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Herbivory as a selective agent on the timing of leaf production in a tropical understory community

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In highly seasonal environments (for example, temperate deciduous forest or tropical dry forest) plant phenologies are often constrained by physiological stress caused by seasonal variation in temperature and moisture[1]. Where climatic fluctuations are less pronounced (for example, tropical marine or lowland wet forest communities) determinants of phenology may include biotic selective pressures such as herbivores, predators, competitors, pollinators or dispersers. Temporal patterns of leaf production vary considerably between tropical forest species, but few species produce leaves continuously throughout the year[2]. Even in aseasonal tropical forests, most species show synchronous peaks in leaf production[2]. Results from this one-year study suggest that herbivores may influence leaf phenology of shade-tolerant understory plants in a Panamanian lowland moist forest. Leaves produced during the dry season or in synchronous flushes receive significantly less damage from herbivores than leaves produced during the wet season or out of synchrony with conspecifics.

For a wide range of tropical and temperate plant species, the average biomass lost to herbivores is greater than the biomass allocated to reproduction[3]. In response to the strong selective pressures of herbivores, plants have evolved a variety of chemical and structural defences[4,5]. In many cases these defences are most effective against herbivores of mature leaves, resulting in the majority of damage occurring during the period of leaf expansion[6]. Although expanding young leaves are often chemically defended, the high levels of water and nitrogen and low toughness make them especially vulnerable to herbivores[6-10]. Because leaves expand for a period of only weeks, the timing of leaf production may influence levels of damage.

It has been suggested that two phenological mechanisms may reduce damage to expanding leaves: (1) producing leaves when herbivore abundance is low, or (2) satiating herbivores with highly synchronous flushes[6,8,11-13]. Trees experimentally defoliated in a Costa Rican dry forest responded by producing a second cohort of leaves[14]. The cohort produced 7-10 days later in the wet season and out of synchrony with the population, received significantly higher levels of damage. This suggests the importance of synchronous leaf production as a possible mechanism for escaping or satiating young-leaf herbivores. Rockwood[14] also observed trees 'anticipating' the wet season and producing leaves at the end of the dry season before the appearance of the herbivores, thereby seasonally escaping damage. Although the majority of tropical species produce leaves synchronously, pioneer or gap species growing in high light often produce leaves continuously. McKey[13] has predicted that the young leaves of these species are unlikely to escape herbivores phenologically and will be defended more frequently by extrafloral nectaries.

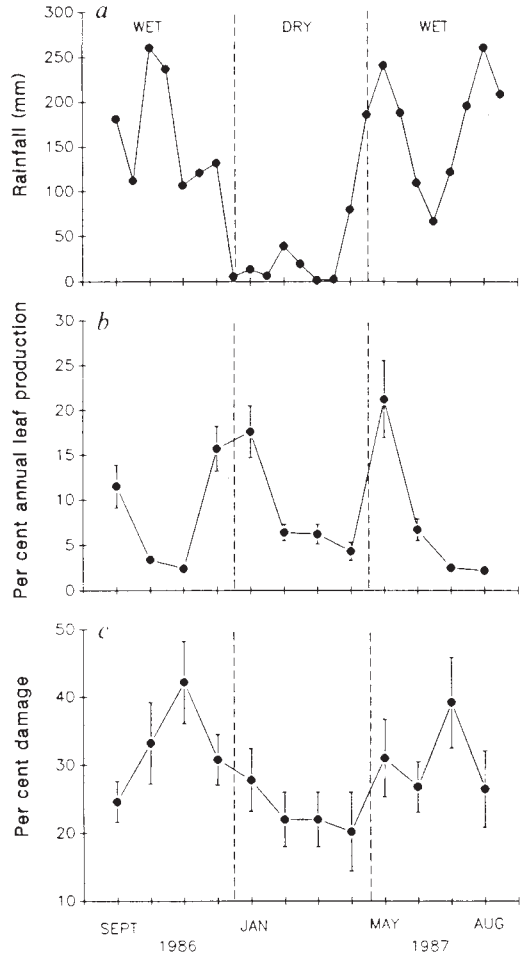

Fig. 1 Rainfall and annual patterns of leaf production and herbivory of saplings (1-2 m) of canopy and understory species in a tropical understory community of Barro Colorado Island, Panama. *a*, Rainfall values (mm) are the semi-monthly totals. Leaf production and herbivory data were collected during the first four days of each month and the mean ±s.e. values for 32 common species of woody plants are presented. *b*, The monthly proportion of annual leaf production for the 32 species. *c*, Monthly damage values are the average of mean values for all species that produced leaves in that month and were measured 30 days later when leaves were expanded. Both leaf area and damage were measured using a plastic grid. The total potential leaf area was estimated to 1 cm^2 and damage was estimated to 0.1 cm^2. This method estimates the potential photosynthetic area lost, but it does not account for the actual area eaten by herbivores (that is, holes created while a leaf is expanding will grow[23]). Species censused were: *Acalypha diversifolia, Alseis blackiana, Beilschmiedia pendula, Capparis frondosa, Cousarea curvigemmia, Desmopsis panamensis, Eugenia oerstedeana, Faramea occidentalis, Guarea guidonia, Guarea* sp. ('hairy'), *Hirtella triandra, Hybanthus prunifolius, Lacistema aggregatum, Mouriri myrtilloides, Ouratea lucens, Poulsenia armata, Pouteria unilocularis, Piper cordulatum, Prioria copaifera, Protium panamenses, P. tenuifolium, Psychotria horizontalis, Quararibea asterolepis, Rheedia edulis, Rinorea sylvatica, Sorocea affinis, Swartzia simplex, Tachigalia versicolor, Talisia princeps, Tetragastris panamensis, Trichilia tuberculata* (*T. cipo* in Croat[15]), *Virola sebifera*. Species nomenclature follows Croat[15].

To investigate the mechanisms of phenological defence, the timing of leaf production and damage to expanding leaves were monitored in shade-tolerant understory plants of Barro Colorado Island, Panama. The forest on this island is classified as tropical moist forest[15,16], but a distinct dry season of approxi-

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mately four months occurs between mid December and mid April (Fig. 1*a*). Thirty two of the most common shade-tolerant woody species (20 individuals per species) were censused monthly for new leaf production from September 1986 to August 1987. I counted all expanding leaves and marked and remeasured a subset the following month to determine the amount of damage that occurred during the period that leaves were expanding (per cent leaf area damaged per month). From these data I calculated the proportion of the annual leaf production and damage levels to young leaves for the individual, species, and the community (all species combined) for each month.

The pattern of leaf production for the 32 species shows distinct peaks at the beginning of the wet season (May), during the wet/dry season transition (December/January) and a smaller peak in the middle of the wet season (September); together these peaks account for 66% of the annual leaf production (Fig. 1*b*). Rates of leaf production did not differ significantly between wet and dry season months (dry, 8.6%; wet, 8.2%; $T = 0.3$, $P > 0.7$). In four of the eight wet season months leaf production was less than 3.5% of the annual production for the community. Although plants can be water stressed during the dry season[17] the three driest months (February, March and April) accounted for 15% of the annual leaf production and their monthly levels exceed those of the four lowest wet season months.

On average, 29% of the potential leaf area is lost during the first month of a leaf's lifetime. Damage to expanding leaves ranged from 42% in November to 20% in April (Fig. 1*c*). For the community, damage during the first month was significantly less for leaves produced during the dry season than leaves produced during the wet season (dry, 23%; wet, 32%; $T = 2.7$, $P < 0.01$). Therefore, 34% of the annual leaf production occurs during the dry season when insect abundance tends to be lowest[18] and damage to expanding leaves was the lowest. These results strongly suggest that levels of damage to expanding leaves are greatly influenced by the seasonality of leaf production.

Although damage levels are lowest during the dry season, leaf production is also limited by water stress and many species produce leaves synchronously at the beginning of the wet season or during the transition from the wet to the dry season. To determine if synchronous leaf production also reduces damage to expanding leaves, I compared the annual average level of damage to each species with the damage level for the species' month of highest leaf production. Damage levels in the peak month of leaf production were lower than the annual average for 23 of the 32 species (Wilcoxon's Sign Rank Test, $T = 99$, $P < 0.005$); therefore, individuals producing leaves in synchrony with conspecifics experienced less damage.

Previous work has identified abiotic factors as the major determinants of plant phenology[1,19–21]. Clearly, abiotic factors (for example, day length, température, humidity and rainfall) can act both as cues and as ultimate selective pressures on phenology. On Barro Colorado Island, higher light levels in the early dry season could facilitate leaf production in understory saplings, and water stress during the end of the dry season may limit growth. This study has shown that in addition to possible abiotic factors, herbivores appear to represent an important biotic constraint on leaf phenological patterns for shade-tolerant understory plants in this tropical moist forest. A review of flowering and fruiting phenology studies also suggests that phenological patterns can be partially explained by the selective pressures of biotic factors (for example, pollinators and predators)[22]. Although abiotic factors are likely to act as the proximate cues, a broader definition of phenology, including the possible influence of both abiotic and biotic factors as the ultimate selective pressures, would help in trying to understand the complex patterns of plant life-cycle events.

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Incubation periods for paediatric AIDS patients

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A recent seroprevalence study of newborns indicates that one in 62 children born in New York City has antibodies to the human immunodeficiency virus (HIV)[1]. The distribution of incubation periods for paediatric patients is needed to estimate future AIDS case loads from these seroprevalence data. Current estimates of incubation periods for paediatric patients are based on limited data[2–5]. We use parametric [5,6] and non-parametric[7,8] methods to analyse incubation periods for 215 paediatric patients with AIDS whose only known route of infection is maternal. We conclude that incubation periods are longer than previously reported[9]; that there is a distinct knee in the incubation period distribution at seven months which suggests two risk populations; and that there is an increase in incidence which is consistent with exponential growth.

Data were taken from paediatric AIDS patient reports in the New York City and New York State AIDS case registries[10] which include all New York State residents age 12 years or less, reported through December of 1987 and diagnosed before August 1, 1987 (Table 1). AIDS diagnosis met the 1985 Centre for Disease Control definition[11]. Of 238 patients, 23 individuals whose mode of transmission was either undetermined or through blood or blood products were removed.

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