Canopy Nutrient Allocation in Relation to Incident Light in the Tropical Fruit Tree *Borojoa patinoi* (Cuatr.)

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Abstract. The relationship of incident photosynthetically active radiation (PAR) and mineral nutrient allocation was evaluated in canopies of *Borojoa patinoi* (Cuatr.) growing in the Chocó rainforest of Colombia, South America. Allocation of P in the canopy was positively correlated with incident PAR, principally because of increased leaf frequency (number of leaves per unit volume of canopy) brought about by local branching, with a smaller contribution from increased specific leaf weight (SLW, leaf dry weight per unit leaf area). The chemical fractionation of P within leaves did not respond to incident PAR. Canopy N allocation also was positively correlated with incident PAR because of increased leaf frequency and SLW. The N partitioning to soluble protein rather than chlorophyll was positively correlated with incident PAR. The allocation of K, Ca, Mg, S, Mn, and Cu also was positively correlated with incident PAR primarily because of increased leaf frequency and secondarily because of increased SLW. The area of individual leaves and the concentration of nutrients in leaf dry weight were not important in determining nutrient allocation responses to incident PAR. Our observations suggest that leaf frequency caused by local branching, followed by changes in SLW, are the primary determinants of canopy nutrient allocation in this tropical fruit tree.

An understanding of the physiological factors influencing the efficiency of nutrient acquisition and use by fruit trees may contribute to the sustainability and productivity of fruit production in the United States, where intensive fertilization of orchard crops is of increasing concern as a source of groundwater contamination (Weinbaum et al., 1992) and in the tropics, where tree fruit production is often limited by low soil fertility (Opeke, 1982). The efficiency of nutrient use by plants has been defined in many diverse ways, as discussed recently by Clark (1990). In the present context, we will consider nutrient efficiency in terms of the economic analogy of resource allocation (Bloom et al., 1985), in which an efficient plant allocates limiting resources in a way that optimizes growth-limiting processes, as typified by photosynthetic C acquisition. In this study, we examined the role of canopy nutrient allocation as a part of overall nutrient efficiency of a tropical fruit tree native to low-P soils.

Leaf N content often is correlated closely with leaf photosynthetic capacity, because both the light-harvesting apparatus and the CO₂-assimilating enzymes have high N contents (DeJong, 1982, 1983). It has been proposed that C gain within plant canopies would be maximized by preferential partitioning of N to leaves receiving higher levels of light (Field, 1983; Mooney and Gulmon, 1979). This hypothesis has been supported by observation of the correlation of light and leaf N content within canopies (Charles-Edwards et al., 1987; DeJong and Doyle, 1985; Hirose and Werger, 1987; Hirose et al., 1988; Klein et al., 1991).

Phosphorus also is important in determining leaf photosynthetic capacity, because of its role in enzyme regulation and in controlling metabolite fluxes (Brooks, 1986; Foyer and Spencer, 1986; Sivak and Walker, 1986). Light and P are relatively scarce

in many environments, and allocation of P to the more illuminated regions of tree canopies also would be expected to maximize plant C gain. Nutrient allocation to a specific portion of the tree canopy can result from an increase in the number of leaves in that portion of the canopy (leaf frequency) or an increase in the nutrient content per leaf. Under conditions of low P availability, leaves likely are produced with the minimum concentration of P required for physiological function, suggesting that P allocation in the canopy would depend more on leaf frequency than on changes in leaf P content. In contrast, N allocation is expected to depend more on changes within individual leaves, since chloroplast N fractions can vary in individual leaves in response to the light environment.

The objectives of this study were to test the following hypotheses: 1) light and P distribution are correlated in tree canopies; and 2) allocation of N and P in tree canopies differ in that P allocation depends more on changes in leaf frequency rather than physiological changes within leaves.

We tested these hypotheses by measuring incident light and nutrient allocation in the canopy of the tropical tree *Borojoa patinoi* growing in the Chocó rainforest on the Pacific coast of Colombia, South America. This tree produces large, fleshy fruit that have a high market value in Colombia, where it is believed that these fruit have tonic and aphrodisiac qualities. Colombian government agencies are investigating *B. patinoi* as a component of sustainable agroforestry production systems for the Chocó forest, a unique tropical rainforest rich in biological diversity that is threatened by rapid deforestation, conversion to annual crops, and soil degradation. *Borojoa patinoi* has large lanceolate leaves typically ≈270 mm long and ≈100 mm wide. Although it is a successful understory species adapted to low-light intensity, *B. patinoi* also adapts to higher light intensities, as evidenced by its occurrence in light gaps, the presence of occasional individuals that emerge from the forest canopy, and its cultivation as a horticultural crop in clearings. The *B. patinoi* canopy is dense, and there is significant self-shading. Individual shoots in the canopy of *B. patinoi* are initiated and grow in all parts of the canopy, in deeply shaded areas as well as more peripheral areas exposed to higher light intensity. These characteristics made it an appropriate subject for this study.

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Materials and Methods

Location. Work was conducted at Bajo Calima (76°56'W, 3°59'30"N), Municipio of Buenaventura, Dept. of Valle del Cauca, at ≈40 m above mean sea level in the Chocó rainforest on the Pacific Coast of Colombia, South America. This site is characterized by an average annual precipitation of 7600 mm, average annual temperature of 26.4°C, and average annual relative humidity of 94%. Soils in the region are generally formed from weathered parent material of low fertility.

Soil analysis. The experiment site's soil was chemically analyzed to reveal imbalances or irregularities in the availability of the nutrients being studied in the tree canopies. Soil samples were collected with a 100-mm auger from three sites within 2 m of the base of the tree used in the first study, then were pooled and analyzed for P fractionation according to the method of Williams (1967) and P fixation according to the method of Fassbender and Igue (1967). Standard chemical analyses of tropical soils were performed as described in Salinas and Garcia (1985).

Plant material. The trees used in this study were 4 to 6 years old, reproductively mature, and ≈4 m high, growing in a light gap created by recent anthropogenic clearing of the surrounding 5 to 10 m of forest.

Canopy measurement of photosynthetically active radiation (PAR). Data reported here represent two sampling periods, the first a detailed study of leaves within a single tree in June 1988, and the second a sampling of five trees from the same location in Mar. 1990. In 1988, 17 leaves were selected from various parts of the canopy with diverse light exposure. We selected the youngest fully expanded leaf on a given branch and avoided leaves showing signs of severe insect herbivory or fungal growth. At 0.5-h intervals, incident PAR was measured at each leaf location over two continuous photoperiods (an afternoon, a complete day, and a morning). Incident PAR was measured with a quantum sensor on a photometer (model Li-188B; LI-COR, Lincoln, Neb.) placed parallel to the leaf adaxial surface and moved back and forth along the midrib of the leaf. Each measurement was integrated for 10 sec. All measurements for a given leaf were numerically integrated to provide values for total incident PAR over the entire measurement interval. Ambient PAR was measured at a height of 2.5 m around the periphery of the canopy.

For the survey of five trees in 1990, 12 leaves were selected in each tree to represent shaded, intermediate, and nonshaded regions of the canopy. Incident PAR for each of the 60 leaves was measured as described previously at midmorning (local time, ≈0900 HR), noon (≈1200 HR), and afternoon (≈1500 HR) in one photoperiod. Immediately following each leaf measurement, ambient PAR was measured as described previously to provide an estimate of leaf irradiation as a percentage of ambient PAR. Mean daily PAR as a percentage of ambient PAR was used to group the leaves in one of three categories: 'low light,' corresponding to leaves receiving 30% or less of ambient PAR, 'medium light' leaves receiving >30% to 60% of ambient PAR, and 'high light' leaves receiving >60% of ambient PAR.

Leaf composition. After the final PAR measurements had been taken, leaves used in both sampling periods were cut from the plant and quickly frozen on dry ice. Chlorophyll a and b were extracted from 4.16-cm² leaf discs in 96% ethanol in darkness at 4°C and quantified spectrophotometrically by the method of Wintermans and Mots (1965). Leaf soluble protein was extracted with 0.05 M tris-HCl at pH 8.8 containing 200 g sucrose and 50 g PVP-40/liter (Robinson and Megarrity, 1975, modified) and determined by the method of Bradford (1976). Lyophilized tissue was analyzed for

crude P fractions using the method of Barr and Ullrich (1963). Leaf total N was determined by the method of Bremner (1965). Leaf content of other elements was determined by digestion (Chapman and Pratt, 1961), followed by atomic absorption spectrophotometry (total Ca, Mg, K, Zn, Cu, Fe, and Mn, using the method of Baker and Smith, 1973), turbidometry (total S, using the method of Tabatabai and Bremner, 1970), and colorimetry (total P, using the method of Murphy and Riley, 1962). Throughout this report, we use 'leaf content' to refer to nutrient content per unit leaf area and the traditional 'leaf concentration' to refer to nutrient content per unit leaf dry weight.

Leaf CO₂ assimilation. Leaf CO₂ assimilation was measured in the field with a portable photosynthesis system (model LI-6000; LI-COR). Because of the high ambient humidity, transpiration and related variables were not measured. For high-light measurements, supplemental illumination of 800 to 900 μmol photon·m⁻²·s⁻¹ was provided by a hand-held, 12-V metal halide lamp. Leaves were enclosed in the LI-COR 4-liter gas exchange chamber for 40 to 60 sec to measure CO₂ depletion, during which time there were no changes in leaf temperature, air temperature, or relative humidity. Dark respiration of CO₂ was measured by enclosing the leaf chamber in a black cloth.

Data analysis. Tree canopies function in three dimensions, whereas nutrient analysis is expressed typically in units without dimension (nutrient concentration) or having two dimensions (nutrient content per unit leaf area or land area). To quantitatively estimate nutrient allocation within a canopy, we developed a characteristic we call "volumetric nutrient allocation" (VNA), calculated as the product of the various components contributing to total canopy nutrient allocation, as follows: VNA = (nutrient concentration) × (specific leaf weight) × (average leaf area) × (leaf frequency), where "leaf frequency" is defined as the number of leaves present in a given volume of the canopy (and "presence" is defined as at least 50% of the leaf within the given volume). Leaf frequency is a function of the frequency of major branches, local branching (leading to changes in the frequency of growing shoots), leaf spacing on growing shoots, and leaf duration. The relative contribution of leaf frequency to total VNA will depend in part on the volume of space in which leaves are counted. In this study, leaves were counted in spheres having a 180-mm radius.

Statistical analysis. The relationship of VNA with the components used in calculating VNA was analyzed by Pearson linear correlation of standardized log-transformed variables. Standardization was necessary to eliminate the impact of unit magnitude on the correlations. Correlation was used instead of regression, because none of the variables was independently controlled; a least-squares approach was indicated to reduce the influence of outliers and error on fundamental relationships. Log transformations were used to reduce problems of autocorrelation and to help linearize the data before correlation. The relationship of light classes and leaf frequency was analyzed as a randomized complete block design with trees as blocks (Wilkinson, 1989). Relationships of leaf characteristics with incident light were analyzed by Pearson linear correlation, because incident light and observed leaf characteristics were dependent variables. Resulting correlation coefficients are conservative, because in some cases the relationships do not appear linear (yet are not amenable to nonlinear regression analysis since, as noted above, there is no independent variable).

Results

The study site's soil was moderately acid, was low in readily available P (shown by Bray I and Bray II values, and the values for

Table 1. Chemical analyses of soil samples from the study site.

	Depth (cm)			
	0 to 25	25 to 40	40 to 50	50 to 70
P (mg·kg ⁻¹)				
Bray I	1.59	2.59	1.59	1.85
Bray II	2.20	3.29	2.06	2.38
Exchangeable P ^z	5.0	6.0	5.5	5.0
Ca compounds-apatitic	19.0	17.0	14.0	15.0
Ca compounds-nonapatitic	5.0	5.0	5.5	6.0
Al compounds	5.5	6.0	7.5	5.0
Fe compounds	73.5	53.0	33.5	47.0
Inert	77.0	79.3	76.5	30.7
Organic	263.7	167.3	137.5	113.7
Total	448.7	333.5	280.0	222.5
P fixation (%)	20.9	20.9	26.0	39.8
N (mg·kg ⁻¹)	6.50	4.26	2.69	1.79
Organic matter (%)	8.02	6.16	4.08	2.82
K (meq/100 g)	0.13	0.08	0.05	0.04
Ca (meq/100 g)	3.05	2.02	1.08	1.04
Mg (meq/100 g)	1.57	1.14	0.58	0.39
Al (meq/100 g)	1.08	1.58	1.83	1.83
Al saturation (%)	18.5	32.8	51.7	55.5
Mn (mg·kg ⁻¹)	77.7	61.6	45.1	32.4
pH	5.15	5.11	5.04	5.12
CEC (meq/100 g)	5.83	4.82	3.54	3.0

^zBy the method of Williams et al. (1967).

exchangeable P from the P fractionation data), and had potentially toxic levels of Mn in the topsoil and Al in the subsoil (Table 1). The high organic matter content of the topsoil would suggest that N was less limiting than P, although without more complete data on N turnover, this is speculative. The high organic matter content at all depths, together with the high proportion of P complexed with organic matter, suggests that the soil parent material was allophane-rich alluvium derived from volcanic soils of the nearby western range of the Andes. Fixation of P was moderate, probably mainly to organic matter-Al complexes. Fair amounts of apatitic P suggest that rhizosphere modification by plants roots might be useful in liberating P in this soil. Base supply and pH did not appear overly problematic for humid tropical vegetation, with the possible exception of low K availability.

During the first period of measurement (1988), ambient PAR above the canopy averaged 289 $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, with a maximum of 556 $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Integrated incident PAR upon the leaves selected for this study ranged from ≈ 2 to 10 $\text{mol photon}\cdot\text{m}^{-2}$ over the measurement period.

Incident PAR was not correlated with leaf P concentration (Fig. 1). Leaf inorganic P, trichloroacetic acid (TCA)-soluble organic P, and TCA-insoluble P fractions were not correlated with changes in incident PAR (33.9% inorganic, 11.7% TCA-soluble organic, and 54.4% TCA-insoluble). Leaf N and leaf chlorophyll were negatively correlated with incident PAR. Leaf soluble protein concentration was positively correlated with incident PAR.

Specific leaf weight (SLW, dry weight per unit leaf area) increased with increasing PAR (Fig 2). Because of the correlation

Fig. 1. Total P, total N, soluble protein, and chlorophyll concentration in individual leaves within a canopy of *B. patinoi* in relation to incident photosynthetically active radiation (PAR) over 2 days in 1988. Incident PAR was not correlated with P concentration, negatively correlated with N concentration ($r = -0.59$, $P \leq 0.01$), positively correlated with soluble protein concentration ($r = 0.48$, $P \leq 0.05$), and negatively correlated with chlorophyll concentration ($r = -0.68$, $P \leq 0.01$).

Fig. 2. Specific leaf weight of individual leaves within a canopy of *B. patinoi* in relation to incident photosynthetically active radiation (PAR) over a 2-day period in 1988. ($r = 0.79$, $P = 0.0001$).

of SLW with PAR, the relationships of PAR with leaf nutrient concentrations ($\text{mg} \cdot \text{kg}^{-1}$) were different than those with leaf nutrient content ($\text{mg} \cdot \text{m}^{-2}$). Leaf P content, leaf N, and leaf soluble protein ($\text{mg} \cdot \text{m}^{-2}$) were positively correlated with PAR (Fig. 3). Leaf chlorophyll content ($\text{mg} \cdot \text{m}^{-2}$) declined slightly and was not correlated with increasing PAR (Fig. 3).

Leaf N content ($\text{mg} \cdot \text{m}^{-2}$) was not correlated with leaf chlorophyll, but it was positively correlated with soluble protein and leaf CO_2 assimilation (Fig. 4). Leaf CO_2 assimilation was measured at ambient PAR levels; thus, it is possible that the relationship between leaf N content and leaf CO_2 assimilation was due to the observed relationship between leaf N content and incident PAR (Fig. 3). We returned to the tree at a later date with portable 12-V halogen lamps that permitted photosynthetic saturation at 800 to 900 $\mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (data not shown). These later measurements demonstrated that leaf CO_2 assimilation at ambient PAR was not substantially less than leaf CO_2 assimilation at high PAR, and that these assimilation rates were highly correlated with each other (Fig. 5). Leaf CO_2 respiration in darkness was not correlated with the PAR environment of the leaf (data not shown).

Leaf frequency, measured as the number of leaf blades within a sphere originating at the insertion point of the reference leaf and extending out in all directions to a radius of 18 cm, was positively correlated with incident PAR (Fig. 6). Changes in leaf frequency were not associated with differences in internode length or the proximity of major branches (data not shown), but they were associated strongly with the degree of local branching. Of the

Fig. 3. Total P, total N, soluble protein, and chlorophyll content per unit leaf area in individual leaves within a canopy of *B. patinoi* in relation to incident photosynthetically active radiation (PAR) over 2 days in 1988. Incident PAR was positively correlated with P content ($r = 0.58$, $P \leq 0.05$), N content ($r = 0.59$, $P \leq 0.05$), and soluble protein content ($r = 0.68$, $P \leq 0.01$), but was not significantly correlated with chlorophyll content.

seven shoots in heavily self-shaded regions of the canopy, all seven were unbranched, whereas of nine shoots selected at random from well-illuminated regions at the periphery of the canopy, eight had branches at the third or fourth node from the apex. Analysis of variance indicated that PAR environment had no effect on internode length (measured with a ruler).

The VNA for P and N were positively correlated with incident PAR (Fig. 7), largely because of the high correlation between leaf frequency and PAR, with a secondary contribution from increased nutrient content per unit area because of increased SLW (Table 2). Because VNA is defined as the product of nutrient concentration, SLW, leaf area, and leaf frequency, it was not possible to determine statistically which of these four variables was most important in controlling VNA responses to light; however, the variation in each of these components of VNA may be an indication of their relative impact. Variables that hold constant will, likewise, not account for much change in VNA in response to light, but high variability [indicated in Table 2 by a high coefficient of variation (cv)] also

Fig. 4. Relationships per unit leaf area of soluble protein content, chlorophyll content, and CO₂ assimilation to N content in individual leaves within a canopy of *B. patinoi*. Nitrogen content was not significantly correlated with chlorophyll content, but was positively correlated with soluble protein content ($r = 0.69$, $P \leq 0.01$), and leaf CO₂ assimilation ($r = 0.75$, $P \leq 0.001$).

Fig. 5. Carbon dioxide assimilation per unit leaf area at saturating PAR (800 to 900 $\mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) in relation to CO₂ assimilation per unit leaf area at ambient photosynthetically active radiation (PAR) (0.1 to 285 $\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, with an average of 99 $\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) in individual leaves within a canopy of *B. patinoi*. Leaf CO₂ assimilation in ambient and saturating PAR were highly correlated ($r = 0.87$, $P \leq 0.0001$).

Fig. 6. Leaf frequency (number of leaf blades within 18 cm of the point of insertion of the reference leaf) within a canopy of *B. patinoi* in relation to incident photosynthetically active radiation (PAR) over a 2-day period in 1988. Leaf frequency was positively correlated with incident PAR ($r = 0.64$, $P \leq 0.05$).

Fig. 7. Volumetric nutrient allocation of N and P within a canopy of *B. patinoi* in relation to incident photosynthetically active radiation (PAR) over a 2-day period in 1988. Incident PAR was positively correlated with volumetric N allocation ($r = 0.52$, $P \leq 0.05$) and volumetric P allocation ($r = 0.55$, $P \leq 0.05$).

may be due to noise or variation not associated directly with changes in VNA. Visual examination of the relationship of the four component variables and VNA showed that leaf frequency, which typically had the highest cv, was most closely associated with VNA, followed by SLW. Leaf area had a relatively high cv but was not closely associated with VNA. Leaf concentrations of chlorophyll, N, P, Mg, and S had low cvs and were not associated with VNA, while other nutrients had fairly high cvs but were not associated with VNA. These relationships are shown for N (representative of a nutrient having a relatively invariant leaf concentration as shown by low cvs) and Fe (representative of a nutrient having a relatively variable leaf concentration as shown by high cvs) (Fig. 8). The contribution of nutrient content per unit area to total VNA was greater for N than for P. Volumetric soluble protein allocation was positively correlated with incident PAR, because of significant correlations with leaf frequency, specific leaf weight, and soluble protein concentration. Volumetric chlorophyll allocation was not correlated with incident PAR. The volumetric allocations of S, Ca, Mg, Fe, Mn, Zn, and Cu were positively associated with incident PAR, primarily because of leaf frequency. The volumetric allocation of Ca and Mg were substantially influenced by nutrient content per unit area because of the combined effects of specific leaf weight and nutrient concentration. Sulfur allocation

followed the pattern of N allocation, as expected. Allocation of Fe, Mn, Zn, and Cu were largely governed by leaf frequency with a secondary contribution from specific leaf weight. Potassium was the only nutrient whose canopy allocation had no association with incident PAR.

A survey of leaves from five trees (data not shown) confirmed the principal results obtained from the detailed analysis of one canopy described previously; however, in the survey, volumetric Zn and K allocations were not correlated with incident PAR, contrary to the study of a single canopy. Total leaf frequency was very highly associated with incident PAR, whereas leaf frequency per shoot axis did not respond to changes in incident PAR (Table 3).

Discussion

Our data show that the distribution of nutrients and PAR are correlated in the canopy of *B. patinoi*. The factors responsible for the allocation of P and total N in the canopy were generally similar. Allocation of P and N in response to PAR did differ in terms of the use of N and P within leaves. Leaf P pools were not responsive to incident PAR, whereas soluble protein content increased with

Table 2. Pearson linear correlation coefficients for incident photosynthetically active radiation (PAR) in relation to volumetric nutrient allocation (VNA) and the components used in calculating VNA in the canopy of *B. patinoi*. VNA values are averages of all light environments.

Variable ²	Mean	SE	CV	<i>r</i>
Leaf area (m ²)	0.0188	0.0012	26.67	0.07 ^{NS}
SLW (g·m ⁻²)	91.588	4.709	21.2	0.79 ^{***}
Leaf frequency (no./m ³)	435.8	37.9	35.9	0.44 ^{NS}
VNA (g·m ⁻³)				
Chlorophyll	3.72	0.38	42	0.33 ^{NS}
Protein	12.23	2.1707	73.17	0.66 [*]
N	10.077	1.26	51.5	0.52 [*]
K	2.799	0.329	48.52	-0.11 ^{NS}
Ca	6.8484	1.1264	67.81	0.64 ^{**}
Mg	5.5331	0.8413	62.69	0.63 ^{**}
S	2.9451	0.5358	75.01	0.58 [*]
P	0.4786	0.0631	54.41	0.55 [*]
Fe	0.0558	0.0097	71.87	0.72 ^{**}
Mn	0.0513	0.0096	77.46	0.64 ^{**}
Zn	0.0188	0.0032	70.59	0.66 ^{**}
Cu	0.0105	0.0016	64.13	0.6 [*]
Nutrient concentration (g·kg ⁻¹ dry weight)				
Chlorophyll	10	0.36	28.34	-0.68 ^{**}
Protein	15	0.9	24.62	-0.48 ^{**}
N	13.4	0.3	10.69	-0.59
K	4.3	0.5	50.94	0.71 ^{***}
Ca	8.5	0.4	20.89	0.3 ^{NS}
Mg	7	0.2	11.75	0.25 ^{NS}
S	4.1	0.2	1.94	-0.18 ^{NS}
Nutrient concentration (μg·g ⁻¹ dry weight)				
P	600	35	67.4	-0.33 ^{NS}
Fe	80.1	0.629	32.3	0.16 ^{NS}
Mn	69.6	3.72	22.07	0.25 ^{NS}
Zn	27.0	2.04	31.178	0.04 ^{NS}
Cu	15.3	0.842	22.70	-0.21 ^{NS}

²Leaf area = average area of individual leaves; SLW = specific leaf weight; Leaf frequency = leaf frequency in number of leaves per unit volume.

NS, *, **, *** Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

Fig. 8. Relationship of leaf nutrient concentration, leaf area, specific leaf weight, and leaf frequency to volumetric nutrient allocation of N and Fe within a canopy of *B. patinoi*.

incident PAR, leading to higher ratios of soluble protein : chlorophyll in high light leaves. The divergent responses of soluble protein and chlorophyll allocation to incident PAR is consistent with previous studies (Björkman, 1981; Vapaavuori and Vuorinen, 1989). In low-light environments, the leaf invests more N in the light harvesting apparatus, because light is limiting photosynthesis, whereas in high-light environments, relatively more N is devoted to the carboxylation enzymes since at high light, CO₂ assimilation is limiting photosynthesis. In *B. patinoi*, N investment in light harvesting was a significant component of total N use, since this species is adapted to low-light levels in the rainforest understory. Our results confirm earlier observations of a correlation of PAR with SLW, and thereby leaf nutrient content in tree canopies (Marini and Marini, 1983; Weinbaum et al., 1989).

Leaf frequency was the most important factor in canopy nutrient allocation. Differences in leaf frequency on a given main branch may have been brought about by differences in the rate of leaf formation, the rate of leaf abscission, leaf spacing, or local branching. One index of leaf age is Ca content, because Ca is retranslocated poorly and tends to accumulate in leaves over time. We did not observe a significant correlation between incident PAR and leaf Ca concentration in mature leaves in the study of one canopy, but did find that high PAR was associated with lower leaf Ca concentration in the survey of five trees (data not shown). To the extent that leaf Ca concentration is simply related to leaf age, this is evidence that leaves in higher light environments were younger, which might result from differences in the rate of leaf initiation. However, the fact that incident PAR had no effect on leaf frequency per shoot axis (Table 3) indicates that increased leaf initiation and other mechanisms that would influence leaf frequency per shoot axis were not important in determining the

overall response to incident PAR. We did not observe that abscission scars were more frequent or recent on branches in low-light environments, arguing against differential leaf abscission as a determinant of leaf frequency. Our data on leaf spacing (internode length on a given shoot) show no significant differences between light environments. The most important determinant of leaf frequency was local branching. Therefore, processes determining canopy architecture were more important than leaf- or chloroplast-related processes in nutrient allocation in the canopy of *B. patinoi*.

Chapin (1980) has proposed that species adapted to low-nutrient environments exhibit relatively efficient nutrient use because of slow growth and slow tissue turnover. Our observations of P allocation in response to local PAR availability support this view, in that the slow 'efficient' growth strategy of *B. patinoi* was conserved at the leaf level even in response to high local PAR intensity. High local PAR intensity was exploited by increased branching, which increases the rate of tissue growth and resource capture in a specific region of the canopy without changing the inherent efficiency characteristics of individual organs, as would be caused by, for example, more rapid leaf turnover.

In considering the implications of the nutrient allocation patterns shown here on C gain, we note that although the quantum sensor we used measured light in the range of PAR, the spectral distribution of that light would be expected to vary in the canopy, with shadier regions of the canopy having qualitatively poorer light for photosynthesis. The association of light quality with light intensity would tend to amplify the functional significance for photosynthesis of the allocation patterns we report here.

Of the 10 nutrients studied, the distribution of all but K in the detailed study and Zn in the survey were correlated with the distribution of PAR, generally in response to increased leaf fre-

Table 3. Effect of light [photosynthetically active radiation (PAR)] environment on variables related to nutrient allocation in the canopy of *B. patinoi*. 'Low light' corresponds to leaves receiving 30 % or less of ambient PAR, 'medium light' to leaves receiving from 30% to 60% of ambient PAR, and 'high light' to leaves receiving >60% of ambient PAR. Data were collected from five trees. Leaf frequency is expressed in terms of the total number of leaves per m³ ('total leaf freq') or only leaves on the same shoot axis as the leaf being measured ('shoot leaf freq'). Data are the mean values.

Variable	Light level						F ^z
	Low		Medium		High		
	(N = 28)	SE	(N = 19)	SE	(N = 13)	SE	
Total leaf frequency	319	(24.6)	577	(51.6)	495	(36)	12.16***
Shoot leaf frequency	246	(21.3)	319	(20.9)	262	(26.2)	1.84 ^{NS}

^{NS}, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

²From analysis of variance.

quency and higher specific leaf weight in better-illuminated regions of the canopy. Leaf frequency and specific leaf weight are fundamental variables that simultaneously affect the majority of leaf constituents. Correlation of nutrient and light distribution may or may not represent adaptive behavior in the context of a particular nutrient. We doubt that all of the mineral nutrients have a direct bearing on the photosynthetic capacity of leaf tissue to the extent that N and P do. Nutrients such as Ca may simply be an integral component of the cost of leaf production and yield only indirect benefits to canopy C gain by facilitating optimum N and P allocation, rather than through direct contributions.

Bloom et al. (1985) proposed that optimum adaptive behavior consists in balancing resource costs and benefits in such a way that resources are colimiting. Our observations prompt the speculation that optimum use of several principal resources (in this case light, N, and P) automatically entails a defined use of a range of other resources (in this case mineral nutrients such as Ca, Mg, etc.) that otherwise may conceivably have other 'optimum' uses. This pattern implies the existence of resource prioritization. Lower priority resources may not benefit from inherent mechanisms to integrate the principal resource constraints (in this case presumably light, N, and P), and, when in short supply, may instead affect growth through Liebig's law of the minimum caused by physiological dysfunction, rather than the colimitation mechanisms proposed by Bloom et al. (1985). The proposal that ecophysiological strategies inherently favor a subset of prioritized resources is supported by the observations of Schulze (1989) to the effect that European forest decline may be brought about by tree strategies to maximize N and C acquisition to the detriment of Ca and Mg nutrition. Resource prioritization also may account for the long-standing observation that nitrogenous fertilizers may overstimulate shoot growth, inducing deficiencies of other nutrients.

Horticulturists may find the concept of VNA useful in developing management practices and genotypes that have reduced nutrient requirements. If *B. patinoi* is representative of other fruit trees, leaf frequency is an important and relatively neglected (although easily measured) determinant of nutrient allocation and light capture in canopies. The same approach could be applied to the spatial analysis of reproductive processes in canopies.

Our observations support the hypothesis that the distribution of light and P are correlated in the canopy of a tropical fruit tree, and suggest that leaf frequency caused by local branching, followed by changes in SLW, are the primary determinants of canopy nutrient allocation.

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