Ecology:

Patterns in the Amount of Leaf Litter Dropped by Hyeronima alchorneoides Trees of Varying Ages:

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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 an asset, a tree can drop them in the form of leaf litter. At La Selva Biological Station, 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 suggests that inter-leaf competition and the permanence of fixed carbon change as H. alchorneoides trees age.

Introduction

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

Assuming that the lifespan of leaves is equal among trees with different numbers of leaves, then the number of leaves falling from a tree per unit time should be in proportion to the number of leaves on that tree. If the ratio of the number of leaves falling per unit time to the total number of leaves on a tree is not equal across trees of varying ages, then there may be evidence for changes in the lifespan of leaves with increasing tree age.

I collected data on leaf litter in three monocultures of Hyeronima alchorneoides, a tropical, non-deciduous tree, to investigate how inter-leaf competition and leaf lifespan change with tree age. Assessment of these relationships may reveal changes in the dynamics of carbon storage as tree age increases. 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 store carbon for a longer period of time than trees that allocate fixed carbon to short-lifespan leaves. Understanding these potential changes in the dynamics of carbon storage across trees of varying ages is an important goal for *H. alchorneoides*, since it is a candidate for reforestation and silviculture efforts in Central America (1).

**Methods**

I studied *Heronima alchorneoides* trees in an experimental monoculture plantation located at the confluence of the Puerto Viejo and Sarapiquí Rivers at La Selva Biological Station, Costa Rica. The monoculture was composed of three adjacent, similarly sized plots. One plot was planted with *H. alchorneoides* trees in 1991, a second in 2001, and a third in 2004 (2). Tree density did not vary between the plots, with one tree planted approximately every three meters. In each plot, I randomly placed three 9-m² 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, allowing for easy identification of recently fallen leaf litter. Within each quadrat I counted recently fallen (red-orange) *H. alchorneoides* leaves 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 in each quadrat.

All of the relationships in these data appeared 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 the total number of leaves per quadrat, average leaf area per quadrat, and total leaf area per quadrat changed with age. All analyses were performed using JMP 5.0.1.2. Because I used a balanced experimental design, the fact that variances did not meet the assumption of equality did not preclude the use of 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; ANOVA, F = 13.32, df = 2, 6, P < 0.01; all means significantly different from one another, Tukey / = 0.05).

The quadrats of one year-old trees had the largest mean leaf size (475.1 ± 57.6 cm²); quadrats of four year-old trees contained intermediate-sized leaves (282.90 ± 20.20 cm²), and quadrats of 14 year-old trees contained the smallest leaves (171.9 ± 26.4 cm²; ANOVA, F = 13.17, df = 2, 6, P < 0.01; all means significantly different from one another, Tukey / = 0.05).

One year-old trees produced the least amount of total leaf litter per quadrat (1267 ± 32 cm²) and four year-old trees produced the most total leaf litter per quadrat (2177 ± 224 cm²). The 14 year-old trees produced an intermediate amount of total leaf litter per quadrat (6130 ± 441 cm²; ANOVA, F = 87.73, df = 2, 6, P < 0.01; all means significantly different from one another, Tukey / = 0.05).

**Discussion**

Although these data show that total area of leaf litter per quadrat peaks at an intermediate age, my 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 lifespans of leaves were equal across trees of different ages, then the number of dropped leaves should be in proportion to the total number of leaves on the tree. However, the four year-old *H. alchorneoides*, which I observed to have fewer canopy leaves when compared to 14 year-old *H. alchorneoides*, produced more leaf litter than the older 14 year-old *H. alchorneoides*. Therefore, the lifespan of leaves is probably not equal for 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 of 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 abscission 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. For example, if tree age is correlated with the susceptibility of leaves to herbivory, and damage by herbivores causes a leaf to become a net cost to a plant, rates of abscission may vary with tree age due to the differential effect of herbivory on young and old trees.

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 increases as a tree grows, every unit of leaf area that is dropped from the canopy is subsequently replaced by at least one unit of 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, and, by dropping leaves, release fixed carbon as CO$_2$ into the atmosphere, an understanding of how rates of carbon fixation and release vary with tree age is important for accurate assessments of the 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 useful 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 abundance across ages, such as potential differences in carbon storage permanence, could be exaggerated in the oldest *H. alchorneoides* trees.

**References**