placed three, 9 m^2 quadrats. Each quadrat was bounded by four trees, with one tree in each corner of the quadrat.

H. alchorneoides leaves turn a reddish-orange color before they fall and become brown as they decompose on the ground, allowing for easy identification of recently fallen leaf litter. Within each quadrat I quantified the abundance of recently fallen (red-orange) *H. alchorneoides* leaf litter and measured the area [leaf length*leaf width] of each leaf. I summed the areas of all individual leaves per quadrat to calculate total area of leaf litter per quadrat.

All of the relationships I examined appear to be non-linear. However, because I had multiple replicates for each tree age, I was able to use one-way ANOVAs to examine how leaf litter abundances (total number of leaves) per quadrat, average leaf area per quadrat, and total leaf area per quadrat change with age (JMP 5.0.1). Because of unequal variances in my samples, I was unable to meet assumptions of normality. However, I had a balanced experimental design and therefore was able to use parametric tests.

RESULTS

The quadrats of one year-old trees contained the fewest leaves (mean ± SE, 2.37 ± 1.93), quadrats of four year-old trees contained the most leaves (11.11 ± 0.68), and quadrats of 14 year-old trees contained an intermediate number of leaves (6.95 ± 0.89; $F = 13.32$, df = 2, 6, $P < 0.01$, all means significantly different from each other, Tukey $\alpha = 0.05$).

The quadrats of one year-old trees had the largest average leaf size (475.1 ± 57.6 cm^2), four year-old tree quadrats contained intermediate-sized leaves (282.90 ± 20.20 cm^2), and 14 year-old tree quadrats contained the smallest leaves (171.9 ± 26.4 cm^2; $F = 13.17$, df = 2, 6, $P < 0.01$, all means significantly different from each other, Tukey $\alpha = 0.05$).

One year-old trees produced the least amount of total leaf litter per quadrat (1267 ± 32 cm^2) and four year-old trees produced the most total leaf litter per quadrat (2177 ± 224 cm^2). The 14 year old trees produced an intermediate amount of total leaf litter per quadrat (6130 ± 441 cm^2; ANOVA, $F = 87.73$, df = 2, 6, $P < 0.01$, all means significantly different from each other, Tukey $\alpha = 0.05$).

DISCUSSION

Although the data I collected show that total area of leaf litter per quadrat peaks at an intermediate age, my informal observations suggest that total canopy cover increases with age. This implies that the lifespan of leaves on 14 year-old trees might be longer than the lifespan of leaves

on four year-old trees. If the lifespan of leaves were equal across trees of different ages, then the number of leaves in the leaf litter should be in proportion to the number of leaves on the tree. However, the four year-old *H. alchorneoides*, which I informally observed to have fewer canopy leaves when compared to 14 year-old *H. alchorneoides*, produced more leaves in its leaf litter than the older 14 year-old *H. alchorneoides*. Therefore, the lifespan of leaves is probably not equal for these trees of different ages; four year-old trees may rapidly drop the leaves they produce.

What might cause these differences in leaf lifespan? Perhaps the short leaf lifespan on four year-old *H. alchorneoides* is a result of high inter-leaf competition for light. Future studies should examine how mutual shading by canopy leaves changes with tree age and determine whether abcission rates and leaf longevity change accordingly.

It is likely that mutual shading by leaves is only one of many factors that may influence the lifespan of leaves. Other factors that influence leaf longevity might differentially affect leaves on trees of different ages. Herbivory, for example, might cause a leaf to be dropped from the canopy, if it causes the leaf to be a net cost to a plant. Leaves on younger trees and older trees could be differentially affected by leaf herbivory.

Regardless of the mechanism, the suspected short lifespan of leaves on four year-old *H. alchorneoides* implies that, all else being equal, carbon fixed by *H. alchorneoides* remains fixed for different periods of time at different stages in the tree's life. Since canopy cover is increasing as a tree grows, every unit leaf area that is dropped from the canopy is subsequently replaced by at least one equal unit leaf area. Therefore, a short leaf lifespan necessitates a high leaf turnover rate and a high allocation of fixed carbon towards leaf replacement. Because trees fix carbon by taking CO_2 out of the atmosphere, differential carbon fixation across tree ages is important in assessing permanence of carbon stores and potential atmospheric CO_2 reduction resulting from planting trees.

This study was limited to the early life stages of *H. alchorneoides.* Obtaining data over the entire lifespan of *H. alchorneoides* would be insightful in understanding the potential influence of leaf longevity on carbon fixation over the entire life of a tree. Because larger trees have more leaves, any possible implications of differences in leaf litter amounts across ages found in my data, such as potential differences in carbon storage permanence, could be exaggerated in the oldest *H. alchorneoides* individuals.

Literature Cited

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