LEAF TURNOVER AND SELF SHADING IN THEOBROMA CACAO

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Abstract

Theobroma cacao is a deciduous understory tree that produces new crops of leaves in flushes 2-4 times per year. I examined if the young vertical red leaves that are not photosynthesizing could potentially shade mature horizontal productive leaves and if the vertical growth form and timing of the flush minimizes self shading. Results indicate that at the same moment young leaves turn green fungi and herbivory increase on mature leaves and large numbers of mature leaves senesce and abscise. The young leaves up until this point allowed four times the amount of light energy pass through than mature leaves. This strategy of development maintains only one population of mature leaves at the end of branches at one time, thus insuring minimal self shading.

Introduction

Theobroma cacao is a deciduous understory tree of lowland rain forests, producing 2-4 flushes of new leaves a year (Hansen, 1983). Young leaves are thin, red, and hang vertically, while mature leaves are dark green, and may move to a horizontal position by the means of two plovini located in the petiole. There is a high leaf turnover rate and young leaves receive very little photosynthetically active radiation (PAR). I generated two hypotheses to explain the growth strategy in T. cacao. 1) The red color and vertical orientation of young leaves is an adaptation to reduce damage in intense sunlight. 2) Young leaves are produced quickly to maintain the high turnover rate, so they grow in a manner that minimizes self shading of more efficient mature leaves.

It is well known that T. cacao is extremely shade tolerant and needs moist soils (Hansen, 1983). I will focus on the second hypothesis, reasoning that T. cacao is an understory plant and must maximize the amount of PAR hitting its leaf surface. It has been shown elsewhere that if the leaf area index is greater than three, then net productivity will tend to be greater if the outer leaves are oriented vertically and the inner and lower leaves are horizontal (Nobel, 1983). I addressed the following questions: 1) Can the leaves produced from the most recent flush potentially shade existing productive leaves? 2) Do the physical properties of young leaves and the timing of development minimize self shading?

Methods

An approximately 50 meter square plot of former T. cacao plantation was chosen on the Las Vegas Trail, La Selva Biological Reserve, Costa Rica. First, I developed a subjective age scale in order to quickly classify leaf age and physical characteristics.

1: Bright red, very delicate, smaller than 10cm length
2: Light orange, larger than 10cm, still delicate,young
3: Light green, Almost full size
4: Dark green, full size
5: Dark green, large, has moved to less than 60° with the horizontal
Mature: Leaf from previous, petiole hardened and internodal stem is woody.

I randomly picked 44 young leaves and 15 mature leaves and tested for leaf transparencies by covering a 35mm SLR camera lens with a leaf centered at the main vein and measuring the f-stop values with a constant bright light pointed at the lens.

Randomly chosen points were located in the study plot, and I collected the following data on the nearest branch, for 39 replicates: 1) age class of the most recently flushed leaves; 2) the number of most recently flushed leaves and the number of mature leaves; 3) orientation in respect to vertical and horizontal of the most recently flushed leaves, and 4) the estimated damage by percent surface area to mature leaves by fungus and herbivory.

Results

Relative leaf transparencies with respect to age class were derived from f-stop values. Results of light absorbance across all age classes show a much greater transparency of the youngest leaves (Table 1).

Using a log transform on the ratio of young leaves to mature results in a good linear correlation with the young leaf age class. The log of the ratio of young leaves to mature leaves is positively correlated with the corresponding young leaf age class ($r = .78$, $n = 39$, $p < 0.01$). Furthermore, the ratio of leaves in age class 3-5 (green young leaves) to mature leaves is significantly greater than the ratio of leaves in age class 1-2 (red young leaves) to mature leaves ($t = 11.8$, $df = 32$, $p < .01$).

The relationship of percent damage to mature leaves with age class of younger leaves is also significantly different from zero ($r = .63$, $n = 39$, $p < .01$).

Discussion

The strategy of T. cacao may be to reproduce very productive leaves that have a short life span, necessitating a high rate of leaf turnover. It appears that T. cacao maintains one generation of photosynthetically active leaves at one time. My results indicate that at the point when young leaves build up chlorophyll and enlarge, mature leaves senesce and abscise resulting in a large increase in the ratio of young leaves to mature leaves. This is a very noticeable change, and may indicate that it is not advantageous for T. cacao to maintain two populations of leaves at one time. This pattern is represented in a simple schematic model in figure 3.

It is advantageous for trees to distribute all the available PAR as evenly as possible (Nobel, 1983). The diagram of branch morphology (Figure 4 shows how two generations of mature (horizontal) leaves would produce much self shading. If a small proportion of a plant was above its photosynthetic saturation point while other leaves in the interior of the tree were not photosynthesizing at an optimal level or even below the compensation point, PAR would be wasted. A shade tolerant species is under selective pressure to maximize photosynthesis. My results show that at the same time young leaves turn green and many mature leaves senesce there is an increase in herbivory and/or fungal growth on the leaves. This may be the result of chemical defenses being shut down in the old leaves and reclaiming nutrients before abscission.

There may be other pressures that result in the vertical orientation of leaves. A thin leaf that absorbs very little light energy and receives very little PAR per unit area should help T. cacao adapt to conditions of direct sunlight. Indeed, in direct sunlight the plovini can move the leaf and control leaf surface temperatures (Hansen, 1983). In addition, the vertical orientation of the delicate leaves may prevent physical damage during rainstorms.

The high population of fungus in the study plot may have added a complication in the study. Fungi infested trees would exhibit earlier turnover of mature leaves.

Because T. cacao generally only maintains one population of mature leaves at one time, it appears that the tree exhibits a preferred investment in young leaves. If mature leaves are in fact generally found below the photosynthetic compensation point, then self shading is intrinsic to the patterns and morphology of leaf turnover.

Table 1 Relative leaf transparencies in T. Cacao with respect to leaf age.

	Leaf Age Class					
	1	2	3	4	5	Mature
Relative light through leaf	3.72	3.20	2.54	2.00	1.38	1.00
S.D.	0.09	0.06	0.12	0.00	0.11	0.08

Figure 1 Comparison of log transformed data of the ratio of numbers of most recently flushed leaves to young leaves with respect to age class, color, and orientation of the most recently flushed leaves.

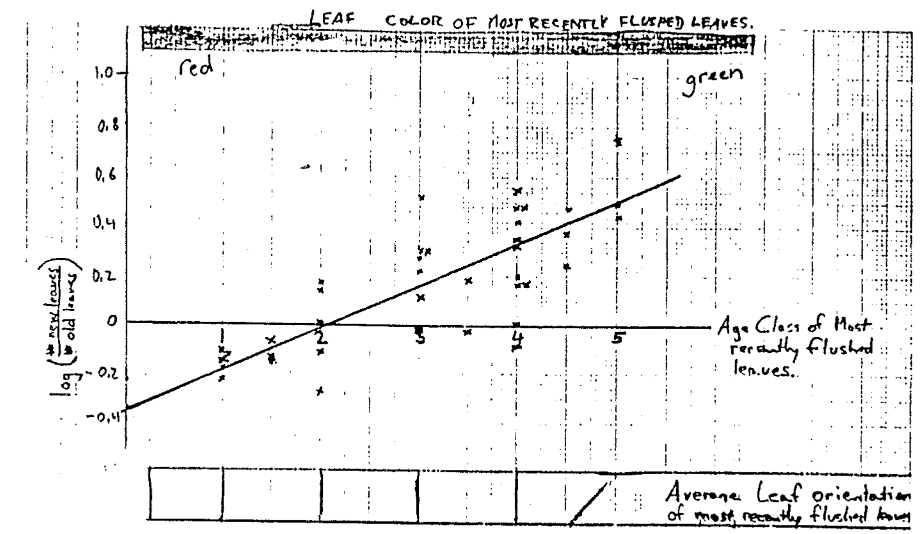


Figure 2 Comparison of estimated percent damage on older leaves to age class of the most recently flushed leaves on the same branch.

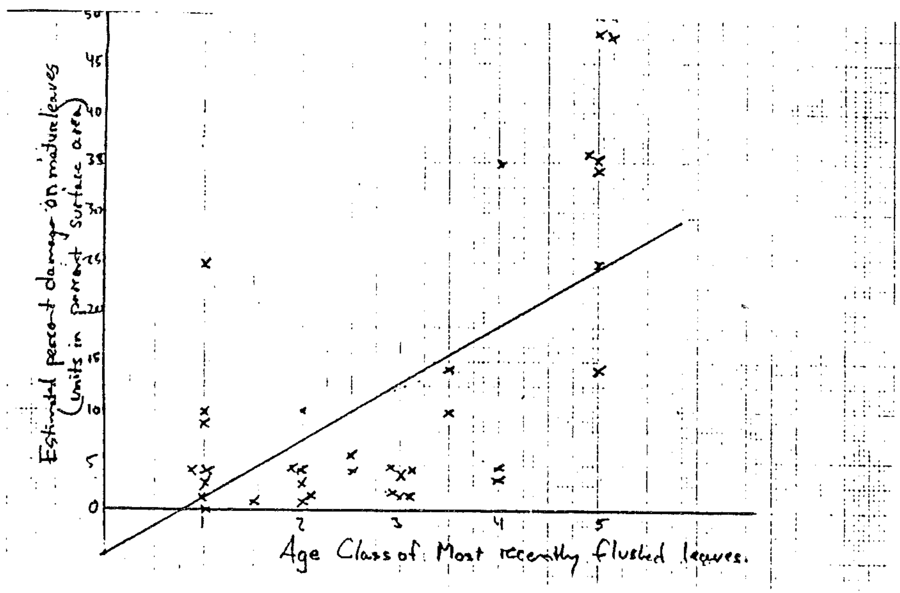
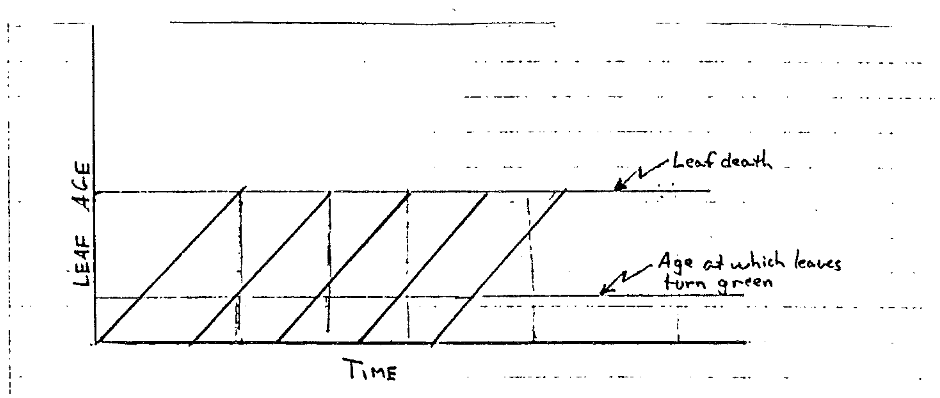


Figure 3 Model of leaf replacement in T. cacao. Each line represents a generation or flush of leaves. Any vertical line determines the age structure of the leaf population at a specific point in time.



Literature Cited

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