Report

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Indigenous Knowledge Informing Management of Tropical Forests: The Link between Rhythms in Plant Secondary Chemistry and Lunar Cycles

This research used knowledge of the indigenous practice of timing nontimber forest product harvest with the full moon to demonstrate that chemicals controlling the decomposition rate of foliage fluctuate with the lunar cycle and may have developed as a result of plant-herbivore interactions. Indigenous knowledge suggests that leaves harvested during the full moon are more durable. Palm leaves harvested during the full moon had higher total C, hemicellulose, complex C and lower Ca concentrations. These chemical changes should make palm leaves less susceptible to herbivory and more durable when harvested during the full moon. This study proposes a mechanism by which plants in the tropics minimize foliage herbivory and influence the decomposition rates of senesced leaves and their durability, especially during the full moon. This research supports the need to use natural life cycles in managing forests and provides a scientific basis for an indigenous community's harvesting practice.

INTRODUCTION

Even though the practice of harvesting agricultural and forest products based on the lunar cycles is common knowledge in many tropical regions, the existence of these practices has not been systematically documented (1) nor has a scientific rationale been presented that explains lunar-based harvesting practices. Lunar-based harvesting is a practice mentioned by indigenous groups to ethnobotanists and social ecologists studying the use and harvest of products in parts of tropical Africa and the tropical Americas (1–6). Many different products, such as rice in Indonesia, (1), certain wet woods in Puerto Rico, and palm fronds for roofing thatch in the American tropics (6) are harvested according to lunar phase. Many harvesters of natural resources in tropical regions such as Belize, Panama, and Puerto Rico believe that it is critical to harvest these resources during the full moon because materials harvested at this phase are perceived to be more durable (6).

The fact that the scientific literature documents a periodicity to plant growth that appears to follow lunar or solar flares supports the hypothesis that indigenous knowledge of harvesting plants has a scientific basis. The rhythmic responses of plants and animals to the lunar cycle have been reported for decades (7, 8) but these results have not been linked to practical management practices. The mechanistic explanations for why these correlations exist between plant growth responses and lunar or sunspot activity have been more difficult to explain. We hypothesized that there was a link between the timing of indigenous communities harvesting products from tropical forests and plant production of secondary defensive chemicals that occur over the short time scales of a lunar cycle. The perception by indigenous communities that products collected during a full moon are more durable suggests that the persistence of harvested plant tissues can be attributed to their lack of susceptibility to degradation and decomposition (e.g. insects and fungi) (9, 10). We hypothesized that changes in the concentrations of these complex secondary plant chemicals would be detectable with changes in the lunar cycle and that palm tissues harvested during the full moon would have higher C concentrations than during the other lunar phases. The purpose of this research was to document whether changes in plant carbon concentrations and secondary chemical production could be detected for palms according to lunar cycles. We were also interested in seeing whether 2 spatially associated species (*Heliconia carabea*, *Palicourea riparia*) of the palm would show similar changes in secondary chemistry with lunar phases. We hypothesized that *H. carabea* would utilize a C-based defensive approach to insect herbivores similar to palms so that the lunar linked fluctuations in plant chemistry should be similar to that hypothesized for *P. montana*. In contrast, we hypothesized that *P. riparia* would utilize a N-based defense against herbivores (since it contains almost twice as much N in its foliage) and would not have lunar phase changes in its secondary chemistry.

The historical and currently wide usefulness of palm species around the world (11–14) make this an ideal species to use in a case study attempting to determine whether there is a scientific basis for harvesting practices being linked to lunar cycles. Palms supply over 390 products from 200 genera for both local and international markets (11) and they are commonly found as both an overstory and understory plant species in the pantropical region (15). In tropical forests of the American, African, and Asian region (14), indigenous communities harvest palms for a variety of nontimber forest product uses, especially as an important source of roofing material (12, 13). In Central America, palms are often harvested for roofing thatch according to lunar phases and local knowledge suggests that fronds harvested during the full moon significantly outlast material harvested during other lunar phases (16).

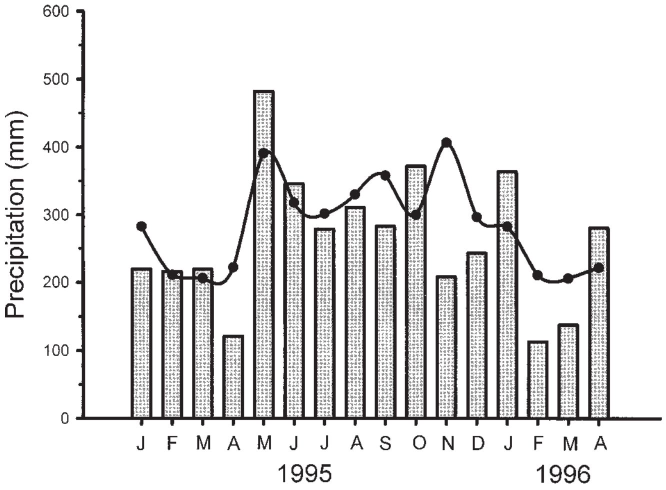
Determining whether there is a scientific basis for this indigenous knowledge is even more important today because of the increased harvesting demands for these products as part of implementing Integrated Conservation and Development Programs (ICDP) throughout the world (17). These international development programs may increase the use and harvesting of palms in a nonsustainable manner as a nontimber forest product (14), and overexploitation and depletion of palms have already been reported (18). In a 1991 Belize-wide census, it was reported that *Sabal mauritiiformis* (bayleaf) was used to thatch 13.5% of the residence roofing and there is an increasing commercial demand for bayleaf thatch by the tourism industry (14, 19). It has been estimated that on average 3500–4500 leaves are required to construct a roof for an average sized home (14). Since indigenous knowledge suggests that palm fronds harvested during the new moon decay within a couple of years while those collected at or around the full moon last for 12–20 years (16), a strategy based on using indigenous knowledge to develop ecological sustainable harvesting practices is worth considering.

MATERIALS AND METHODS

Sampling sites and harvested plant characteristics: Plant tissues were collected in a subtropical wet forest called the Tabonuco forest zone of the Luquillo Experimental Forest (LEF) (18°10'N, 65°30'W) in northeastern Puerto Rico. Peak precipitation (average 400 mm month^{-1}) occurs between the months of May and November, with drier periods recorded between January and April (inputs average 200–250 mm month^{-1}) (20). Mean monthly air temperatures average between 21–24°C throughout the year (20). Precipitation data for 1995–1996 are provided in Figure 1 for the research site. This subtropical wet forest is dominated by *Dacryodes excelsa* (tabonuco), *Prestoea montana* (sierra palm), *Sloanea berteriana,* and *Cecropia schreberiana*. The understory contained many plant species, but was dominated by *Danea nodosa*, *Ichnanthus palens*, *Heliconia carabea*, *Palicourea riparia*, *Piper glabrescens*, *Pilea inegualis*, *Prestoea montana*, and *Scleria canescens.*

Foliage samples were collected from the following 3 species growing in the understory of this forest: *Prestoea montana* (sierra palm), *Heliconia carabea*, and *Palicourea riparia. Palicourea riparia* is a dicot shrub species, and the 2 other species are monocots. *Heliconia carabea* and *P. montana* are predominantly found growing in clumps along streams and in tree-fall gaps close to streams while *P. riparia* is found growing throughout the forest. Palms were the focus of this study, but samples were also collected from the other 2 species to test how general might be the relationship between plant chemistry and lunar phases. Samples were collected from El Verde and Bisley Experimental Watersheds, 2 study sites at LEF (2 watersheds were sampled at Bisley—Bisley 3 and Bisley 5).

Figure 1. Monthly precipitation data are presented for the subtropical forest, Bisley Experimental Watershed, Luquillo Experimental Forest, Puerto Rico. The 10-yr average precipitation for each month is given as a line drawing above the bar graphs which represent the monthly precipitation summaries from January 1995 to April 1996.



Foliage sampling methods: In 1996, tissue samples were harvested from plants growing in the understory of the Tabonuco forest over 2 lunar cycles (see Fig. 2) and were collected consecutively at each lunar phase during the months of January-March. Sampling occurred during the following dates to correspond to each of the lunar phases (number of individual plants sampled is given in parentheses for *P. montana*, *H. carabea* and *P. riparia*, respectively): *i*) first quarter–January 10, 1996 (n = 13; 6; 3); *ii*) full moon–February 4, 1996 (n = 21; 10; 10); *iii*) last quarter–February 12, 1996 (n = 10; 3; 3); *iv*) new moon–February 19, 1996 (n = 11; 3; 3); *v*) first quarter–February 26, 1996 (n = 11; 4; 4); *vi*) full moon–March 5, 1996 (n = 11; 3; 3); *vii*) last quarter–March 11, 1996 (n = 5; 4; 3); *viii*) new moon–March 17, 1996 (n = 11; 4; 4). All plants were tagged so that they would not be subsequently sampled during later lunar phases.

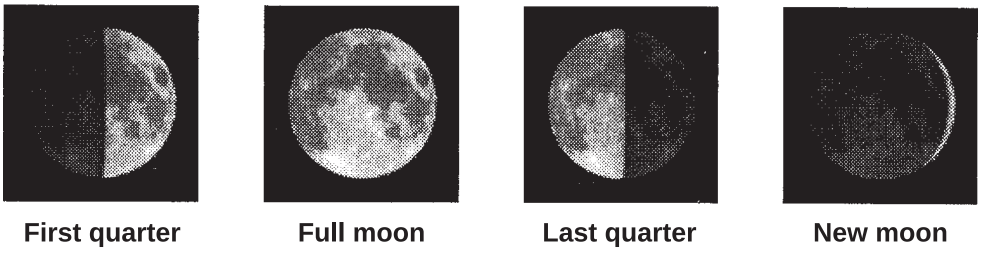
Foliar samples of *P. montana* were collected from 2–3 m tall plants, i.e. size of palms typically used to harvest leaves for roof thatch (14). Since *P. montana* typically maintains 4–6 fronds, all samples were taken from the 3rd and 4th oldest palm fronds from the newest shoot. For each palm frond, tissue samples were collected at the base, mid-section and top of the frond (the center rib was not included) and combined per individual plant. After collection, all samples were immediately frozen and subsequently prepared for chemical analyses. The understory palms included in the sampling were not reproducing during the study period.

Palicourea riparia and *H. carabea* tissues were collected from plants that were 1–2 m in height. *Palicourea riparia*, a shrub, was sampled by collecting an equal number of leaves from each of the 3 canopy-height zones of one plant. Each *P. riparia* leaf sample was collected from one plant. For *H. carabea*, one leaf was collected from each sampled plant, the second oldest leaf.

Chemical analyses of tissues: Each sample of plant tissue collected during the 8 sampling dates was analyzed for total carbon and nitrogen using a LECO CHN-600 Analyzer. For the Puerto Rico samples, element concentrations (Ca, K, Mg, P, Al, Mn, Zn) were determined using a Perkin-Elmer Optima 3000 Inductively Coupled Plasma Spectrophotometer on sulfuric acid-hydrogen peroxide digested tissues. Secondary chemistry of leaf tissues was determined using standard cell-wall fractionation and fiber analyses to obtain lignin, polyphenolics, cellulose, hemicellulose, and soluble sugar fractions (21, 22). When there were no significant differences in the chemistry data for palm foliage collected in Puerto Rico during the 2 times of each lunar phase, data are combined to present the results in Table 1. No significant changes in specific leaf area (g cm^{-2}) were recorded between the different sampling dates for any of the species.

Statistical analyses: One-way ANOVA's using Duncan's Multiple Range Test with alpha set at 0.05 was used to test for significant differences in tissue chemistry within a species and

Figure 2. Phases of the lunar cycle.



First quarter **Full moon** **Last quarter** **New moon**

Prestoea montana **growing in the understory of a Tabonuco forest, Luquillo Experimental Forest, Puerto Rico. Photo: K. Vogt.**

across the lunar phases using SAS (version 6.11) for Windows (SAS 1990, SAS/STAT user's guide. SAS Institute, Cary, NC. USA).

RESULTS AND DISCUSSION

Changes in *P. montana* Foliage Chemistry with Lunar Cycles

Rhythmic behavior in plants and animals is ubiquitous and many studies have confirmed that organisms as well as tides have intrinsic rhythms with the lunar cycle (7). Recent articles have provided evidence that plant growth dynamics such as tree stem diameter and tree radial growth are linked to lunar nodal tides or sunspot activity (8, 23, 24). In this study, short-term changes were detected in the chemistry of palm leaves collected during the different phases of the moon suggesting that there might be a scientific explanation for the lunar related harvesting practices used by indigenous communities.

Indigenous knowledge suggests that palm leaves harvested during the full moon are more durable than those harvested during the new moon. The results of this study support the idea that there is a chemical basis for the perceived greater durability of leaves harvested during the full moon and that palm leaves harvested during the full moon would decompose at slower rates (10, 25). During this study, those elements known to regulate the rate at which foliage decomposes in this tropical forest in Puerto Rico (10) either increased or decreased in concentration so that palm leaves collected during the full moon would have decomposed at a slower rate while those collected during the new moon would decompose at a faster rate.

The amount of total C and complex C in plant tissues is an effective predictor of the decay rates of palm tissues and the ability of plants to protect themselves against herbivores; typically higher C levels decrease decomposition and herbivory rates (10, 26). During this study, C levels increased significantly for *P. montana* foliage during the full moon compared to the new moon

Table 1. Concentrations of secondary plant chemicals and elements for *Prestoea montana* fronds collected by lunar phase in the Luquillo Experimental Forest, Puerto Rico (x ± SE)*.

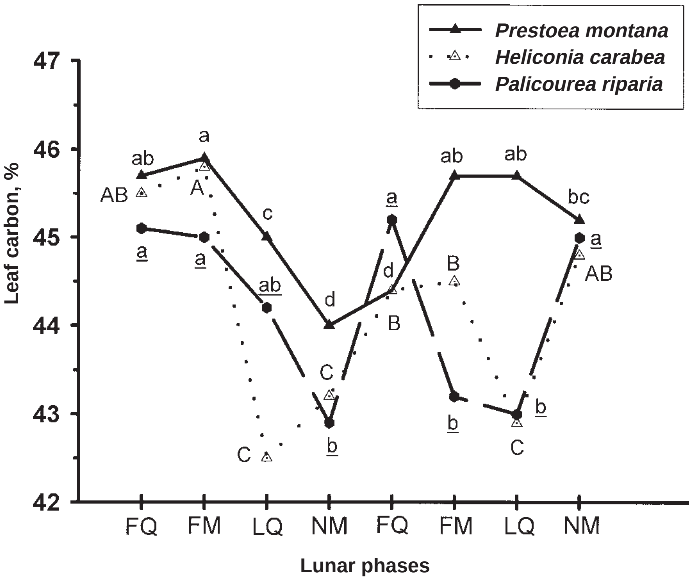
	First quarter	Full moon	Last quarter	New moon
C:N ratio**	30.9a	29.9a	28.1b	28.2b
N, %	1.45 ± 0.02a	1.55 ± 0.01b	1.60 ± 0.01c	1.59 ± 0.01c
C, %	44.4 ± 0.1a	45.8 ± 0.02b	45.7 ± 0.1b	44.0 ± 0.04a
P, $g\ kg^{-1}$	87 ± 4a	98 ± 1a	100 ± 1a	92 ± 2a
K, $g\ kg^{-1}$	564 ± 36a	764 ± 198a	743 ± 58a	758 ± 145a
Mg, $g\ kg^{-1}$	419 ± 16a	444 ± 7a	434 ± 5a	426 ± 22a
Ca, $g\ kg^{-1}$	701 ± 39a	628 ± 8b	697 ± 6a	748 ± 21a
Soluble sugars, %	29.2 (1.7)ab	29.2 (0.3)a	29.4(0.4)a	30.9 (0.5)b
Hemicelluloses, %	15.2 (0.6)a	17.1 (1.1)b	16.3 (1.6)ab	15.7 (0.4)a
Cellulose, %	34.1 (1.3)a	33.5 (2.1)a	32.3 (3.2)a	34.0 (0.9)a
Complex C, %***	19.2 (0.1)a	19.2 (0.3)a	18.4 (0.3)b	17.2 (0.2)c

* Sample size for nutrient analyses for each lunar phase was: n = 24 for first quarter; n = 33 for full moon; n = 15 for last quarter; n = 22 for new moon. Sample size for secondary chemistry analysis was n = 15 for the first quarter, n = 33 for full moon, n = 10 for last quarter and n = 8 for the new moon.

** Mean values followed by the same lower case letter are not significantly different from one another when comparing within the same analysis by row.

***Complex C = Polyphenolic and/or lignin compounds

Figure 3. Carbon concentrations of *Prestoea montana, Heliconia carabea* and *Palicourea riparia* foliage collected during the 8 sampled lunar phases at the Luquillo Experimental Forest, Puerto Rico. The sampling dates are given consecutively starting from the left side of the X-axis with FQ – January 10, 1996; FM – February 4, 1996; LQ – February 12, 1996; NM – February 19, 1996; FQ – February 26, 1996; FM – March 5, 1996; LQ – March 11, 1996; NM – March 17, 1996. Mean values followed by the same letter (lower case for *Prestoea*, lower case underlined for *Palicourea*; upper case for *Heliconia*) are not significantly different when comparing within a species for the 8 sampling points at P = 0.05. (FQ = first quarter; FM = full moon, LQ = last quarter and NM = new moon).



(Fig. 3). For example, *P. montana* leaves harvested during the full moon had significantly higher C than leaves harvested during the new moon when comparing results from the first lunar cycle for which data were collected (i.e. February 4 full moon *vs* February 19 new moon) (Fig. 3). A similar pattern of change in foliar C contents was recorded for *P. montana* leaves collected during the second lunar cycle (i.e. March 5 full moon *vs* March 17 new moon) except the differences were only significant at P = 0.08. When combined data were analyzed for each lunar phase for the 2 cycles (Table 1), C in the foliage differed significantly when comparing the full moon and new moon phases (n = 110, F-crit$_{3,102}$ = 2.69, P = 0.012). Significant differences were also recorded between the first and last quarter phases of the moon; however, the variability between sampling dates did not allow for a pattern to be detected (Fig. 3).

The significantly higher total C levels in palm leaves harvested during the full moon were also reflected in the significantly higher complexed C (i.e. polyphenolic and/or lignin compounds) and higher hemicellulose concentrations measured during this lunar phase (Table 1). The small difference in complexed C contents of *P. montana* foliage recorded between the full moon and new moon are at a level that are relevant at the system level since palm fronds decay rates are controlled by polyphenolic concentrations at levels of 1–2% (10). Leaves harvested during the new moon had the lowest complex C levels compared to the other lunar phases while the highest complex C levels were measured during the full moon and during the first quarter (Table 1). The complex C fraction measured during this study is comprised of a high portion (22%) of phenolic type fragments that are of nonlignin origin based on pyrolysis gas chromatography mass spectrometry analysis (27). Whether these polyphenolic compounds are those that increase in levels during the full moon is not known. Plants growing in tropical regions do have higher polyphenolic concentrations in their tissues compared to temperate zone species and the total concentrations recorded for *P. montana* foliage is at the high end of what has been measured for 46 canopy tree species (i.e. 2.6–22.6%) in a lowland neotropical rain forest (26).

We cannot explain why hemicellulose levels would change significantly with lunar cycles except that this is part of the carbon reallocation occurring within a plant. The lower soluble sugars concentrations of leaves harvested during the full moon (Table 1) could be part of internal plant reallocation but would also be important in reducing herbivory and decomposition rates of foliage during this period. During this study, no differences were detected in the amount of cellulose contained in *P. montana* leaves with lunar phases (t = 1.71, P = 0.36) suggesting this extraction fraction does not change during the short time interval of one lunar cycle.

Even though studies conducted in the temperate zone suggest that N levels are inversely related to the rate of decomposition of foliage litter (28), decomposition studies in the tropics have found no correlation between initial N concentrations and decay rates for several tree species (29, 30). Therefore, one could hypothesize that significant changes in the N concentration of *P. montana* foliage would not be detected when comparing leaves harvested during the full moon to the new moon, and N contents of foliage should not be well correlated to the different persistence levels of harvested palms. During this study, N concentrations did vary in palm leaves collected during the different phases of the 2 lunar cycles, but these changes did not correlate with the full moon and new moon as was recorded for total C (Figs 3 and 4). In general, palm leaves collected during the full moon had intermediate N levels compared to the other lunar phases while the highest levels were measured during both the last quarter and new moon; however, the most significant changes in N were not confined to the full moon and new moon phases. This pattern is easier to observe when combining data from the 2 lunar phases of the two lunar cycles (Table 1). For this analysis, the lowest N levels were found for *P. montana* leaves collected during the first quarter, followed by significantly higher N levels during the full moon, but the highest N levels were recorded during the last quarter and the new moon.

Calcium has been positively correlated with increasing plant growth, resulting in faster decay rates in the tropics (30). In this forest, Ca is a nutrient that limits the decomposition activity of microbes and Ca alone was the best predictor of decay rates (r^2 = 0.64) (29). This suggests that Ca levels should change in response to lunar phases and would help to explain the different durability levels of palms harvested during the full moon and new moon. During this study, Ca concentrations were significantly lower in *P. montana* foliage collected during the full moon compared to the other three phases of a lunar cycle; this pattern was opposite of what was recorded for total C (Table 1). These results suggest that Ca may be one factor that needs to be considered when examining the changing durability of harvested palm leaves with lunar phases.

The other elements (i.e. K, Mg, P, Al, Mn, and Zn) analyzed during this study did not vary significantly with lunar phases (Table 1). The lack of significant changes in concentrations of these elements in leaf tissues with lunar phases is interesting because these elements have not been found to be important in controlling the decomposition rates of litter tissues in this forest (30).

Changes in Foliage C and N of Associated Plant Species with Lunar Cycles

The lunar correlated patterns of change in total C measured for *P. montana* leaves were also observed for the other understory monocot species, but not for the shrub species sampled during the same lunar phases in this forest (Fig. 3). As had been hypothesized, *H. carabea* had similar significant changes in foliage C as did *P. montana* (i.e. higher C levels during the full moon and lower levels during the new moon) (Fig. 3). In contrast, *P. riparia* did not show this pattern.

Both *P. montana* and *H. carabea* had foliage N concentrations

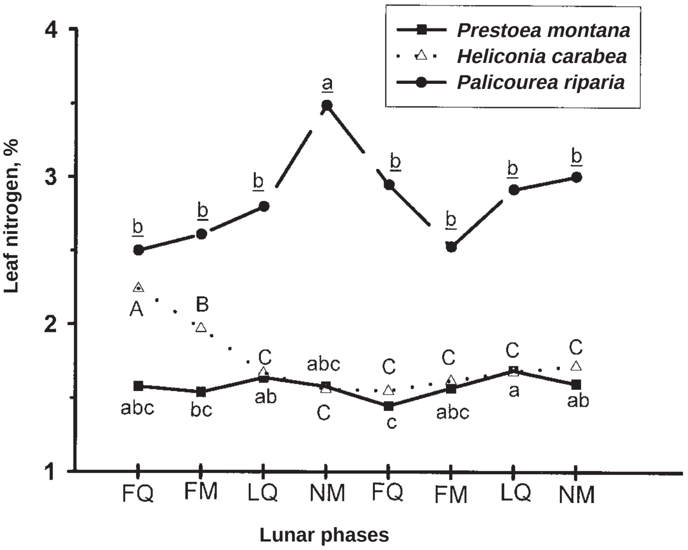


Figure 4. Nitrogen concentrations of *Prestoea montana, Heliconia carabea* and *Palicourea riparia* foliage collected during the 8 sampled lunar phases at the Luquillo Experimental Forest, Puerto Rico. The sampling dates are given consecutively starting from the left side of the X-axis with FQ – January 10, 1996; FM – February 4, 1996; LQ – February 12, 1996; NM – February 19, 1996; FQ – February 26, 1996; FM – March 5, 1996; LQ – March 11, 1996; NM – March 17, 1996. Mean values followed by the same letter (lower case for *Prestoea*, lower case underlined for *Palicourea*; upper case for *Heliconia*) are not significantly different when comparing within a species for the 8 sampling points at P = 0.05. (FQ = first quarter; FM = full moon, LQ = last quarter and NM = new moon).

that were half as high as what was measured for *P. riparia*. In contrast to changes measured in foliage C, both *P. montana* and *H. carabea* had no detectable changes in the N concentrations of foliage with specific lunar phases (Fig. 4). While *P. riparia* had no detectable pattern of change in foliage C with specific lunar phases, significant increases in foliage N were measured during the new moon (February 19 new moon) compared to the other phases of both lunar cycles (Fig. 4). For *P. riparia*, N levels above 3% were only recorded during the new moon phase of the lunar cycle.

No research has been conducted to show the type of chemical defenses used by *P. riparia* to defend itself against insect herbivores; however, this study suggests that it might be N and not C based. Both *P. montana* and *H. carabea* appear to have a C based defensive method to protect themselves against the high herbivory rates that exist in the tropics. These results suggest that developing strategies for harvesting nontimber forest products based on lunar cycles will be successful for some species but cannot be generally applied to the forest. It will be important to consider the type of chemical defense mechanism used by a plant against herbivores, and the physiological response of plants and herbivores to microclimate (see next section).

Proposed Mechanisms for Lunar Linked Changes in Plant Chemistry

Insect-caused herbivory is greater in the tropics than in temperate regions causing insects and plants to have developed strong evolutionary relationships (31). The tropics are known to have a higher number of different insect herbivores that plants have to protect themselves against and overall greater levels and higher diversity of defenses (9, 32). The greater commitment of plants to defenses in the tropics than in temperate regions is thought to be a result of the greater herbivore pressures (31). Insects have also been observed to be more abundant and active with increasing lunar illumination (33–39). Therefore, lunar-correlated changes in foliar chemistry could be induced by changes in insect activity. The link to herbivory and the potentially changing dynamics of herbivores in relationship to lunar cycles is one mechanism that could explain changes in plant secondary chemistry at short temporal scales.

High herbivore pressure has caused plants to develop a variety of strategies to defend themselves. In general, species susceptibility to herbivory depends on many factors with the most important being leaf structure, leaf age, and their nutrient and secondary chemical compositions; these latter factors are those that result in plant tissues being of lower nutritional quality to herbivores (26, 31, 40). Insects are also able to rapidly change their behavior in response to the chemistry of plant tissues. They selectively consume plants with higher foliar nutrient concentrations and are less attracted to leaves with decreased amounts of nutrients and secondary phenolics in excess of their normal diet (41, 42). Low nitrogen and water contents have been repeatedly associated with reduced preferences and performance of insects (43) while the amount of fiber in leaf tissues poses digestive and mechanical problems to herbivores and is negatively associated with herbivory (26).

In the tropics, plants respond to herbivory by increasing their production of tannins, phenolics, or other secondary chemicals at the contact point of herbivory, and/or by translocating more N out of tissues or by complexing N with secondary plant chemicals (29, 44, 45). If these chemicals are formed in response to changing population levels of herbivores, there should be direct links to the decomposition/breakdown rates of these harvested materials since these chemicals do control the rate at which these processes occur (29). Therefore, plant leaves exposed to lower herbivory rates might have higher N and lower amounts of phenolic and/or lignin compounds which should feedback to increase decomposition rates. This explanation supports the hypothesis that plants have evolved to respond to higher periods of insect activity during the full moon by changing the concentrations or allocation of secondary chemicals in leaves.

How much microclimate contributed to our ability to detect the plant secondary changes with lunar cycles during this study needs to be addressed. In the tropics, the relationships between rainfall and herbivory is presently unclear with mixed results reported in the literature. Even at the LEF, herbivory has been reported to be the highest during the wet season (46), constant throughout the year (47) or to be the most severe after long droughts (46). The relationship between climate and herbivory pressures may be important to understand the cyclic pattern of herbivory and the ability to detect the plant chemistry changes recorded during this study. However, this will require detailed sampling of temporal changes in insect herbivores which, as of now, does not exist. However, one study conducted in this Tabonuco forest did report increased insect abundance during the middle of the dry season in February (48) which coincided with the tissue sampling dates of this study. It would be important to determine whether our ability to detect the chemical changes in some of the plants with lunar phases is due to a co-occurrence of high insect herbivore populations during the time of sampling so that plants are actively protecting their tissues and how much the drier period affects the measured variables. What is clear is that plants have to deal with cycles of insect herbivory that are regulated by the temporal frequency of climate and disturbances (49, 50).

This study highlights the importance of managing ecosystems according to natural life cycles, as well as the importance of using indigenous knowledge as a basis for selecting indicators for assessing forest health and condition. Moreover there has been considerable discussion about the need to manage for large-scale disturbances (e.g. fires, hurricanes, El Nino) but less about managing according to life cycles (e.g. harvesting after seed fall, reducing fishing and hunting during critical reproductive periods, etc.). This paper provides a good example of how basic knowledge can provide effective management tools.

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