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Primary Productivity and Resource Use in *Metrosideros polymorpha* Forest as Influenced by Nutrient Availability and Hurricane Iniki

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN AGRONOMY AND SOIL SCIENCE AUGUST 1995

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Abstract

Primary productivity and resource use was measured in montane *Metrosideros polymorpha* forest across a $4.1 \times 10^6$ year chronosequence where available pools of soil nitrogen and phosphorus varied with site age. At the oldest site, N, P and a mix of other essential nutrients applied in complete factorial combination to 32 plots demonstrated P limitations to above-ground net primary productivity (ANPP) as predicted by conceptual models of soil development and weathering. This in contrast to N limitations previously demonstrated in geologically young soils. The response to P was that of an initial increase in photosynthetic area followed by increased wood production.

Following hurricane Iniki, leaf area index (LAI) was reduced by 3% to 58%, but recovered to near pre-hurricane values by nine months. Live fine root mass was reduced by 44%, was not related to reductions in LAI, and took two years to recover. Stem damage was largely that of branch removal but some stems were tipped or snapped and large trees were damaged with greater frequency than small trees. Fine litterfall was 1.4 times the annual input while
nutrient transfers from the canopy to forest floor approximated that of a typical year. During litter decomposition there was an initial mass loss of nutrients from both leaves and twigs, followed by immobilization of N and P. Stem growth and ANPP decreased for a year and then recovered to near pre-hurricane values. Both ANPP and production per unit leaf area increased in response to increased P availability.

Across the chronosequence, primary productivity was greatest where available pools of soil N and P were greatest, but differences between sites were small and there was no consistent pattern for above- versus below-ground allocation. *M. polymorpha* within a site appears to adjust to N and P availability by increasing radiation conversion efficiency (RCE) when nutrient availability is relatively high and by increasing nutrient use efficiency (NUE) when availability is low. A negative correlation between RCE and foliar nutrient resorption supports the idea that a trade-off exists between RCE and leaf characteristics affecting NUE.
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Chapter 1
Introduction

Background

Forest productivity is affected by a variety of factors including but not limited to the availability of essential nutrients, the manner in which these nutrients are used and become available for re-use, and radiation interception. Earlier studies have shown that acquisition of critical resources is a function of supply. But when productivity is limited by some resource, re-allocation and growth responses may be such that uptake or capture of that resource is increased. Similarly, those resources which are the most limiting may be used more efficiently. Studies supporting these hypotheses suggest that productivity, allocation and resource use efficiency change in a predictable manner with the availability of limiting resources.

Ecosystem properties such as nutrient availability are influenced by soil development and weathering and by the succession of biological assemblages. Phosphorus and other rock-derived nutrients are present as primary minerals at the beginning of soil development. \( P \) weathers into
biologically available forms early, but in the long term becomes less available because of its conversion to recalcitrant organic and adsorbed forms (Walker & Syers 1976, Crews et al. 1995). In contrast, nitrogen is absent from parent material, gradually accumulating with time as soils and vegetation develop (Vitousek et al. 1983; Bormann & Sidle 1990). Consequently, during pedogenesis, biologically available nutrients increase over time to some maximum, after which availability declines (Walker & Syers 1976; Fox et al. 1991).

It has been suggested that N availability could limit biological activity early in soil development, but P availability should limit it late (Walker & Syers 1976; Vitousek & Walker 1987). Net primary production in relatively undisturbed ecosystems may, therefore, follow a pattern similar to that of nutrient availability; low productivity early in ecosystem development increasing to some maximum and then declining as these systems age (Mueller-Dombois 1986; Bormann & Sidle 1990). Furthermore, one might expect that resource use and allocation by organisms will shift as ecosystems progress from one point to the next along this hypothetical nutrient availability
curve. Variation in the above versus below ground biomass ratio of trees on sites differing in nutrient availability is an example of one such shift in allocation (Vitousek and Sanford 1986, Gower and Vitousek 1989).

Jenny (1961, 1980) suggested that variations in soil and ecosystem properties can be viewed as the function of a number of state factors. The major state factors include climate, organisms, topographic relief, parent soil material and time. Theoretically, varying one state factor while holding all others constant will demonstrate the effect of that factor on otherwise related systems. A key underlying theme in the following chapters is that soil fertility changes in a predictable manner over time through development and weathering processes if other state factors are held relatively constant. These changes in soil fertility affect the components of ecosystem productivity and resource use efficiency.

The Hawaiian Islands provide a unique opportunity to study the relationships between ecosystems as a function of time. The islands result from the movement of the Pacific tectonic plate over a stationary convective plume or "hot spot" in the Earth's mantle (Clague and Dalrymple 1987).
The plume now lies under the southeastern edge of the chain of islands which extends some 2600 km, increasing in age from southeast to northwest.

The basaltic parent material of which the islands are constructed is for the most part uniform in chemical composition (Wright and Helz 1987). Under the influence of comparable climatic conditions and potential vegetation, soils derived from this parent material should develop similarly across the island chain. Therefore, with careful selection, it is possible to identify a series of sites representing a chronosequence of otherwise related ecosystems across the Hawaiian Island chain. Such a chronosequence was recently described (Crews et al. 1995). The studies contained in this dissertation make use of five of the six sites described. The sixth site was omitted because its forest was in a state of advanced decline or dieback; a phenomenon characteristic to Hawaiian Metrosideros forests (Mueller-Dombois 1987).

The following chapters maintain a focus on forest productivity across the chronosequence. The sites range in age from 300 years to approximately 4.1 million years and are characterized by changes in nitrogen and phosphorus.
availability but are otherwise very similar (Crews et al. 1995). The study is part of a collaborative research project. Nitrogen availability has been characterized by Riley and Vitousek (1995). Phosphorus availability and quantification of the forms of phosphorus in the soil has been characterized by Crews et al. (1995). Growth limitation by nitrogen has been demonstrated by Vitousek et al. (1993) at the youngest site on the chronosequence.

In 1992, hurricane Iniki, a powerful category 4 storm, passed directly over the oldest of the sites thereby complicating initial research objectives. Earlier site descriptions and measurements by the author and others made it irresistible to include a study of the damage and recovery processes induced by this high energy disturbance.

This dissertation includes three closely related studies. The first of these studies examines phosphorus limitation to primary productivity in a Metrosideros polymorpha dominated forest on a highly weathered soil and was conducted at the oldest of the chronosequence sites. The study was designed to determine whether the predicted decrease in P availability during soil weathering is realized to the point where forest productivity is limited
by P to a greater extent than other essential nutrients.
The study will complement research completed at the youngest
site on the chronosequence where nitrogen was demonstrated
to be the most limiting essential nutrient (Vitousek et al.
1993).

The second study examines primary productivity and
resource use across the chronosequence. The study is
designed to (a) measure the production responses of
Metrosideros polymorpha dominated forests to a measured
gradient of nutrient availability, and (b) determine whether
the efficiency of resource use and relative biomass
investments into different components of productivity
function to optimize the acquisition and use of a critical
resource under conditions of limitation.

The third study examines the damage and recovery
processes in a Metrosideros polymorpha dominated forest at
the oldest of the chronosequence sites as a result of
Hurricane Iniki. The study examines damage to the canopy,
roots and stems. Measurements of litter decomposition and
changes in litter nutrient mass through leaching,
mineralization and immobilization are used to evaluate the
fate of nutrients transferred from the canopy to the forest
floor. Since hurricane Iniki struck an experiment site where fertilizer applications were made during the previous two years, recovery of the forest relative to nutrient availability was examined.

**Chronosequence Site Descriptions**

Sites were selected with relatively uniform parent material, rainfall, elevation and dominant vegetation (Crews *et al.* 1995). Three sites are located on the island of Hawaii, the youngest and most geologically active in the island chain. Soils of the chronosequence sites were derived from volcanic tephra deposits ranging in age from 300 to $1.4 \times 10^6$ years (Crews *et al.* 1995). A possible exception is the oldest site where it is difficult to determine the form of the parent material at such a late weathering stage.

Each site supports a closed canopy forest with *Metrosideros polymorpha* as the dominant tree species. Several other genera including *Cibotium*, *Cheirodendron*, *Ilex*, *Coprosma* and *Vaccinium* account for most of the remaining cover and species richness increases from the
youngest to the oldest site (Crews et al. 1995). None of the sites are known to have been cleared by humans.

All sites are near 1200 m elevation and have a mean annual temperature near 16 C (Atlas of Hawaii, 1983); and receive ≈ 2500 mm of precipitation annually (Giambelluca et al. 1986). Sites are located on undissected volcanic shield surfaces or shield remnants (at the oldest sites) with minimal slope (< 6%). Site locations across the Hawaiian Islands are indicated in Figure 1.1.

Soil N and P pools have been described in detail for all the sites (Riley & Vitousek 1995, Crews et al. 1995). In general, foliar N and P concentrations follow the same pattern as that of plant available soil N and P pools across the chronosequence (Vitousek et al. 1995). For the purposes of comparing relative site fertility, foliar N and P concentrations are presented with the following site descriptions. Measures of biologically available N and P are presented in Table 1.1.

**Thurston**

The youngest site is near Thurston lava tube on the southeast slope of Kilauea volcano at 1178 m elevation in
Hawaii Volcanos National Park. The soil is considered to be ≈ 300 years old, having developed on several tephra deposits ranging in age from 200 to 400 years old (Crews et al. 1995). Previous fertilization experiments (Gower & Vitousek 1989; Vitousek et al. 1993) indicate that NPP at the site is limited by nitrogen primarily. Mass based foliar N concentration in glabrous M. polymorpha leaves is 0.87%; foliar P is 0.060% (Vitousek et al. 1995).

Laupahoehoe

The site is located in the Laupahoehoe Forest Reserve on the northeast flank of Mauna Kea at 1170 m elevation. Access was by Blair Road from the town of Laupahoehoe. Soils at Laupahoehoe developed in 1 x 10^4 to 3 x 10^4 year old tephra deposits and ecosystem development at the site is considered to have begun ≈ 2 x 10^4 years before present (Crews et al. 1995). Foliar N is highest at this site at 1.42% and P = 0.101% (Vitousek et al. 1995).
Kohala

The site is located in the Kohala mountains on the southeast slope at 1122 m elevation. Access was through the Hawaii Preparatory Academy and Parker Ranch. The parent material from which the Kohala soils are derived were deposited \( \approx 1.5 \times 10^5 \) years before present (Crews et al. 1995). Foliar analyses indicates the highest P availability and high N availability; \( N = 1.14\% \) and \( P = 0.113\% \) (Vitousek et al. 1995).

Kokekole

This site is near Puukolekole at 1210 m elevation in the Kamakou Preserve which is managed by the Nature Conservancy of Hawaii, Molokai. The soils at Kokekole are believed to be derived from tephra deposits originating from Puukolekole \( \approx 1.4 \times 10^6 \) years ago (Crews et al. 1995). Foliar \( N = 1.06\% \) and \( P = 0.085\% \) (Vitousek et al. 1995).

Kokee

Kokee is located at 1134 m elevation in the Na Pali - Kona Forest Reserve on the island of Kauai. Access is by
the Alakai trail in Kokee State Park. Soils at the site are derived from materials originating $3.9 \times 10^6$ to $4.3 \times 10^6$ years before present. An estimated age of $4.1 \times 10^6$ years is used for the site (Crews et al. 1995). Foliar $N = 0.86\%$ and $P = 0.061\%$ (Vitousek et al. 1995).
References


Kokee
4.1 x 10^6 yr

Kolekole
1.6 x 10^6 yr

Kohala
1.4 x 10^5 yr

Laupahoehoe
2 x 10^4 yr

Thurston
300 yr

Figure 1.1. Map of Hawaii. The locations of the five sites that form the montane rainforest chronosequence and estimated land surface ages are noted.
Table 1.1. Soil pH and availability of N and P across the chronosequence.

<table>
<thead>
<tr>
<th>Site</th>
<th>pH in H₂O</th>
<th>In situ resin extractable nutrients (μg bag⁻¹ d⁻¹)</th>
<th>Gross N-min. (mg m⁻² d⁻¹)</th>
<th>N-nitr.</th>
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<tr>
<td>Thurston</td>
<td>5.02</td>
<td>0.20, 3.01, 0.22</td>
<td>195, 33</td>
<td></td>
</tr>
<tr>
<td>Laupahoehoe</td>
<td>3.57</td>
<td>1.21, 8.12, 4.25</td>
<td>---, ---</td>
<td></td>
</tr>
<tr>
<td>Kohala</td>
<td>4.09</td>
<td>2.19, 4.90, 0.31</td>
<td>432, 52</td>
<td></td>
</tr>
<tr>
<td>Kolekole</td>
<td>3.77</td>
<td>0.51, 4.02, 10.53</td>
<td>---, ---</td>
<td></td>
</tr>
<tr>
<td>Kokee</td>
<td>3.99</td>
<td>0.41, 4.12, 10.29</td>
<td>647, 112</td>
<td></td>
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Adapted from Crews *et al.* 1995.
Chapter 2

Phosphorus Limitation of Leaf Area and Net Primary Productivity on a Highly Weathered Soil

Abstract

We tested the hypothesis that P was the nutrient limiting net primary production of a native *Metrosideros polymorpha* forest on a highly weathered montane tropical soil in Hawaii. A factorial experiment used all combinations of three fertilizer treatments: nitrogen (N), phosphorus (P) and a mix of other essential nutrients (OE), consisting primarily of mineral derived cations and excluding N and P. P addition, but not N or OE, increased leaf area index within 12 months, foliar P concentration measured at 18 months, and stem diameter increment within 18 months. Stem growth at 18 months was even greater when trees fertilized with P also received the OE treatment. N and P additions increased leaf litterfall and N and P in combination further increased litterfall. The sequence of responses suggests that increased available P promoted an increase in photosynthetic area which led to increased wood...
production. P was the essential element most limiting to
primary production on old volcanic soil in contrast to the N
limitation found on young volcanic soils.

Introduction

Phosphorus and other rock-derived nutrients are present
as primary minerals at the beginning of soil development. P
weathers into biologically available forms early, but in the
long term becomes less available because of its conversion
to recalcitrant organic and adsorbed forms (Walker & Syers
1976, Crews et al. 1995). In contrast, nitrogen is absent
from parent material, gradually accumulating with time as
soils and vegetation develop (Vitousek et al. 1983; Bormann
& Sidle 1990). Consequently, during pedogenesis,
biologically available nutrients increase over time to some
maximum, after which availability declines (Walker & Syers
1976; Fox et al. 1991).

It has been suggested that N availability could limit
biological activity early in soil development, but P
availability should limit it late (Walker & Syers 1976;
Vitousek & Walker 1987). Net primary production in
relatively undisturbed ecosystems may, therefore, follow a
pattern similar to that of nutrient availability; low productivity early in ecosystem development increasing to some maximum and then declining as these systems age (Mueller-Dombois 1986; Bormann & Sidle 1990). In line with these predictions of nutrient availability and ecosystem response, it was demonstrated that N is the element most limiting to net primary productivity (NPP) in Metrosideros polymorpha Gaud. forests on young volcanic soil in Hawaii (Vitousek et al. 1987; 1993; Walker & Aplet 1994).

Experimental fertilizations have shown that tropical forest trees respond to applications of N and P with increases in NPP and that the response to N or P may be affected by the relative age of the soil. On a young volcanic Dystrandept in Hawaii, tree stem diameter, litterfall and treefern growth increased after fertilization with N, but there was no response to P or a mix of other essential elements (Vitousek et al. 1993; Walker & Aplet 1994). On a montane Humitropept in western Venezuela, Tanner et al. (1992) measured increased tree growth in response to fertilization with N and P and reported evidence of N limitation. Evidence for which element(s) limit production of the naturally occurring vegetation later in
soil development is generally lacking, but in a highly weathered Amazonian oxisol near San Carlos Venezuela, fine roots proliferated in P-fertilized ingrowth cores (Cuevas & Medina 1988).

The Hawaiian Islands are well suited to the study of ecosystems in relation to their development and function across a soil chronosequence. The basaltic parent material is, for the most part, uniform in chemical composition (Wright & Helz 1987) and geologic age of the islands increases from southeast to northwest. In this study we examine nutrient limitation of an *M. polymorpha* dominated forest on one of the oldest montane soils in the Hawaiian Islands. The study was designed to determine whether the predicted decrease in P availability on this highly weathered soil is realized to the point where forest productivity is limited by P to a greater extent than by other essential nutrients. The site was selected to match the young site fertilized by Vitousek *et al.* (1993) in elevation, annual precipitation, slope position, and dominant vegetation, and a similar experimental design was used. The site is the oldest in a well-defined chronosequence of soils derived from similar substrates.
beginning with an age of approximately 300 years at the youngest site on the island of Hawaii (Crews et al. 1995).

Site Description

The study site is located in the Na Pali - Kona Forest Reserve in Kokee State Park, island of Kauai, Hawaii (22°08' N and 159°38' W) at 1134 m elevation. The site is on a ridge top remnant with a geologic age estimated to be between 3.9 and 4.3 million years (Clague & Dalrymple 1988). The soil is mapped as a clayey ferritic isomesic Plinthic Acrorthox (Soil Survey Staff 1972) revised to an Acrudox (Soil Survey Staff 1992). Mean annual precipitation is 2500 mm (Giambelluca et al. 1986).

Vegetation is characterized by a closed forest canopy composed predominantly of Metrosideros polymorpha Gaud. var. glaberrima (H. Lev.) St. John, with Syzigium sandwichensis (A. Gray) Nied., Cheirodendron trigynum (Gaud.) A. Heller and Cheirodendron platyphyllum (Hook. & Arnott) Seem. subspecies kauaiense (Kraj.) Lowry and a fern understory.

Total soil P at the site was 0.44 kg P m⁻² to a depth of 50 cm with a soil bulk density of 0.80 g cm⁻³. Of this, 25% was organic P, 27% was secondary mineral P and 48% was
occluded inorganic P (Crews et al. 1995). Resin-extractable inorganic P was 16.0 μg g⁻¹ in the organic layer and 5.0 μg g⁻¹ in the mineral A horizon (T. Crews, pers. comm.). By comparison with the low availability of P, N is relatively available. During 30-day laboratory incubations, net N mineralization rate was 26.4 mg N m⁻² day⁻¹ and net nitrification rate was 16.4 mg N m⁻² day⁻¹ (Riley & Vitousek, 1995).

**Methods**

**Experimental Design:**

DBH of all tree stems greater than 50 mm were recorded in each of 42 plots measuring 10 x 10 m prior to the application of treatments. In early March 1991 a fertilization experiment was started on the 32 most similar plots. Treatments were applied to the 20 x 20 m area encompassing each plot to provide a 5 m border. The three main treatments were N and P applied at the annual rate of 100 kg ha⁻¹ yr⁻¹ each, and a mix of other essential (OE) nutrients (excluding N and P) which consisted of K (100 kg ha⁻¹ yr⁻¹), Ca (100 kg ha⁻¹ yr⁻¹), Mg (58 kg ha⁻¹ yr⁻¹), S (40 kg ha⁻¹ yr⁻¹), Fe (8 kg ha⁻¹ yr⁻¹), Mn (8 kg ha⁻¹ yr⁻¹), Zn (8 kg ha⁻¹ yr⁻¹),
lyr\(^{-1}\)), Cu (2.25 kg ha\(^{-1}\)yr\(^{-1}\)) and B (0.75 kg ha\(^{-1}\)yr\(^{-1}\)). P was applied as treble super phosphate and N was applied as a mixture of urea and ammonium nitrate, each fertilizer supplying equal amounts of N. The OE treatment included muriate of potash, dolomite, gypsum and Granusol, an agricultural micronutrient mix.

Treatments were applied at two levels: zero or plus. The initial fertilizer application was equal to the annual rate. Subsequent applications began six months later and were made in semi-annual allotments, each equal to half the annual rate. Eight factorial combinations of N, P and OE treatments were randomly assigned to plots in four blocks.

The experiment was analyzed as a randomized complete block ANOVA. Fixed model F tests were performed on the three main treatments and all interactions (Snedecor & Cochran 1980). An alpha of .05 was used for determining significance. All statistical tests were performed on log-transformed data in order to homogenize variance. Tables and figures use arithmetic means and standard errors for simplicity in presentation.
Field Measurements:

Spring-loaded dendrometer bands were installed on six M. polymorpha trees per plot and diameter growth was measured every six months for eighteen months. The first six months of growth were excluded from analysis to allow for settling of the dendrometer bands (Keeland & Sharitz 1993).

LAI was estimated optically using a LI-COR LAI 2000 plant canopy analyzer, which uses gap fraction analysis of diffuse radiation transmittance to indirectly estimate LAI (Welles & Norman 1991). This method may underestimate LAI where canopy elements are strongly clumped or aggregated in space, such as in conifers. Gower and Norman (1991) found that four conifer species required a correction factor ranging from 1.49 to 1.67 for accurate estimation of LAI by the LI-COR LAI 2000. A correction factor of 2.63 was determined by Smith et al. (1993) for Douglas-fir. However, the method agreed with direct harvest estimates in red oak (Gower & Norman 1991) and a variety of tropical hardwoods (Harrington & Fownes 1995). Preliminary results from tree harvest on the island of Hawaii indicate that a correction factor for M. polymorpha canopy LAI may be equally high (D. 25
Herbert & J. Fownes, unpublished data). Despite the underestimate in LAI, it is nevertheless directly related to differences among our treatments in light absorption by canopies. Because the study area is in a State Park, native rainforest trees could not be harvested to determine a site-specific calibration factor. Therefore, we used the optical method to detect relative differences among treatments, and no correction factor has been applied to the results presented here.

LAI was estimated from six points within each plot at 6, 8 and 12 months. No LAI estimates were made at 18 months because of extensive canopy damage from Hurricane Iniki (September 11, 1992) which reduced pre-hurricane LAI by as much as 60%.

N and P concentrations and leaf mass per area (LMA) were measured in early September 1992, 18 months after initial fertilizer application. The most recently fully expanded sun leaves were obtained from the uppermost part of the canopy. Area was measured with a LI-COR LI-3100 area meter, after which samples were dried at 70 C. Leaves were ground and then acid-digested in a block digester using a persulfate procedure with a mercuric oxide catalyst. N and
P concentrations were determined using an Alpkem auto-analyzer.

Monthly fine litterfall collections began at the end of September 1991, six months after initial fertilization. Collections were made using four 0.2 m² frame traps in each plot. Litterfall collections were taken through September 1, 1992, after which canopy damage from the hurricane eliminated treatment effects.

Allometric Equations and Biomass Estimation:

Wood biomass (W), including boles, branches and twigs, was estimated using an allometric equation generated from the destructive sampling of 45 M. polymorpha trees ranging in size from 1.0 to 38 cm basal diameter (D), harvested from several different sites on the Island of Hawaii (Gerrish 1988; J. Raich, unpubl. data; G. Aplet, unpubl. data). Regression of ln W versus ln D produced the equation ln W = 2.619 + 3.034 * ln D (r² = 0.977, P < .0001, Sy.x = .548).

Height improved the regression (r² = 0.983, P < .0001, Sy.x = .345), but since we did not have heights for all trees we use only D in our allometric equation. The correction factor exp(Sy.x²/2) was applied to counteract bias from
logarithmic transformation (Baskerville 1972; Sprugel 1983). The final equation was $W = 15.945 * D^{3.034}$ where $D$ is measured in cm and $W$ is predicted in g.

**Estimates of Production:**

Above ground net primary production (ANPP) was estimated as the sum of the change in wood biomass and the fine litterfall on a per area basis. Annual litterfall was estimated from the available pre-hurricane values. The change in wood biomass was estimated by applying the allometric equation for biomass, as described above, to stem diameters at the beginning and end of each measurement interval. There was no evident relation between radial stem growth and initial stem diameter to suggest that differences in diameter increment were dependent on initial stem diameter, so the mean growth increment of measured trees in each treatment plot were applied to all trees within the plot to estimate wood production on a stand basis. As an index of growth efficiency, production per unit leaf area was calculated as ANPP from 6 to 18 months divided by LAI at 12 months.
Results

Canopy Response to Fertilization:

LAI increased with P application by 8 months and increased further by 12 months after initial fertilizer application (Table 2.1). All plots without P amendments exhibited reductions in LAI during the interval for which data are available (Figure 2.1). That LAI was maintained or increased when P was applied suggests extended leaf retention or increased leaf initiation in response to increased availability of P.

P addition nearly doubled foliar P and significantly decreased LMA (Table 2.1). N addition did not increase foliar N and had no effect on LMA.

Annual litterfall increased with both N and P addition (Table 2.2). Leaf litterfall increased in response to N addition beginning in November, 1991, and in response to P in addition to N beginning in May, 1992. The magnitude of litterfall responses to N and P were approximately equal. A positive interaction of N with P began in July 1992 and continued through the end of the experiment (Figure 2.2). Patterns for litterfall including twigs were similar to
those for leaf litter, except for winter months when storms increased twig litter.

**Stem Growth:**

Stem diameter initially increased in response to the combined P and OE treatments (Table 2.3). Later (12 to 18 months) there were increases in response to P and N separately, and to the combined P and OE treatment. Cumulative increment for the year (6 to 18 months) was greatest among P treatments with a positive and significant interaction when P and OE were applied in combination. Diameter increment never increased when OE was applied without P.

**Production:**

From 6 to 12 months there was an interaction of P with OE where wood production was greatest when both treatments were combined (Table 2.4). From 12 to 18 months wood production was greatest in P treatments without significant interactions. Cumulative wood production for the year (6 to 18 months) was greatest for P treatments while other nutrients and their interactions were non-significant. ANPP
(wood production plus leaf and twig litterfall) increased with P application (Table 2.5). Production per unit leaf area did not differ significantly among treatments (Table 2.5).

Discussion

The first measurable responses to P application were increased LAI and litterfall. Although foliar P increased, increased ANPP was apparently caused by increased leaf area and not increased production per unit leaf area. However, the interaction between P and OE (p = .074), suggested that had the experiment continued longer there may have been increased production per unit leaf area when P plus OE were combined. N also increased canopy production as measured by increased leaf litterfall, a persistent effect first observed six months prior to the litterfall response in P treatments. Both N and P had the effect of increasing canopy production but in different ways. N application increased litterfall while LAI did not change significantly, indicating that leaf production and turnover increased. P application increased litterfall after an increase in LAI, suggesting increased leaf initiation or retention.

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A reduction in foliar N:P ratio was the result of increased foliar P concentration in the P treatment plots. This change occurred without a significant increase in foliar N even when fertilizer N was applied. Also, foliar N did not decrease when LAI increased suggesting that N did not become limiting in supply when both P availability and LAI increased. N is known to affect maximum rates of photosynthesis in many plants (Field & Mooney 1986), but foliar P may also limit photosynthesis when P availability is low (Reich & Schoettle 1988).

The decrease in LMA in P treated plots suggests that the increased available P had an effect on leaf structure. Lower LMA in nutrient sufficient leaves is supported in other observations (Chabot & Hicks 1982; Reich et al. 1991; Vitousek et al. 1995). LMA and mass-based net photosynthesis were negatively correlated in 23 Amazonian tree species (Reich et al. 1991). High foliar nutrient concentrations in mature leaves are positively correlated with decomposition rate (Tanner 1981; Cuevas & Medina 1988; Constantinides & Fownes 1994), which in turn, could affect nutrient cycling.
Increased stem diameter increment and wood production generally followed canopy responses in a progression similar to that measured in other forest fertilizations (Miller & Miller 1976). Diameter increment increased in response to P, but was greater when applied in combination with OE. Increases in response to N were also seen late in the experiment. Wood production per plot, which incorporates stem density, also increased in the P treatments, but this did not become readily apparent until late in the experiment. An interaction of P with OE showing increased mean wood biomass increment was not significant after the 6 to 12 month interval, and there was no increased wood production in response to N.

Changes in canopy leaf mass were not included in our estimate of ANPP due to the effects of Hurricane Iniki which brought the study to an early conclusion. Therefore, ANPP was probably underestimated in plots which had a net increase in LAI, that is all P treatments. Despite this potential error there was a strong response to P, supporting the hypothesis that ANPP at the site is limited by the lack of biologically available P.
The persistent effect of increased stem diameter increment when OE was applied with P, the early effect of N on litter production and the late effect of N on stem diameter increment suggests that other nutrients were in short supply at the site and may impose secondary limitations on production. The probability that other nutrients secondarily limit ANPP is not surprising since reductions in the total amounts of Ca, Mg, K and S can occur early during normal soil weathering processes (Walker & Syers 1976; Fox et al. 1991). The availability of N through mineralization processes may be regulated by P availability (Vitousek & Howarth 1991) which could help to explain the early increase in litterfall and the late stem diameter response when N availability was increased by fertilization.

Notwithstanding secondary limitation or the effect of other nutrients on some components of productivity, ANPP increased when P availability was increased. The response clearly demonstrates P limitation on a weathered soil as predicted by Walker & Syers (1976) and Vitousek & Walker (1987).
References


Vitousek PM, Van Cleve K, Balakrishnan N & Mueller-Dombois D (1983). Soil development and nitrogen turnover in montane rainforest soils on Hawaii'i. Biotrop. 15:268-


Table 2.1. Treatment effects on LAI (m²/m²) at 12 months, foliar P and N (% dry mass) and LMA at 18 months (g m⁻²). Values are means with standard errors in parentheses. P, N and other elements, OE (K, Ca, Mg, S, Fe, Mn, Zn, Cu, and B), were applied in factorial combination at rates described in the text. P increased LAI (3.1 vs. 2.4; \( p = .001 \)), foliar P (0.060% vs. 0.104%; \( p < .001 \)) and decreased LMA (174 vs. 193 g m⁻²; \( p = .046 \)).

<table>
<thead>
<tr>
<th>P Trt.</th>
<th>- N</th>
<th>+ N</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAI</td>
<td>- P</td>
<td>2.3 (.31)</td>
</tr>
<tr>
<td></td>
<td>+ P</td>
<td>2.6 (.15)</td>
</tr>
<tr>
<td>Leaf P%</td>
<td>- P</td>
<td>.058 (.005)</td>
</tr>
<tr>
<td></td>
<td>+ P</td>
<td>.100 (.009)</td>
</tr>
<tr>
<td>Leaf N%</td>
<td>- P</td>
<td>.802 (.061)</td>
</tr>
<tr>
<td></td>
<td>+ P</td>
<td>.850 (.031)</td>
</tr>
<tr>
<td>LMA</td>
<td>- P</td>
<td>211 (19)</td>
</tr>
<tr>
<td></td>
<td>+ P</td>
<td>183 (14)</td>
</tr>
</tbody>
</table>

- OE  + OE

| - N | 2.4 (.27) | 2.7 (.17) |
| + N | 3.1 (.30) | 3.3 (.40) |
| - N | .063 (.004) | .057 (.003) |
| + N | .104 (.008) | .095 (.012) |
| - N | .856 (.030) | .844 (.056) |
| + N | .840 (.018) | .935 (.023) |
| - N | 175 (4) | 191 (10) |
| + N | 190 (14) | 150 (7) |
Table 2.2. Treatment effects on annual litterfall leaves and on total litterfall (g dry mass m$^{-2}$ yr$^{-1}$). Values are means with standard errors in parentheses. Treatments as presented in Table 2.1. Leaf litter was increased by N (455 vs. 376 g m$^{-2}$, $p = .001$) and P (446 vs. 385 g m$^{-2}$, $p = .007$). Total litterfall was also greater among N (580 vs. 484 g m$^{-2}$, $p = .003$) and P (574 vs. 489 g m$^{-2}$, $p = .006$) treatments.

<table>
<thead>
<tr>
<th>P Trt.</th>
<th>- N</th>
<th>+ N</th>
<th>- N</th>
<th>+ N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaves</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- P</td>
<td>340 (17)</td>
<td>414 (33)</td>
<td>372 (16)</td>
<td>416 (41)</td>
</tr>
<tr>
<td>+ P</td>
<td>394 (26)</td>
<td>510 (31)</td>
<td>401 (30)</td>
<td>481 (33)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- P</td>
<td>423 (27)</td>
<td>520 (45)</td>
<td>483 (18)</td>
<td>532 (52)</td>
</tr>
<tr>
<td>+ P</td>
<td>517 (33)</td>
<td>627 (40)</td>
<td>512 (38)</td>
<td>641 (51)</td>
</tr>
</tbody>
</table>
Table 2.3. Treatment effects on stem diameter growth (mm). Diameter increments are separated into semi-annual intervals to illustrate the progression of responses. Values are means with standard errors in parentheses. Treatments as presented in Table 2.1. In the second interval diameter increment was increased by P (1.6 vs. 1.0 mm, \( p = .010 \)) and N (1.5 vs. 1.1 mm, \( p = .049 \)). P increased annual increment (2.5 vs. 2.0 mm; \( p = .046 \)). P x OE was significant in the first interval (\( p = .005 \)), second interval (\( p = .025 \)) and annual increment (\( p = .010 \)).

<table>
<thead>
<tr>
<th>Months</th>
<th>P Trt.</th>
<th>- N</th>
<th>+ N</th>
<th>- N</th>
<th>+ N</th>
</tr>
</thead>
<tbody>
<tr>
<td>6 to 12</td>
<td>- P</td>
<td>1.2 (.23)</td>
<td>1.2 (.11)</td>
<td>0.7 (.20)</td>
<td>0.5 (.11)</td>
</tr>
<tr>
<td></td>
<td>+ P</td>
<td>0.7 (.18)</td>
<td>1.1 (.17)</td>
<td>0.9 (.09)</td>
<td>1.2 (.31)</td>
</tr>
<tr>
<td>12 to 18</td>
<td>- P</td>
<td>1.3 (.32)</td>
<td>1.4 (.17)</td>
<td>0.8 (.13)</td>
<td>0.8 (.14)</td>
</tr>
<tr>
<td></td>
<td>+ P</td>
<td>1.0 (.06)</td>
<td>2.0 (.45)</td>
<td>1.4 (.28)</td>
<td>1.9 (.40)</td>
</tr>
<tr>
<td>6 to 18</td>
<td>- P</td>
<td>2.5 (.55)</td>
<td>2.6 (.27)</td>
<td>1.5 (.31)</td>
<td>1.3 (.13)</td>
</tr>
<tr>
<td></td>
<td>+ P</td>
<td>1.7 (.19)</td>
<td>3.1 (.60)</td>
<td>2.2 (.35)</td>
<td>3.1 (.64)</td>
</tr>
</tbody>
</table>
Table 2.4. Treatment effect on wood production (g dry mass m⁻²yr⁻¹). Production is separated into semi-annual intervals to illustrate the progression of responses. Values are means with standard errors in parentheses. Treatments are as presented in Table 2.1. Wood production increased in response to P in the second interval (401 vs. 297 g m⁻², \( p = .015 \)) and for the entire year (662 vs. 442 g m⁻², \( p = .027 \)). P x OE was significant in the first interval (\( p = .049 \)).

<table>
<thead>
<tr>
<th>Months</th>
<th>P Trt.</th>
<th>- N</th>
<th>+ N</th>
<th>- N</th>
<th>+ N</th>
</tr>
</thead>
<tbody>
<tr>
<td>6 to 12</td>
<td>- P</td>
<td>258 (62)</td>
<td>239 (36)</td>
<td>137 (29)</td>
<td>145 (29)</td>
</tr>
<tr>
<td></td>
<td>+ P</td>
<td>218 (42)</td>
<td>239 (52)</td>
<td>289 (35)</td>
<td>298 (128)</td>
</tr>
<tr>
<td>12 to 18</td>
<td>- P</td>
<td>282 (79)</td>
<td>291 (54)</td>
<td>176 (45)</td>
<td>240 (58)</td>
</tr>
<tr>
<td></td>
<td>+ P</td>
<td>246 (35)</td>
<td>437 (155)</td>
<td>461 (84)</td>
<td>459 (150)</td>
</tr>
<tr>
<td>6 to 18</td>
<td>- P</td>
<td>540 (141)</td>
<td>530 (90)</td>
<td>313 (69)</td>
<td>385 (60)</td>
</tr>
<tr>
<td></td>
<td>+ P</td>
<td>464 (63)</td>
<td>676 (206)</td>
<td>750 (112)</td>
<td>757 (274)</td>
</tr>
</tbody>
</table>
Table 2.5. Above ground net primary production (g m$^{-2}$ yr$^{-1}$) and growth efficiency (g m$^{-2}$ leaf area yr$^{-1}$) in response to fertilizer treatments. Values are means with standard errors in parentheses. Treatments are as presented in Table 2.1. ANPP was significantly greater when P was applied (1236 vs. 931 g m$^{-2}$; $p = .006$).

<table>
<thead>
<tr>
<th>P Trrt.</th>
<th>- N (139)</th>
<th>+ N (107)</th>
<th>- N (83)</th>
<th>+ N (84)</th>
</tr>
</thead>
<tbody>
<tr>
<td>+ P</td>
<td>964</td>
<td>1050</td>
<td>795</td>
<td>916</td>
</tr>
<tr>
<td></td>
<td>981 (88)</td>
<td>1303 (224)</td>
<td>1262 (100)</td>
<td>1398 (265)</td>
</tr>
<tr>
<td>- P</td>
<td>441 (107)</td>
<td>463 (70)</td>
<td>329 (22)</td>
<td>342 (25)</td>
</tr>
<tr>
<td>+ P</td>
<td>374 (29)</td>
<td>370 (54)</td>
<td>424 (61)</td>
<td>433 (68)</td>
</tr>
</tbody>
</table>

ANPP/LA
Figure 2.1. Leaf area index (m²/m²) in -N -P (open triangles), +N -P (filled triangles), -N +P (open circles) and +N +P (filled circles) treatment plots. The values are means +/- standard errors.
Figure 2.2. Monthly leaf litterfall (g dry mass/m²) for October, 1991 through August, 1992. Values and symbols are the same as in Figure 1.
Chapter 3

Forest Productivity and Efficiency of Resource Use Across a Chronosequence of Tropical Montane Soils

Abstract

We tested the hypothesis that plants adjust to nutrient availability by altering carbon allocation patterns and nutrient use efficiency (NUE), but are constrained by trade-offs between NUE and radiation conversion efficiency (RCE). Net primary production (NPP), NUE and RCE were measured in montane Metrosideros polymorpha forest across a $4.1 \times 10^6$ yr chronosequence in which available soil N and P pools change with site age. NPP was lowest at the young site and peaked at the $1.5 \times 10^5$ yr site. In contrast to theories of carbon allocation relative to limiting resources, no consistent trend was detected for above- versus below-ground allocation in the M. polymorpha dominated forests. RCE followed a pattern similar to that of NPP across the chronosequence while the pattern of NUE was inverse to that of RCE, peaking
at the youngest and oldest sites. A negative correlation between RCE and foliar nutrient resorption supports the idea that a trade-off exists between RCE and leaf characteristics affecting NUE.

**Introduction**

Nutrient availability is an important factor governing net primary productivity (NPP), patterns of carbon allocation, and resource-use efficiency (RUE). Patterns of NPP can be usefully analyzed as the product of resource supply, resource acquisition and RUE. We examined these factors along a well-defined gradient of soil nutrient availability in a chronosequence of tropical montane forest ecosystems to determine the mechanisms and patterns of plant response.

Resource supply, specifically nutrient availability, changes over the course of soil and ecosystem development. Relationships between soil age and soil nutrient pools have been illustrated with the use of chronosequences (Walker & Syers 1976; Crews et al. 1995). Chronosequences have also been used to describe relationships between nutrient availability and productivity (Bormann & Sidle 1990), foliar
nutrients (Vitousek et al. 1995), plant assemblages (Kitayama in press) and successional replacement (Bormann & Sidle 1990; Kitayama et al. 1995). Crews et al. (1995) recently described a chronosequence across the Hawaiian Islands with substrate ages from 300 to $4.1 \times 10^6$ yr where available soil nutrients change systematically from the youngest to oldest sites, all of which are dominated by a single species, Metrosideros polymorpha. Phosphorus at the youngest site is mostly in the form of primary minerals, while more labile forms increase at the $2 \times 10^4$ to $1.5 \times 10^5$ yr sites. Recalcitrant forms of P dominate at the oldest sites (Crews et al. 1995). Nitrogen accumulates from the youngest site to the oldest site (Riley & Vitousek 1995). Foliar nutrient concentrations in M. polymorpha tend to follow a pattern across the chronosequence similar to that of nutrient availability: the highest N concentrations occur at the $2 \times 10^4$ yr site, the highest P concentrations at the $1.5 \times 10^5$ yr site, and decreased concentrations of both nutrients at the ends of the chronosequence (Vitousek et al. 1995).

Resource acquisition by plants can be modified by relative shifts in carbon allocation between above- and
below-ground components (Tilman 1988). For example, nutrient stressed plants may increase nutrient uptake by investing a greater proportion of carbon resources in roots (Chapin 1980; Gower 1987; Aerts et al. 1991). Nutrient sufficient plants should increase photosynthetic area or produce high-nutrient leaves with a greater capacity for photosynthesis (Chabot & Hicks 1982; Reich et al. 1991). Increased leaf mass per unit area (LMA), leaf longevity (Chapin 1980; Reich et al. 1991), decreased foliar nutrient concentration and photosynthetic rates (Chabot & Hicks 1982; Reich et al. 1991) are often associated with low nutrient availability.

Plants may adjust to variation in nutrient availability by altering nutrient use efficiency (NUE). Defining NUE as the amount of biomass produced per unit nutrient taken up from the soil, Hirose (1975) hypothesized that plants growing in nutrient impoverished sites would be more efficient in their use of available nutrients than plants growing in more fertile sites. Among plant communities, shifts in NUE might be explained by successional replacement of species leading to more or less efficient communities (Chapin 1980, Chapin & Kedrowski 1983). Within a species
there may be phenotypic variation in nutrient conserving characteristics (Kost & Boerner 1985). Some studies have shown an inverse relationship between nutrient availability and NUE in both plants (Hirose 1975; Shaver & Melillo 1984) and in ecosystems (Vitousek 1982). In other cases, there was either no relationship (Birk & Vitousek 1984) or NUE increased with nutrient availability (Fownes 1985; Lathja 1987). Pastor et al. (1984) found that nitrogen use efficiency along an N availability gradient was low with very low N availability, increased as N increased and then declined. The pattern suggests a shift from biomass maintenance to increased net carbon gain as N becomes more available and reduced nitrogen use efficiency at relatively high N availability.

Resorption of nutrients from senescing leaves reduces dependency on nutrient uptake from the soil and can be viewed as a component of NUE. In some cases, the proportion of one or more nutrients resorbed has been shown to be greater at nutrient impoverished sites (Boerner 1984; Lathja 1987; Chapin & Moilanen 1991; Pugnaire & Chapin 1993). However, in other cases the opposite pattern has been found
Another measure of RUE is radiation conversion efficiency (RCE) which is measured as NPP per unit absorbed light (g MJ$^{-1}$). Production of plant biomass is linearly proportional to absorbed radiation when other resources are not limiting (Monteith 1977). The relationship holds for both temperate and tropical trees (Linder et al. 1985; Cannell et al. 1987; Harrington & Fownes 1995; Saldarriga and Luxmore 1991; Wang et al. 1991) and may differ between species or within a species under altered nutrient availability (Monteith 1977; Waring 1983). When Sitka spruce was fertilized with N, RCE increased from 0.33 to 0.43 g mol$^{-1}$ (Wang et al. 1991) suggesting that RCE can be improved when nutrients become more available. Foliar N is positively correlated with photosynthetic rate (Field & Mooney 1986) and P has been shown to be positively correlated with photosynthetic rate in white pine seedlings (Reich & Schoettle 1988).

Since low nutrient availability is associated with nutrient conserving mechanisms including low nutrient leaves, there may be a physiological trade-off in which
increased NUE occurs at the expense of RCE. The basic form of the trade-off pattern is an inverse relation between a species performance under one constraint versus another (Fownes 1995). A related example is the trade-off between intrinsic water-use efficiency and NUE measured in plants under conditions of water limitation (Field et al. 1983; Lajtha & Whitford 1989; Harrington et al. 1995).

In Hawaii, *M. polymorpha* exhibits a high degree of both phenotypic (Stemmerman & Ihse 1993) and genotypic variation (Aradhya et al. 1991). The species has an extremely wide ecological amplitude, occurring from near sea level to tree line at 2500 m on Mauna Loa, Island of Hawaii, and from bog to dry forest. Given the adaptability of the species, we hypothesized that *M. polymorpha* forests will have increased NUE at the ends of the chronosequence where N and P limitation have been demonstrated. Furthermore, NPP should reach a maximum where nutrient availability and foliar nutrients peak. Phenotypic adjustments to nutrient availability should be apparent as proportional differences in above- versus below-ground biomass or production allocation patterns. Because photosynthetic rates are related to foliar nutrient status, we hypothesized that RCE
should be positively correlated with foliar nutrients.
There should be an inverse relationship between RCE and NUE
if nutrient stressed plants adjust nutrient conserving
characteristics.

**Site Descriptions**

Five sites were selected along a soil chronosequence in
the Hawaiian Islands described in detail by Crews *et al.*
(1995). All sites are near 1200 m elevation and have a mean
annual temperature near 16°C (Atlas of Hawaii, 1983) and
receive \( \approx 2500 \) mm of precipitation annually (Giambelluca *et al.*
1986). Sites are located on undissected volcanic shield
surfaces or shield remnants (at the oldest sites) with
minimal slope (< 6%). Soils of the chronosequence sites
were derived from volcanic tephra deposits ranging in age
from 300 to \( 1.4 \times 10^6 \) years (Crews *et al.* 1995). A possible
exception is the oldest site where it is difficult to
determine the form of the parent material at such a late
weathering stage. Each site supports a closed canopy forest
with *Metrosideros polymorpha* as the dominant tree species.
Several other genera including *Cibotium*, *Cheirodendron*,
*Ilex*, *Coprosma* and *Vaccinium* account for most of the

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remaining cover and species richness increases from the youngest to the oldest site (Crews et al. 1995). None of the sites are known to have been cleared by humans. Sites will hereafter be referred to as Thurston (300 yrs), Laupahoehoe (2 x 10⁴ yrs), Kohala (1.5 x 10⁵ yrs), Kolekole (1.4 x 10⁶ yrs) and Kokee (4.1 x 10⁶ yrs).

Resin extractable P increases by a factor of ten from Thurston to Kohala (Table 3.1) and then declines by 80% at Kokee (Crews et al. 1995). Nitrogen mineralization increases from 195 to 647 mg m⁻² day⁻¹ and nitrification increases from 33 to 112 mg m⁻² day⁻¹ from Thurston to Kokee (Riley & Vitousek 1995).

Methods

Two 10 m radius plots were established at Thurston, Kohala and Kolekole sites; two 15 m radius plots were used at Laupahoehoe (because of larger trees at the site). At Kokee, we used four 10 x 10 m plots that were already defined for controls in a fertilizer study (Herbert & Fownes 1995). All trees 30 mm or larger at 1.3 m height (DBH) within the plots were identified and DBH recorded. Because M. polymorpha grows slowly and stem surfaces are often
convoluted, a ring was painted around each stem at DBH to reduce error involved in measurement of increment growth. Diameter increments were measured for one year beginning in October 1993.

**Litterfall Collections:**

Monthly fine litter collections (including twigs < 1 cm diameter) were made for twelve months beginning in October 1993. Collections were made using nine 0.2 m² frame traps per plot except for Kokee where four litter traps were used per plot. Litter collections were sorted into leaf and twig components and weighed after drying to constant weight.

**Leaf Area Index (LAI):**

LAI was estimated optically using a LI-COR LAI 2000 plant canopy analyzer at two to three month intervals. Regularly scheduled measurements were not possible due to frequent rain or mist at the study sites and the effect of water droplets on the LAI 2000 optics. The LAI 2000 uses gap fraction analysis of diffuse radiation transmittance to indirectly estimate LAI (Welles & Norman 1991). This method underestimates LAI where canopy elements are strongly
clumped or aggregated in space, but a correction factor can be determined from the ratio of projected LAI to true LAI at the appropriate level of aggregation (Gower & Norman 1991, Smith et al. 1993). Our correction for *M. polymorpha* is based on tree harvests at the University of Hawaii Hamakua Research Station, Island of Hawaii, at 810 - 830 m elevation. Ten plots having a projected LAI (measured by the LAI 2000) ranging from 1.4 to 3.6 were sampled. Linear regression of allometric LAI against optical LAI gave a correction in which LAI = -1.16 + 2.44 * optical LAI (appendix A).

**Fine Roots:**

Fine roots (< 2.0 mm diameter) were sampled from each plot using a 3 cm diameter core. Sample depth varied from site to site because of soil and root growth characteristics. Sample depth was determined as that depth which included 90% of fine roots in the upper 50 cm of the soil profile by subsampling from excavated soil pits at each site. On this basis, samples were taken to 12 cm at Kokee, 20 cm at Kolekole and 30 cm at Kohala and Thurston. Samples at Laupahoehoehoe were taken to 50 cm, but since fine roots...
penetrated below 1 m at this site a depth determination based on 90% inclusion was not made. Five cores per plot were collected at Kokee and 9 were collected from all other plots (coefficient of variation ranged from 33 to 47). Within 48 hours, cores were sieved and washed in tap water and roots less than 2 mm diameter were separated from the washed sample in a water bath. Roots were classified as live or dead based on color and texture, oven dried to constant weight and recorded to the nearest 0.001 g.

**Soil Respiration and Below Ground Production:**

Soil CO₂ flux was measured using the soda-lime absorption method (Edwards 1982; Cropper, Ewel & Raich 1985; Raich & Nadelhoffer 1989). Sixty grams of soda-lime, oven dried to constant weight at 105 °C, was contained in soil tins having a 79 mm diameter opening. Tins were opened and placed under inverted chambers covering 645 cm² soil surface for 20 to 26 hours. The difference in soda-lime oven dry weight, multiplied by the correction factor 1.4 (Edwards, 1982), represented CO₂ absorbed. To avoid root damage, chambers were inserted into a 1 cm deep groove in the soil surface, maintained between measurements with a plastic
ring. Measurements were taken once a month from five chambers per plot except for Kokee where three chambers per plot were used. Measurements during heavy rainfall events were avoided because changes in water-filled pore space could result in a flush of CO₂ from the soil.

An annual flux of soil CO₂ was calculated for each site and used to estimate carbon allocation to roots by the carbon budget method, assuming steady state of soil carbon pools. As such, a simple carbon budget (inputs = outputs) can be used to place upper limits on below-ground carbon allocation in forest ecosystems (Raich and Nadelhoffer 1989). Assuming that the primary soil carbon inputs are litterfall and below-ground carbon allocation, and the major pathway to carbon loss is respiration, below-ground carbon allocation can be calculated as carbon flux from the soil minus carbon input from litter. An approximate carbon fraction of 0.5 was used to estimate litterfall carbon inputs from litterfall dry mass.

**Allometric Equations and Biomass Estimation:**

Wood biomass (W), including boles, branches and twigs, was estimated using an allometric equation generated from
the destructive sampling of 45 *M. polymorpha* trees ranging in size from 1.0 to 38 cm basal diameter (D), harvested from several different sites on the Island of Hawaii (Gerrish 1988; J. Raich, unpubl. data; G. Aplet, unpubl. data).

Regression of ln W versus ln D produced the equation ln W = 2.619 + 3.034 * ln D (r² = 0.977, P < .0001, Sₓₓ = .548).

Height improved the regression (r² = 0.983, P < .0001, Sₓₓ = .345), but since we did not have heights for all trees we use only D in our allometric equation. The correction factor exp(Şₙₓₓ²/2) was applied to counteract bias from logarithmic transformation (Baskerville 1972; Sprugel 1983).

The final equation was W = 15.945 * D¹.034 where D is measured in cm and W is predicted in g dry weight.

**Estimates of NPP and NUE:**

Above ground net primary production (ANPP) was estimated as the sum of the change in wood biomass and annual fine litterfall on a per area dry weight basis. The change in wood biomass was estimated by applying the allometric equation for biomass, as described above, to stem diameters at the beginning and end of the measurement interval. The fraction of soil respiration attributed to
roots was used to represent below-ground carbon allocation. Total NPP was measured as the sum of ANPP and root production. As an index of NUE we used the ratio of NPP to nutrient mass cycled through litter annually. While nutrients cycled through litterfall do not fully represent nutrient uptake, Nadelhoffer et al. (1983) found a strong correlation between N uptake by vegetation and N mass in litterfall. NPP was also examined in relation to canopy foliar nutrient pools and nutrient turnover time.

LMA, Foliar Nutrients and Nutrient Resorption:

Full sun and mid-canopy Metrosideros leaves were collected from all sites. The youngest fully mature leaves (behind an expanding whorl or mature bud) were collected from each twig sampled and a minimum of five trees per plot were sampled. Leaves collected from each stratum were pooled into a single collection for each plot, stored in plastic bags and refrigerated. Senesced M. polymorpha leaves were collected within 24 hours of falling onto screens placed on the forest floor. Leaf area was measured using a LI-COR 3100 area meter within 48 hours of
collection. Samples were then dried at 70 C to constant weight to determine LMA.

Foliar nutrient concentrations were determined for senesced, sun- and mid-canopy leaves. The dried samples were ground and acid-digested in a block digester using a semimicro-Kjeldahl procedure with a mercuric oxide catalyst. Total N concentration (Alpkem method A303-S071, 1990) and total P concentration (Alpkem method number A303-S050, 1990) were determined using an Alpkem auto-analyzer.

The fraction of nutrient resorbed during leaf senescence was normalized to calcium concentration to correct for mass loss during senescence (Vitousek and Sanford 1986) and was estimated as 1 minus the quotient of nutrient/Ca in leaf litter and nutrient/Ca in green leaves (sun and mid-canopy leaves pooled). Canopy N and P pools were estimated as the product of LAI, LMA and foliar nutrient concentration. Nutrient turnover in the canopy was measured as the ratio of canopy nutrient pool and nutrient lost in annual litterfall.
Intercepted radiation was estimated using the function

\[ I = R \times (1 - e^{-kLAI}) \]

where \( I \) = intercepted radiation, \( R \) = incident radiation, and \( k \) is the extinction coefficient.

Incident radiation for the Thurston site was obtained from the Hawaiian Sugar Planters Association, Area, Hawaii which receives meteorological data from the Hawaii Volcanos National Park headquarters. Incident radiation at all other sites was measured using LICOR LI200S pyranometers and either a Campbell Scientific CR21 or CR10M data logger. Measurements were taken every 60 s and averaged hourly. Hourly averages were multiplied by 3600 (s hr\(^{-1}\)) and summed for monthly total MJ m\(^{-2}\) estimates. Estimates of LAI and \( k \) were obtained with a LICOR LAI 2000 optical canopy analyzer (LICOR Inc., 1990). Because the LAI 2000 calculates \( k \) and LAI on the basis of light extinction, uncorrected LAI values were used in estimates of intercepted radiation by the canopy. Average intercepted radiation between successive LAI estimates was calculated using the sum of incident radiation during the time interval and the average \( k \) and LAI values. RCE (g MJ\(^{-1}\)) was calculated as the quotient of NPP and \( R_i \).
Results

Total basal area of trees > 30 mm ranged between 32 and 38 m² ha⁻¹, 81 to 88% of which was comprised of M. polymorpha (Table 3.2). The 2 x 10⁴ year old Laupahoehoe site had the largest trees and standing biomass. But there was no relationship between site age or nutrient availability and stand biomass. Furthermore, there was no consistent relationship in the above versus below ground biomass ratio or leaf versus fine root biomass ratio relative to site age or nutrient availability.

NPP ranged from 1.4 to 2.4 kg m⁻² yr⁻¹ with the highest mean NPP measured at the 1.5 x 10⁵ year old Kohala site, declining toward either end of the chronosequence (Figure 3.1.A). However, within-site variability could not be separated from that between sites where mean differences ranged from 1.8 to 2.3 kg m⁻² yr⁻¹. Below-ground components of NPP across the chronosequence followed a pattern similar to total NPP with the exception of the Kolekole site where high twig litter inputs reduced the fraction of soil respiration attributed to root production. RCE (g NPP MJ⁻¹) followed a pattern similar to that measured for NPP across the chronosequence, but more pronounced (Figure 3.1.B).
Mean RCE at Kohala was 136% that at Thurston and 125% that at Kokee. One plot was excluded as an outlier from intercepted radiation estimates at Kokee. An underestimate in LAI was indicated by an anomalous stem diameter to leaf area relationship. Furthermore, due to the location of the plot near the edge of a cliff, intercepted radiation may have also been underestimated.

Concentrations of both N and P in recently fully expanded *M. polymorpha* sun and mid-canopy leaves were low at the youngest and oldest sites. Nitrogen concentrations increased to a maximum at the $2 \times 10^4$ year old Laupahoehoe site and then showed successive decreases to the $4.1 \times 10^6$ year old Kokee site (Figure 3.2.A). Phosphorus concentrations varied similarly with substrate age, except that P reached its maximum at Kohala before declining. In general, both nutrient concentration and nutrient mass per unit leaf area was greater in sun leaves than in mid-canopy leaves with the exception of the Kolekole site. At Kolekole, tree crowns were less stratified and differences between sun leaves and mid-canopy leaves were not evident (Table 3.3).
In contrast, resorption of N and P from senescing leaves was greatest at the youngest and oldest sites and lowest at Laupahoehoe and Kohala, illustrating an inverse relationship with foliar nutrient concentration across the chronosequence (Figure 3.2.B). NPP per unit N and P returned to the soil in leaf litter was greater at the youngest and oldest sites (Figures 3.3.A & 3.3.B). Production per unit total canopy N and P showed a different pattern, with the lowest production per unit nutrient occurring at the youngest site and generally increasing with site age (Figures 3.3.C & 3.3.D). However, there was a long residence time for both N and P in the canopy at the youngest site, decreasing at Laupahoehoe and Kohala, and increasing again at the Kolekole and Kokee sites; a pattern similar to that measured for nutrient resorption but inverse to foliar nutrient concentration across the chronosequence (Figure 3.3.E & 3.3.F).

Both LMA and nutrient resorption were negatively correlated with foliar N and P concentration (Figure 3.4). High LMA leaves were retained longer (Figure 3.5), while leaf turnover interval decreased with both increased foliar P ($p = .030, r^2 = .394$) and N ($p = .050, r^2 = .332$).
RCE was positively correlated with either increased foliar N or P, regardless of site age (Figures 3.6.A and 3.6.B). Although NPP varied across the chronosequence, NPP was not dependent on foliar N or P concentrations alone (Figures 3.5.C & 3.5.D).

RCE was negatively correlated with resorption of both N and P from senescing leaves (Figures 3.7.A & 3.7.B), suggesting an inverse relationship between RCE and internal conservation of nutrients.

Discussion

There was a general pattern of increased NPP at sites on the chronosequence where N and P availability increased. However, differences in mean NPP between sites were small relative to available N and P in soils across the chronosequence (Crews et al. 1995). Furthermore, differences in NPP and the components of NPP (wood, leaves and roots) were not correlated with foliar N or P concentration. By contrast, ANPP at the oldest site was positively correlated with foliar P concentration after fertilization with P and N, but there was no relation between ANPP and foliar N (Herbert & Fownes 1995).
another location near the youngest site, stem growth and photosynthetic rate in *M. polymorpha* were correlated with foliar N concentration after fertilization, but not P (Vitousek et al. 1993). Increased NPP with after fertilization increased foliar nutrients at the young and old sites suggests a phenotypic adjustment to low nutrient availability and a response to increased availability of a limiting nutrient. NPP of *M. polymorpha* forests at multiple sites having a broad range of natural fertility do not show the same relationship with foliar N or P concentration, suggesting adaptation to within-site conditions and a range of phenotypic adjustments across sites.

Contrary to the hypothesis that plants allocate carbon resources in such a way that capture of a limiting resource is optimized, we found the highest fine root mass and highest carbon allocation to roots at the most fertile site. Furthermore, there was no relationship between site fertility and the ratio of leaf to fine root mass or leaf to below-ground carbon allocation. Confirming this result is the finding that root ingrowth cores at three of the sites (Thurston, Kohala and Kokee) had a similar pattern of low
Patterns of resource use in relation to site age and nutrient availability were more distinct. Production per unit N or P uptake was greatest at the ends of the chronosequence and low at the more fertile sites. Low production per unit nutrient in canopy biomass at the youngest site seems contrary to the pattern, but is probably linked to low foliar nutrient concentrations and greater LMA. Photosynthetic capacity is positively correlated with foliar N concentration (Field & Mooney 1986) and the high LMA characteristic of the site is associated with increased leaf longevity which in turn would slow turnover of canopy nutrient pools (Chapin 1980; Chabot and Hicks 1982; Reich et al 1991). The result is low RCE but high NUE associated with increased leaf longevity, long residence time for nutrients in the canopy and high production per unit nutrient cycled back to the soil through litterfall.

Another mechanism increasing NUE at the ends of the chronosequence was the increased fraction of foliar N and P resorbed. High resorption of both N and P was measured at both ends of the chronosequence, even though fertilization
experiments demonstrated that productivity was limited by N at Thurston (Vitousek et al. 1993) and by P at Kokee (Herbert & Fownes 1995). It appears that resorption of N and P is not independent.

RCE increased from Thurston to Kohala and then decreased; a pattern similar to that of NPP but inverse to that of NUE. The relationship between RCE and foliar nutrient concentration suggests that RCE is controlled, at least in part, by nutrient availability. This concept is supported by previous research where RCE increased in response to fertilizer additions (Monteith 1977; Wang et al. 1991). In the present study RCE decreased as the fraction of either N or P resorbed increased. Functionally, this is a trade-off in which high photosynthetic capacity associated with high nutrients in leaves occurs at the expense of efficient nutrient recycling.

We conclude that changes in _M. polymorpha_ forest NPP are small in relation to changes in available soil nutrient pools. The effect of increased foliar nutrient concentration at more fertile sites is to increase RCE, probably through increased photosynthetic capacity. NPP is apparently maintained at nutrient limited sites because of
increased efficiency of nutrient use and internal recycling. Rather than alter carbon allocation to roots to improve uptake of a limiting nutrient, *M. polymorpha* adjusts to nutrient availability by adjusting NUE.
References


Table 3.1. Soil pH and availability of N and P across the chronosequence.

<table>
<thead>
<tr>
<th>Site</th>
<th>pH in H₂O</th>
<th>In situ resin extractable nutrients (μg bag⁻¹ d⁻¹)</th>
<th>Gross N-min.</th>
<th>N-nitr. (mg m⁻² d⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thurston</td>
<td>5.02</td>
<td>0.20 3.01 0.22</td>
<td>195</td>
<td>33</td>
</tr>
<tr>
<td>Laupahoehoe</td>
<td>3.57</td>
<td>1.21 8.12 4.25</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Kohala</td>
<td>4.09</td>
<td>2.19 4.90 0.31</td>
<td>432</td>
<td>52</td>
</tr>
<tr>
<td>Kolekole</td>
<td>3.77</td>
<td>0.51 4.02 10.53</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Kokee</td>
<td>3.99</td>
<td>0.41 4.12 10.29</td>
<td>647</td>
<td>112</td>
</tr>
</tbody>
</table>

Adapted from Crews et al. 1995.
Table 3.2. Stem basal area, % of total basal area of *Metrosideros polymorpha*, biomass and LAI across the chronosequence.

<table>
<thead>
<tr>
<th>Site</th>
<th>BA (m² ha⁻¹)</th>
<th>Met. Wood (%)</th>
<th>Leaves (%)</th>
<th>Live roots (&lt; 2 mm)</th>
<th>LAI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thurston</td>
<td>36.7 (1.1)</td>
<td>81 (21)</td>
<td>17.6 (0.9)</td>
<td>1.52 (0.03)</td>
<td>8.0 (0.7)</td>
</tr>
<tr>
<td>Laupahoehoe</td>
<td>32.0 (1.7)</td>
<td>83 (82)</td>
<td>10.1 (0.1)</td>
<td>2.03 (0.30)</td>
<td>7.1 (0.3)</td>
</tr>
<tr>
<td>Kohala</td>
<td>36.6 (3.1)</td>
<td>83 (27)</td>
<td>8.6 (0.7)</td>
<td>2.66 (0.10)</td>
<td>5.8 (0.3)</td>
</tr>
<tr>
<td>Kokee</td>
<td>38.1 (2.8)</td>
<td>86 (13)</td>
<td>14.5 (1.5)</td>
<td>2.72 (0.69)</td>
<td>7.5 (0.8)</td>
</tr>
<tr>
<td>Kokee</td>
<td>36.8 (7.0)</td>
<td>88 (46)</td>
<td>7.8 (1.1)</td>
<td>2.18 (0.16)</td>
<td>4.4 (0.6)</td>
</tr>
</tbody>
</table>
Table 3.3. Nutrient concentration and LMA of glabrous and pubescent *Metrosideros polymorpha* leaves at sites on the chronosequence.

<table>
<thead>
<tr>
<th></th>
<th>Thurston pubescent</th>
<th>Thurston glabrous</th>
<th>Laupahoehoe</th>
<th>Kohala</th>
<th>Kolekole</th>
<th>Kokee</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sun</td>
<td>Mid</td>
<td>Sun</td>
<td>Mid</td>
<td>Sun</td>
<td>Mid</td>
</tr>
<tr>
<td>N %</td>
<td>0.82</td>
<td>0.81</td>
<td>0.76</td>
<td>0.79</td>
<td>1.42</td>
<td>1.34</td>
</tr>
<tr>
<td>P %</td>
<td>0.063</td>
<td>0.052</td>
<td>0.052</td>
<td>0.056</td>
<td>0.094</td>
<td>0.088</td>
</tr>
<tr>
<td>N g m⁻²</td>
<td>2.08</td>
<td>1.78</td>
<td>1.65</td>
<td>1.45</td>
<td>2.23</td>
<td>1.70</td>
</tr>
<tr>
<td>P g m⁻²</td>
<td>0.160</td>
<td>0.115</td>
<td>0.112</td>
<td>0.103</td>
<td>0.147</td>
<td>0.112</td>
</tr>
<tr>
<td>LMA g m⁻²</td>
<td>256</td>
<td>222</td>
<td>217</td>
<td>184</td>
<td>157</td>
<td>127</td>
</tr>
</tbody>
</table>
Figure 3.1. (A) NPP and the additive components of primary productivity. Values are means +/- one standard error. (B) RCE across the chronosequence. The solid line is plotted through site means. The open symbol represents an outlier at the Kokee site where LAI, intercepted radiation or both were underestimated (See text).
Figure 3.2. (A) Mean foliar N (triangles) and P (circles) in sun- and mid-canopy leaves and (B) fraction of nutrient resorbed from *Metrosideros polymorpha* leaves during senescence. Closed symbols represent pubescent leaves at the youngest site.
Figure 3.3. (A) NPP per unit N and (B) P uptake using litterfall nutrients as an index. (C) NPP per unit N and (D) P in the canopy foliar nutrient pool. (E) N and (F) P turnover time in years in the canopy foliar nutrient pool.
Figure 3.4. (A) Change in LMA relative to foliar N and (B) P concentration. (C) Nutrient resorption relative to foliar N and (D) P concentration as indicated by senesced leaf nutrient concentration. Dashed lines delimit the 95% confidence interval.
Figure 3.5. Leaf turnover time in years relative to LMA. Dashed lines delimit the 95% confidence interval.

\[ p = .001 \]
\[ r^2 = .674 \]
Figure 3.6. Changes in RCE relative to (A) foliar N and (B) P concentration and relationship between NPP and (C) foliar N and (D) P concentrations. Dashed lines delimit the 95% confidence interval. Open symbol in C and D as in figure 1B.
Figure 3.7. RCE versus nutrient resorption as a function of (A) foliar N and (B) P resorption illustrates a trade-off in photosynthesis and nutrient conserving mechanisms. Dashed lines delimit the 95% confidence interval. Open symbol as in figure 1B.
Hurricane Damage and Recovery of a Native Hawaiian Rainforest and the Impact of Experimentally Altered Nutrient Availability

Abstract

Hurricane Iniki damaged a forest dominated by Metrosideros polymorpha where we had previously studied nutrient limitation to forest productivity on a highly weathered soil. Leaf area index was reduced by 3% to 58%, but recovered to near pre-hurricane values by nine months. Live fine root mass was reduced by 44% and took two years to recover. Stem damage was largely that of branch removal but some stems were tipped or snapped and large trees were damaged with greater frequency than small trees. Fine litterfall was 1.4 times the annual input while nutrient transfers from the canopy to forest floor approximated that of a typical year. During litter decomposition there was an initial mass loss of nutrients from both leaves and twigs, followed by immobilization of N and P. Stem growth and above-ground net primary productivity (ANPP) decreased for a
year and then recovered to near pre-hurricane values. Both ANPP and production per unit leaf area increased in response to P fertilizer applications.

Introduction

Hurricanes and other large-scale disturbances influence forest structure. Resistance to damage may differ among species or, or within species, among age or size classes (Foster 1988, Gresham et al. 1991, Putz & Sharitz 1991, Reilly 1991, Walker 1991), thereby affecting species composition or population structure. Recovery following such disturbances may be affected by the degree of damage sustained (Walker 1991, Merrens & Peart 1992), but also by the availability of essential resources. Recent studies suggest that hurricane induced transfers of canopy biomass and nutrients to the forest floor increase nutrient availability, (Lodge et al. 1991, Whigham et al. 1991), but the effect of altered nutrient availability on recovery has not been measured. In the present study, we examine the impact of a hurricane on a montane tropical rainforest, the
On September 11, 1992, Hurricane Iniki struck the island of Kauai in the Hawaiian Islands. The storm passed directly over a montane native rainforest dominated by *Metrosideros polymorpha* (Gaud.) where we were measuring above-ground net primary productivity (ANPP) in response to fertilizer applications (Herbert & Fownes 1995). Knowledge of site characteristics and stand structure allowed for accurate measurement of hurricane damage and subsequent recovery processes as affected by nutrient availability. Our objectives in the ensuing study were to (i) assess hurricane damage in relation to stand structure; (ii) determine the relationship between above-ground and below-ground damage and recovery processes; (iii) evaluate hurricane induced litterfall, the associated transfer of nutrients from the canopy to the forest floor, nutrient mineralization and immobilization processes through two years of decomposition; (iv) measure the impact of damage on subsequent stem growth and ANPP; and (v) evaluate the role of nutrient availability in recovery.
Studies of hurricane damage elsewhere have shown that crown damage was proportional to exposure as a function of tree size (Foster 1988, Gresham et al. 1991, Reilly 1991, Walker 1991) or local topography (Foster & Boose 1992, Boose et al. 1994). On Kauai, six Acacia koa (Gray) forests having a range in stature and LAI were defoliated in proportion to pre-hurricane LAI (Harrington et al. in press), but the effect could not be separated from site topographic variation. We hypothesized that crown damage would be proportional to crown area. The increase in LAI among P fertilized plots allowed for a direct comparison of canopy reduction relative to exposed canopy area within a single location with a uniform topographic relief.

A large decrease in fine roots was measured after Hurricane Hugo struck forests in Puerto Rico (Parrota & Lodge 1991). Experimental gap creation resulted in a 40% decline in live fine root biomass within two months, while six months after Hurricane Hugo there was a 70-77% decline (Silver & Vogt 1993). The decreased fine root biomass may be a consequence of crown damage and leaf area reduction. Fownes and Anderson (1991) found that fine root mass was sensitive to changes in leaf area in two fast-growing tree
species. We predicted that following Hurricane Iniki there would be a decline in live fine root biomass proportional to the reduction of LAI and that regrowth of fine roots would be proportional to LAI recovery.

Directly associated with canopy damage was a large transfer of fine litter to the forest floor, much of which was green or incompletely senesced. The result was a large flux of nutrients from the canopy to the forest floor (Lodge et al. 1991, Whigham et al. 1991, Harrington et al. in press). In the montane forests of Kauai, Hawaii, senesced M. polymorpha leaves are low in nutrient content and decompose slowly, immobilizing both N and P (Crews et al. 1995). Because nutrient concentrations of green M. polymorpha leaves are also low, though greater than senesced leaves (Crews et al. 1995, Herbert & Fownes 1995), we expected that green leaves would also immobilize N and P during the first year of decomposition. Woody fine litterfall should only increase nutrient immobilization during decomposition. Since forest ANPP on the highly weathered soil at the site is limited by P (Herbert & Fownes in press), nutrient immobilization could affect recovery of damaged trees.
Defoliation following disturbance should result in reduced stem growth (Harrington et al. in press; Grace 1995). However, in Yucatan, relative growth rate of surviving stems increased after hurricane Gilbert (Whigham et al. 1991). Hurricane damage at the Hubbard Brook Experimental Forest, New Hampshire, USA, caused an immediate increase in radial growth of surviving trees, probably due to increased availability of light and other resources to survivors (Merrens & Peart 1992). Since there appeared to be low mortality immediately following the hurricane, we hypothesized that decreased LAI should decrease diameter increment, which would recover only after LAI recovered.

Hawaiian M. polymorpha forests form mosaics of "cohorts" made up of trees of apparently similar age (Mueller-Dombois 1987). It has been hypothesized that hurricanes and other catastrophes maintain the forested landscape in this simplified size/age-structure (Mueller-Dombois 1992a, b) due to size-specific mortality. Large trees sustain damage due to a greater exposed profile (Foster 1988, Gresham et al. 1991, Reilly 1991, Walker 1991, Harrington et al. in press), while small trees are damaged

In addition to structural damage from hurricanes, there may be a physiological impact related to the loss of photosynthetic area and fine roots. A possible mechanism underlying senescence of aging M. polymorpha cohorts is an increase in respiratory sink to leaf biomass ratio (Gerrish 1990). Removal of leaf area from large trees which may already be suffering such a respiratory debt could increase mortality. Therefore, we expect that higher mortality will occur among large trees because of the combined effects of greater crown damage and the physiological impact of reduced leaf area. The effect may be to simplify stand-structure as hypothesized by Mueller-Dombois (1987, 1992a, 1992b).

Because P was found to be the most limiting element to productivity prior to the hurricane, we expected added P to affect the recovery process. We continued to measure ANPP and fine root biomass for two years following the hurricane. We hypothesized that increased P availability in P fertilized plots would enhance recovery of net primary productivity.
Site Description

The study site is located in the Na Pali - Kona Forest Reserve in Kokee State Park, island of Kauai, Hawaii (22°08' N and 159°38' W) at 1134 m elevation. The site is on a ridge top remnant with a geologic age estimated to be between 3.9 and 4.3 million years (Clague & Dalrymple 1988). The soil is mapped as a clayey ferritic isomesic Plinthic Acrorthox (Soil Survey Staff 1972) revised to an Acrudox (Soil Survey Staff 1992). Mean annual precipitation is 2500 mm (Giambelluca et al. 1986).

Vegetation is characterized by a closed forest canopy composed predominantly of Metrosideros polymorpha Gaud. var. glaberrima (H. Lev.) St. John, which accounts for 88% of the stem basal area. Other tree species include Syzigium sandwichensis (A. Gray) Nied., Cheirodendron trigynum (Gaud.) A. Heller and Cheirodendron platyphyllum (Hook. & Arnott) Seem. subspecies kauaiense (Kraj.) Lowry. The understory is primarily fern with alien Hedychium gardnerianum and Rubus spp.
Physical Characteristics of Hurricane Iniki

Hurricane Iniki was classified as a category 5 storm (on the Saffir-Simpson scale) with wind speeds of 230 km hr\(^{-1}\) gusting to 280 km hr\(^{-1}\) (National Weather Service 1992). Iniki had a high speed of passage estimated at 32 to 40 kilometers per hour, which may have reduced its impact. Hawaii Civil Defense authorities estimated that major damage covered 75% to 80% of the Island of Kauai, making it the most powerful storm to have struck the Hawaiian Islands in at least 90 years. The path of storm took the eye of Iniki directly over our study site in Kokee.

Methods

Experimental Design

In early March 1991, eighteen months prior to the hurricane, a fertilization experiment was started (Herbert & Fownes 1995). Thirty-two 10 x 10 m plots, each with a 5 m border, were selected for similarity in species composition, total basal area and diameter distribution of stems. The three main treatments were N and P applied at the annual rate of 100 kg ha\(^{-1}\) each, and a mix of other essential (OE) nutrients (excluding N and P), including K, Ca, Mg, S, Fe,
Mn, Zn, Cu and B as described in Herbert & Fownes (1995). Treatments were applied at six month intervals at two levels: zero or plus in eight factorial combinations of N, P and OE and randomly assigned to plots in four blocks.

**Statistical Analyses**

Treatment effects on plot-level damage and recovery were analyzed using a randomized complete block ANOVA. A split-plot ANOVA with two levels of stem diameter as the subplot was used to determine the influence of both tree size and treatment (Snedecor & Cochran 1980). Data were log transformed when appropriate to meet the assumptions of ANOVA. When proportions were used, an arc sine transformation of the square root of the value between zero and one was used (Snedecor & Cochran 1980). An alpha of .05 was used for determining significance in all cases. For clarity, results are presented as arithmetic means or fractions.

**Leaf Area Index (LAI)**

LAI was estimated optically using a LI-COR LAI 2000 plant canopy analyzer, which uses gap fraction analysis of
diffuse radiation transmittance to estimate LAI indirectly (Welles & Norman 1991). This method underestimates LAI where canopy elements are strongly clumped or aggregated in space, but a correction factor can be determined from the ratio of projected LAI to actual LAI at the appropriate level of aggregation (Gower & Norman 1991, Smith et al. 1993). On the basis of destructive tree harvest on the island of Hawaii, we found a correction factor of 2.5 for M. polymorpha (Appendix A) but report optical values here.

Measurements of LAI before the hurricane were made in August and October 1991, and in March 1992. Post-hurricane measurements of LAI were made at three month intervals beginning in September 1992. The difference between the March 1992 measurement and the post-hurricane September 1992 measurement was used as the best estimate of defoliation caused by the hurricane.

Fine Roots

Fine roots (< 2.0 mm diameter) were sampled to a depth of 10 cm from each plot using a 51 mm diameter core. The sample depth included 90% of all fine roots in the upper 50 cm of the soil profile (D. Herbert unpublished data). Five
to six cores per plot were collected (coefficient of variation = 16 to 40 by plot, 25 - 45 by treatment at first sampling) at two weeks, 3, 6, 12, and 24 months after the hurricane. Cores were refrigerated at 6 - 7°C within 24 h of collection. Fine roots were separated from cores within four weeks of collection (ten weeks for the 18 month samples). Cores were sieved and washed in tap water and roots less than 2 mm diameter were separated from the washed sample in a water bath. Roots were classified as either live or dead based on color and texture and oven dried to constant weight at 70°C.

Litterfall Collections

Monthly fine litter collections (including twigs <1 cm diameter) began at the end of September 1991, six months after initial fertilization. Collections were made using four 0.2 m² frame traps per plot. Litter collections were made through October 1994.

Litterfall caused by the hurricane was separated into senesced and green fractions of M. polymorpha leaves, other miscellaneous leaves and twigs. Other collections were not separated into green and senesced components. Suspended
litter was not measured but added to litter collections over the next six months.

Litterfall Nutrients

Tissue nutrient concentrations were determined for the main litter components separated from hurricane litter. Samples were dried at 70°C, ground, and acid-digested in a block digester using a semimicro-Kjeldahl procedure with a mercuric oxide catalyst. Total N concentration (Alpkem method A303-S071, 1990) and total P concentration (Alpkem method number A303-S050, 1990) were determined using an Alpkem auto-analyzer. Samples for K, Ca and Mg analysis were dry-ashed at 500°C for 4 h, then dissolved in nitric acid and analyzed using atomic absorption spectrophotometry.

Decomposition

The rates of mass loss, nutrient immobilization and mineralization were measured over 24 months for green and senesced M. polymorpha leaves and green and senesced twigs, the four largest components of hurricane-caused fine litterfall. Thirty-five samples of each tissue type were air-dried for eight weeks, weighed to the nearest 0.01 g and
sewn into 15 x 15 cm 1.0 mm nylon mesh bags. Samples consisted of approximately 3 g of leaves or 5 g of twigs. A subsample of each tissue type was oven dried at 70°C to constant weight to determine the air dry/oven dry conversion. These subsamples were then ground and analyzed for N, P, K, Ca, and Mg concentration by the methods described earlier. Values obtained were used to estimate initial oven-dry weight and nutrient content of the decomposition samples.

Litter bags were placed on the forest floor at the field site in December 1992. Five randomly selected sample bags of each tissue type were collected at 1, 3, 6, 12, 18 and 24 months. At the 24 month collection, twig sample bags were reduced to three. Samples were oven dried at 70°C to constant weight, recorded to nearest 0.001 g and analyzed for nutrient content.

**Stem Growth**

Spring-loaded dendrometer bands were installed on six *M. polymorpha* trees per plot at the end of February 1991. Diameter growth was measured every six months through September 1994.
Structural Stem and Crown Damage

DBH of all stems greater than 3.0 cm was measured in September 1994. A rating system for structural crown damage (loss of branches) and uprooting (tilting of stems) was used to determine damage to all stems. Tree crowns suffering less than or greater than 25% branch loss were scored either 0 (relatively undamaged) or 1 (damaged). Severity of crown damage was further separated into two categories; 25 - 50% structural crown loss, and greater than 50% loss, including decapitation. Uprooting (no-tilt vs. tilt) was also separated into two severity categories; less than 45° and greater than 45°. Stems were then classified into one of four recovery groups; dead, epicormic growth only, good recovery of foliage and no apparent damage. To determine the effect of tree size on damage and recovery, stems were separated into two size-classes; greater than 10 cm DBH and less than 10 cm DBH. Only two size classes were used due to the limited size distribution.

For each plot, the proportion of all trees in each damage category and size class was recorded. Proportions
were then analyzed for influence of either treatment, size-class or interaction of treatment and size-class using ANOVA, as described earlier.

Allometric Equations and Biomass Estimation

Wood biomass (W), including boles, branches and twigs, was estimated using an allometric equation generated from the destructive sampling of 45 *M. polymorpha* trees ranging in size from 1.0 to 38 cm basal diameter (D), harvested from several different sites on the Island of Hawaii (Gerrish 1988; J. Raich, unpubl. data; G. Aplet, unpubl. data).

Regression of ln W versus ln D produced the equation ln W = 2.619 + 3.034 * ln D (r² = 0.977, P < .0001, Sy.x = .548).

The correction factor exp(Sy.x²/2) was applied to counteract bias from logarithmic transformation (Baskerville 1972; Sprugel 1983). The final equation was W = 15.945 * D³.034

where D is measured in cm and W is predicted in g.

Estimates of Production

Above ground net primary production (ANPP) was estimated as the sum of the change in wood biomass and fine litterfall. The change in wood biomass was estimated by
applying the allometric equation for biomass, as described above, to stem diameters at the beginning and end of each measurement interval. Prior to the hurricane, there was no clear relation between radial stem growth and initial stem diameter to suggest that differences in diameter increment were dependent on initial stem diameter, so the mean growth increment of measured trees in each treatment plot was applied to all trees within the plot to estimate wood production on a stand basis. Production per unit leaf area was calculated as ANPP divided by LAI.

Results

Damage

LAI reductions ranged from 3% to 59% with reductions positively correlated with pre-hurricane LAI (Figure 4.1). Prior to the hurricane, LAI had increased in plots with P additions (Herbert & Fownes 1995). After the hurricane there was no significant difference between treatments, and LAI reductions had been greatest among P treatments with a P*N interaction.

Structural damage to individual tree crowns (25% to complete crown loss) occurred in 34% of the trees surveyed
(Table 4.1). Analysis by split-plot ANOVA using DBH size class as the subplot showed that the proportion of large tree crowns damaged (> 10 cm DBH) was greater than that of small trees (Table 4.2). N fertilized plots had an increased frequency of crown damage and there was a significant interaction of N with DBH class measured as an increased proportion of trees sustaining moderate crown loss (25 - 50% loss). P increased the proportion trees incurring severe crown loss (> 50% loss) and the effects of N and P were additive.

A total of 71 trees, equally split between size classes, were either moderately or severely uprooted. No pattern was detected for this form of damage by either tree size or fertilizer treatment.

Mortality occurred in 53 of the more severely damaged trees. Only three of these cases involved partial uprooting without the added influence of structural crown loss. The remaining deaths were associated with crown reductions, included 34.6% of large trees and 38.3% of small trees with structural crown loss > 50%.
Litterfall, decomposition and nutrient transfer

Fine litterfall caused by the hurricane was 5.76 T ha$^{-1}$ in controls and 8.48 T ha$^{-1}$ in N + P treatments (Table 4.3) with significantly greater quantities in N and P treatments and an N*P interaction. The treatment effects correspond with those measured for LAI reductions. The litterfall measured in control plots was 1.4 times the total of the previous year, but twig and fine woody debris input was more than 3 times that of the previous year.

Fine litter nutrient concentrations were low with senesced twigs having the lowest concentration of N, P and K (Table 4.4). However, nutrients in senesced litter were elevated relative to earlier measurements, suggesting that leaves were incompletely senesced. Senesced *M. polymorpha* leaves from the hurricane contained .7% N and .035% P compared with .37% N and .022% P in earlier measurements at the site (Crews *et al.* 1995). The proportionately large mass of senesced twigs diluted nutrient concentration of the bulk litterfall mass. Nutrient transfer from the canopy to the soil was comparable to that of the previous years litterfall with slight increases in K and Ca and a decrease in P (Table 4.5). For this estimate we assumed that
nutrient concentrations of senesced leaves from hurricane induced litter approximates typical annual litterfall chemistry given that typical litter at the site includes senesced, incompletely senesced and some green leaves.

Mass loss was linear and slow for both green and senesced *M. polymorpha* leaves and twigs (Figure 4.2). After the first month there was little difference in decomposition rates of green and senesced materials. By 24 months, mass loss for twigs was 26%. Mass loss in green and senesced leaf litter was 59 and 63% respectively.

In the first month of decomposition there was a net release of N, P and K from all tissue types (Figure 4.2). By twelve months, all tissues began immobilizing P and green tissues began to immobilize N. By 24 months, both senesced and green tissues mineralized P and immobilized N. Senesced tissues tended to immobilize more P and N than their green counter-parts, while twigs immobilized more P and N than did leaves.

**Changes in growth and productivity**

**Fine Roots**

Fine root mass sampled two to three weeks after the hurricane is considered to represent pre-hurricane mass,
although some mortality may have occurred by the time of the sampling. Live fine root mass sampled at this time was greatest for P fertilized plots but the difference was not significant. Fine root biomass had decreased to 71% of original within three months, and to 56% by six months (Figure 4.3). As was the case for reductions in LAI, live fine root biomass decreased the most in P treatments. However, there was no relation between fine root mass loss and the decrease in LAI when regressed against each other (Figure 4.4). Live fine root mass began to increase at 12 months and returned to original by 24 months. At 24 months, live fine root mass was greatest in P treatments, similar to the trend seen in the original P treatment samples.

Leaf Area

The initial increase of LAI following the hurricane was rapid and was affected by treatment with the greatest increases seen in P fertilized plots (Dec. 1992). However, subsequent high wind events in August, 1993 and March, 1994 reduced LAI to levels similar to those measured immediately after the hurricane (Figure 4.5.A). By 18 months, LAI again increased, with P treatments showing significant increases.
over treatments lacking P. The effect of P treatments remained at 24 months. Recovery after two years approached original LAI but never reached pre-hurricane LAI (Figure 4.5.A).

Litterfall

Litterfall never decreased substantially in the months following the hurricane, probably due to inputs from suspended dead branches (Figure 4.5.B). Pulses of increased litterfall were seen to coincide with high wind events and large decreases in LAI. Prior to the hurricane, litterfall was greatest in N and P treatments.

By 13 months after the hurricane there was a small but significant elevation of monthly litterfall in N and P treatments (Figure 4.5.B). By 22 months, increased litterfall was seen in response to both N and P \((p < .001)\) and a pattern similar to that seen before the hurricane re-emerged.

**Stem Diameter Growth Increment**

Stem diameter increment had increased in response to P before the hurricane. Six months later, stem growth had
decreased substantially in all treatments (Figure 4.6.A). In most cases, diameter increment continued to drop at 12 months. An exception was the P -N treatments in which stem growth rate did not change between six and 12 months. In the second year, stem diameter increment approached pre-hurricane values, showing a significantly greater increment in P treatments beginning at 12 months and continuing through 24 months.

Above Ground Net Primary Production

ANPP dropped rapidly after the hurricane and remained low through the two years of measurement (Figure 4.6.B). Significant increases were seen in P treatments by 18 months, and production approached pre-hurricane values. Production per unit leaf area, E (g m⁻² LA), generally increased but the trend can not be separated from fluctuation before the hurricane (Figure 4.6.C). However, during recovery, E was significantly greater in P treatments (p = .032 at March 1994; p = .047 at September 1994).
Discussion

Defoliation has been reported as the most common type of damage caused by hurricanes (Brokaw & Walker 1991; Whigham et al. 1991). Similarly, on Kauai, large decreases in LAI were measured in the present study and in nearby *Acacia koa* forests (Harrington et al. in press). LAI reductions were proportionate to pre-hurricane LAI. Previously measured differences in LAI among plots were no longer evident, supporting the hypothesis that increased leaf area, which may be associated with an increase in aerodynamic drag, made trees more susceptible to wind damage (Brokaw & Grier 1991; Foster 1988; Harrington et al. in press; Reilly 1991). The high variability in the amount of defoliation across fertilizer treatments relative to controls may be due, in part, to reduced leaf mass per unit area reported earlier in P treatments (Herbert & Fownes 1995).

Live fine root mass declined over six months but reductions were not as large as those reported in Puerto Rico following hurricane Hugo where reductions ranged from 70% to near 100% (Parotta & Lodge 1991; Silver & Vogt 1993). Decline in live fine root mass may be related to defoliation
(Fownes & Anderson 1991), but on Kauai, reductions in fine roots and LAI were not proportional. Parrota & Lodge (1991) suggested that fine root reductions following hurricane Hugo may have been caused by physical disturbance to tree root systems by swaying and partial uprooting of stems during the storm.

We had predicted that fine roots and foliage would recover together. But root recovery was slow, taking a full two years, and did not show fluctuations such as those seen in LAI. By optical methods, LAI never fully recovered at two years, but this may have been an artifact of the method of measurement. Optical methods underestimate LAI when leaves are clustered (Gower and Norman 1991; Smith et al. 1993). Removal of branches from tree crowns may have increased the clustering of new leaves around remaining branches and, therefore, underestimated post-hurricane LAI relative to pre-hurricane measures. Nevertheless, LAI recovery was rapid during the three to nine month period following Iniki. Whigham et al. (1991) saw similar rapid foliage recovery following complete defoliation of a forest by hurricane Gilbert in the Yucatan Peninsula.
We also noted large reductions in LAI at 12 and 18 months which were associated with high wind events and accompanied with large litterfall pulses. The LAI reductions suggest increased susceptibility of new leaves and shoots to further disturbance. *M. polymorpha* leaves are sclerophyllous and typically persist two years or longer (Porter 1972). Rapid production of less sclerophyllous, less durable leaves after defoliation may involve a trade-off compared to more durable, longer-lived leaves.

Structural crown loss was the second most evident form of above ground damage, followed by tipping of stems. Although tipping was infrequent and observed equally in both size classes, large stems sustained a greater frequency of structural crown damage than did small stems; a result consistent with earlier observations elsewhere (Lugo *et al.* 1983; Putz & Sharitz 1991; Reilly 1991; Walker 1991). Disproportionate damage among treatments might further implicate increased wind drag on crowns with increased LAI.

The impact of hurricane Iniki on demographic factors in the study area appeared to be minimal. Mortality occurred in only 20 trees over 10 cm dbh and few large canopy gaps were formed. Synchronization of Hawaiian *M. polymorpha*
forest population structure is largely a function of cohort senescence but may also be induced by severe storms (Mueller-Dombois 1987). Low mortality following hurricane Iniki suggests that hurricanes have a smaller impact on M. polymorpha forests that lack predisposing conditions such as decreased vigor associated with older even-aged stands (Mueller-Dombois 1987).

Fine litterfall deposited in control plots during Iniki was 1.4 times the annual rate which is comparable to that measured at several sites after hurricane Hugo (Frangi & Lugo 1991; Lodge et al. 1991). Elevated litterfall in the following months was probably due to the suspended fraction. After hurricane Hugo in El Verde, Puerto Rico, as much as 46% of hurricane induced litter was suspended on broken crowns and fine woody fractions remained suspended for as long as one year (Lodge et al. 1991).

Nutrient transfers from the canopy to the forest floor were approximately equal to annual inputs. Following hurricane Hugo, it was suggested that litterfall loads would initially increase nutrient availability (Lodge et al. 1991), but that reduction in fine root mass would limit uptake by vegetation (Parrota and Lodge 1991) leading to
nutrient export. Increased nitrogen trace gas fluxes supported this prediction (Steudler et al. 1991). Sanford et al. (1991) speculated that litter mass would immobilize nutrients until decomposition proceeded to a point where mineralization exceeds immobilization. On Kauai, early N and P leaching from litter likely increased available pools, but increased N trace gas flux was not detected following Iniki (Riley, personal communication). Since fine root mass was not lost to the extent measured in Puerto Rico, uptake by vegetation may not have been as affected until nutrient pools were sequestered by immobilization.

In contrast to some observations of growth following high mortality (Merrens & Peart 1992; Whigham et al. 1991), M. polymorpha stem diameter growth decreased in the year following Iniki. In addition to reduced photosynthetic area, decreased stem growth could also reflect increased production of new leaves and perhaps roots while competition for available resources remained relatively high.

Damage to the forest during hurricane Iniki was related to fertilizer treatment, but this was apparently a result of increased susceptibility to wind damage due to the increased leaf area and perhaps increased succulence of the young
shoots supporting new leaves. Relative to controls, recovery was rapid where increased P availability had increased production per unit leaf area. The pattern suggests that under higher nutrient availability, the system had become more susceptible to disturbance. But the relative increase in recovery suggests that the modified system had also become more resilient.
References


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Table 4.1. Structural stem damage frequencies. Values in parentheses represent the percentage of all individuals in each category.

<table>
<thead>
<tr>
<th>Type</th>
<th>DBH &lt; 10 cm freq. (%)</th>
<th>DBH &gt; 10 cm freq. (%)</th>
<th>Total freq. (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uproot &lt; 45°</td>
<td>21 (3.3)</td>
<td>15 (4.1)</td>
<td>36 (3.6)</td>
</tr>
<tr>
<td>Uproot &gt; 45°</td>
<td>24 (3.8)</td>
<td>11 (3.0)</td>
<td>35 (3.5)</td>
</tr>
<tr>
<td>Crown loss &lt; 50%</td>
<td>72 (11.3)</td>
<td>139 (37.6)</td>
<td>211 (20.9)</td>
</tr>
<tr>
<td>Crown loss &gt; 50%</td>
<td>70 (11.0)</td>
<td>46 (12.4)</td>
<td>116 (11.5)</td>
</tr>
<tr>
<td>Decapitation</td>
<td>11 (1.2)</td>
<td>9 (2.4)</td>
<td>20 (2.0)</td>
</tr>
<tr>
<td>No damage</td>
<td>446 (69.8)</td>
<td>156 (42.2)</td>
<td>602 (59.7)</td>
</tr>
</tbody>
</table>
Table 4.2. Structural crown loss by size class and fertilizer treatment. Values represent the arithmetic mean proportion of trees damaged within each treatment with standard errors in parentheses. Analyses were performed on arc sine transformed proportions. Large stems incurred more damage than small stems ($p < .001$) and an interaction with N increased the occurrence of moderate (25 - 50%) crown loss ($p = .033$). Overall, N increased the occurrence of crown loss ($p = .004$) and P increased the occurrence of severely damaged crowns ($p = .018$).

<table>
<thead>
<tr>
<th>Crown Loss Category</th>
<th>Size class</th>
<th>Treatment</th>
<th>25 - 50%</th>
<th>&gt; 50%</th>
<th>Pooled</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt; 10 cm DBH</td>
<td>-N -P</td>
<td>.08 (.01)</td>
<td>.10 (.01)</td>
<td>.18 (.01)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+N</td>
<td>.13 (.02)</td>
<td>.11 (.02)</td>
<td>.24 (.02)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+P</td>
<td>.12 (.01)</td>
<td>.14 (.01)</td>
<td>.27 (.02)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+N +P</td>
<td>.12 (.02)</td>
<td>.18 (.01)</td>
<td>.30 (.02)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pooled</td>
<td>.11 (.02)</td>
<td>.13 (.02)</td>
<td>.25 (.02)</td>
</tr>
<tr>
<td></td>
<td>&gt; 10 cm DBH</td>
<td>-N -P</td>
<td>.28 (.01)</td>
<td>.06 (.01)</td>
<td>.34 (.02)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+N</td>
<td>.46 (.02)</td>
<td>.17 (.01)</td>
<td>.63 (.01)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+P</td>
<td>.32 (.02)</td>
<td>.18 (.01)</td>
<td>.50 (.01)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+N +P</td>
<td>.43 (.02)</td>
<td>.18 (.02)</td>
<td>.60 (.02)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pooled</td>
<td>.37 (.03)</td>
<td>.15 (.02)</td>
<td>.52 (.03)</td>
</tr>
</tbody>
</table>
Table 4.3. Fine litterfall mass by component and treatment (T ha\(^{-1}\)). Values are arithmetic means with standard errors in parentheses. Analyses performed on log transformed data. Total litterfall was greatest in N (p = .036) and P (p < .001) fertilized plots. P treatments had increased senesced leaf (p = .003), green leaf (p = .001) and green twig (p = .017) litter. N increased green leaf litter (p = .010) and there was an N*P interaction increasing green leaf (p = .021) and green twig (p = .040) litter.

<table>
<thead>
<tr>
<th>Fertilizer treatment</th>
<th>(-N) - (P)</th>
<th>(+N) - (P)</th>
<th>(-N) + (P)</th>
<th>(+N) + (P)</th>
<th>Annual (-N) - (P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Senesced leaf</td>
<td>0.68 (.06)</td>
<td>0.75 (.06)</td>
<td>0.84 (.05)</td>
<td>0.92 (.08)</td>
<td>3.40 (.17)</td>
</tr>
<tr>
<td>Green leaf</td>
<td>1.34 (.19)</td>
<td>1.60 (.13)</td>
<td>1.79 (.20)</td>
<td>2.50 (.27)</td>
<td></td>
</tr>
<tr>
<td>Senesced twig</td>
<td>3.03 (.20)</td>
<td>3.17 (.29)</td>
<td>3.60 (.12)</td>
<td>3.46 (.32)</td>
<td>0.83 (.11)</td>
</tr>
<tr>
<td>Green twig</td>
<td>0.71 (.09)</td>
<td>0.77 (.16)</td>
<td>1.02 (.20)</td>
<td>1.60 (.22)</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>5.76 (.43)</td>
<td>6.29 (.25)</td>
<td>7.25 (.43)</td>
<td>8.48 (.63)</td>
<td>4.23 (.27)</td>
</tr>
</tbody>
</table>
Figure 4.4. Fine Litterfall Nutrients (kg ha\(^{-1}\)) for control plots.

<table>
<thead>
<tr>
<th>Type</th>
<th>N</th>
<th>P</th>
<th>K</th>
<th>Ca</th>
<th>Mg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Senesced leaf</td>
<td>5.34</td>
<td>0.26</td>
<td>1.38</td>
<td>4.51</td>
<td>1.24</td>
</tr>
<tr>
<td>Green leaf</td>
<td>11.22</td>
<td>0.62</td>
<td>5.12</td>
<td>7.55</td>
<td>1.94</td>
</tr>
<tr>
<td>Senesced twig</td>
<td>10.60</td>
<td>0.34</td>
<td>1.83</td>
<td>26.77</td>
<td>3.65</td>
</tr>
<tr>
<td>Green twig</td>
<td>4.00</td>
<td>0.26</td>
<td>2.26</td>
<td>5.59</td>
<td>0.64</td>
</tr>
<tr>
<td>Total</td>
<td>31.16</td>
<td>1.48</td>
<td>10.59</td>
<td>44.42</td>
<td>7.47</td>
</tr>
</tbody>
</table>

Annual Fine Litterfall Nutrients (kg ha\(^{-1}\)) for control plots.

<table>
<thead>
<tr>
<th>Type</th>
<th>N</th>
<th>P</th>
<th>K</th>
<th>Ca</th>
<th>Mg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Senesced leaf</td>
<td>24.49</td>
<td>1.32</td>
<td>7.23</td>
<td>24.22</td>
<td>6.55</td>
</tr>
<tr>
<td>Senesced twig</td>
<td>2.93</td>
<td>0.09</td>
<td>0.50</td>
<td>7.35</td>
<td>1.01</td>
</tr>
<tr>
<td>Total</td>
<td>30.42</td>
<td>1.91</td>
<td>7.73</td>
<td>31.59</td>
<td>7.56</td>
</tr>
</tbody>
</table>
Table 4.5. Nutrient concentration of fine litter. Values represent concentrations (%) for composite samples of each tissue type.

<table>
<thead>
<tr>
<th>Tissue type</th>
<th>N</th>
<th>P</th>
<th>K</th>
<th>Ca</th>
<th>Mg</th>
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</thead>
<tbody>
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<td>.75</td>
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Figure 4.1. Reduction in LAI versus pre-hurricane LAI. Inset uses control plots only.
Figure 4.2. Fraction of initial nutrient mass in (A) senesced leaves, (B) green leaves, (C) senesced twigs and (D) green twigs. Filled circles = mass, open circles = N, filled triangles = P, open triangles = K, filled diamonds = Mg and open diamonds = Ca.
Figure 4.3. Change in fine root biomass by fertilizer treatment during two years following Iniki. Values plotted are means +/- one standard error. Solid lines = fine and dashed lines = dead. Filled circles = +P +N, open circles = +P -N, filled triangles = -P +N and open triangles = -P -N.
Figure 4.4. Reduction in LAI versus reduction in live fine root mass.
Figure 4.5. Patterns in (A) LAI and (B) litterfall by fertilizer treatment beginning one year prior to hurricane Iniki. Values plotted are means +/- one standard error. Symbols are as in figure 3. See table 3 for litterfall due to the hurricane.
Figure 4.6. (A) Stem diameter increment, (B) ANPP and (C) E by fertilizer treatment beginning one year prior to hurricane Iniki. Values plotted are means +/- one standard error. Symbols represent treatments as in figure 3.
Appendix A

Effects of Clumping in a Broad-Leaf Canopy on Estimates of Leaf Area Index by the Gap-Fraction Method Using the LI-COR LAI-2000

Abstract

We compared leaf area index (LAI) estimates of a broad-leaf tropical hardwood (Metrosideros polymorpha) from an optical method (LI-COR LAI-2000) with harvest and allometry. There was a strong relationship between LAI estimates by the two methods, but the LAI-2000 consistently underestimated LAI. Similarly, clumping of leaves within shoots, determined from the relationship between projected shoot area and actual leaf area within the shoot, yielded a relationship in which projected area was consistently lower than leaf area. The slope of the relationship between the two estimates of LAI and that of projected shoot area and leaf area were not statistically different, suggesting that clumping of leaves within shoots may account for underestimates by the indirect method. A shoot level correction factor can be used to adjust the estimates of LAI.
by the LAI-2000 upward when aggregation of canopy elements occurs within shoots.

Introduction

Indirect estimation of leaf area index (LAI) is important when destructive sampling must be limited or completely avoided. We used the LI-COR LAI-2000 (LI-COR Incorporated, Lincoln Nebraska) in an earlier study to monitor changes of LAI in a Hawaiian rainforest dominated by a broad-leaf hardwood, Metrosideros polymorpha Gaud. (Herbert & Fownes in press). The study site was within the boundaries of the Na Pali - Kona Forest Reserve in Kokee State Park where destructive sampling was not an option. We suspected that the LAI-2000 was underestimating LAI but that values recorded were nonetheless proportional to the true LAI. In this paper we test for bias in estimates by the LAI-2000 when used with broad-leaf trees in which canopy elements are strongly aggregated.

The LAI-2000 uses canopy gap-fraction analysis of diffuse radiation transmittance to indirectly estimate LAI (Welles 1990). Other methods which utilize gap-fraction analysis include measurement of sunfleck area on the forest.

The assumption of random canopy elements is notably violated in conifers because needles are closely aggregated in shoots, often with extreme overlap or clumping (Norman & Jarvis 1975, Gower & Norman 1991, Smith et al. 1993). By using a direct method to estimate LAI (allometric), Gower and Norman (1991) demonstrated a strong positive correlation with LAI-2000 measurements in four conifer plantations and one broad-leaf plantation. However, LAI was underestimated in the conifer plantations by as much as 40%. The ratio of total projected area of all needles within a shoot to the projected silhouette area of the intact shoot was found to provide a reliable correction factor to the values obtained with the LAI-2000. Gower and Norman (1991) suggested that
shoots could be treated as independent, randomly distributed foliage elements and that a correction to the gap-fraction method could be arrived at by determining the level of needle aggregation within shoots. In another study, *Pseudotsuga menziesii* LAI was similarly underestimated by 62% with the LAI-2000, with 74% of the error being attributable to confinement of needles within branches (Smith et al. 1993). Broad-leaf species having more random patterns of leaf orientation, including *Quercus rubra* (Gower & Norman 1991), *Eucalyptus* spp. (Norman & Campbell 1989), *Eucalyptus camaldulensis*, *Acacia auriculiformis*, *Gliricidia sepium* and *Leucaena diversifolia* (Harrington and Fownes 1995), do not appear to show the same bias toward underestimation of LAI by the gap-fraction method.

*M. polymorpha* is an evergreen broad-leaf hardwood with exaggerated clumping of leaves within shoots. As such, the species exhibits a non-random leaf orientation pattern similar to that seen among conifers. We hypothesized that the gap-fraction method will underestimate *M. polymorpha* canopies in a manner similar to conifers. Further, we hypothesize that underestimates will be due, at least in part, to the clumping of leaves within shoots.
Study Site

Field work was conducted at the University of Hawaii Hamakua Research Station, Paauilo, island of Hawaii (20°02' N and 155°22' W) at 790 to 840 m elevation. The site has been converted from forest to pasture but has numerous small monospecific natural groves of *M. polymorpha* with grass understory. Ten groves of *M. polymorpha* were selected to represent a range of LAI (1.4 to 3.6) as measured in a preliminary survey using the LAI-2000.

Methods

Indirect measurement of stand LAI

A single plot, having a minimum radius of 6 m (maximum 11 m radius), was established within each grove. The LAI of each plot was measured using the LAI-2000 in January 1995. Two LAI-2000 units were used; a remote unit programmed to take light readings every 15 seconds in the open pasture (above-canopy), and a mobile unit used to take readings below the canopy within each plot. Readings were taken under a cloudless sky, early in the morning so that solar elevation was low and sensors could view uniform, diffuse skylight to the NW. Opaque masks obscuring a 270° view of
the sensors were used to exclude direct beam solar radiation from the SE. A compass and levelling bubble were used to align the mobile unit with the remote unit so that both sensors viewed the same quadrant of the sky. Measurements were made at nine randomly selected locations near the center of each plot. Each plot was measured twice and the computed LAI values averaged.

After all data were collected, below-canopy and the corresponding above-canopy measurements were combined based on time of measurement. Because of the open understory and small size of the plots, values from the lower three rings of silicon detectors (viewing at angles below 32° from vertical) were omitted from computations of LAI as these rings were viewing canopy transmittance beyond the perimeter of the measurement plots.

**Direct measurement of stand LAI**

Dimensional analysis was used to directly determine LAI. An inventory of stem diameter at 1.3 m height (DBH) was completed for each plot. Two trees were randomly selected from each plot for harvest. Most trees were single-stemmed at DBH, but one harvested tree was multi-
stemmed. A total of 22 stems ranging from 5 to 35 cm DBH were felled. Fresh weight of the crown of each stem, including leafy twigs 1 cm diameter or less, was recorded to the nearest 0.01 kg. Twelve to 20 leafy twigs were randomly selected from each stem crown and defoliated to determine the leaf to twig mass ratio which was used to estimate total crown leaf mass. Fresh leaf mass per unit area (LMA) was measured to the nearest g cm$^{-2}$ on a subsample of leaves. Subsample area was measured with a LI-COR LI-3100 area meter. LMA and crown leaf mass were then used to determine the total leaf area per harvested stem.

Linear regression was used to derive an allometric relationship between DBH (cm) and leaf area (LA). LA was estimated by applying the allometric equation to all stems within a plot and LAI was calculated as m$^2$ LA/m$^2$ plot area.

**Clumping of Leaves within Shoots**

Each leafy twig (shoot) from the crown subsample was photographed in profile against a 1 m scale prior to defoliation. Photographs were then projected against a point-grid to determine the area of the projected shoot.
profile (m²), measured as the number of points intercepted by the projection divided by the number of points per unit area relative to the 1 m scale (Grace & Fownes in prep.). Shoots were then completely defoliated and total LA for each shoot was measured with a LI-COR LI-3100. The relationship between total LA within shoots and projected shoot profile was determined by linear regression analysis. An incomplete photographic record of subsampled shoots for two of the 22 harvested stems reduced our shoot LA vs. projected shoot profile sample to 20.

Results

Regression analysis of LA against DBH yielded the equation $\text{LA} = 0.028 \times \text{DBH}^{2.55}$ (Figure A.1). The coefficient of determination, $r^2$, was 0.87 and the standard error of estimate, $S_{y.x}$, was 0.48. The range of LAI among plots using the direct method was 2.55 to 7.99, but the range of LAI using the indirect method was substantially lower, 1.56 to 3.55. Linear regression of direct LAI against indirect LAI illustrates a strong positive relation between the two methods ($r^2 = 0.78$, $S_{y.x} = 0.74$) (Figure A.2).
The projected shoot profile was similarly low when compared with shoot leaf area. But linear regression of shoot leaf area against projected shoot profile also illustrated a strong relation \((r^2 = 0.85, \text{Sy.x} = 0.27)\) (Figure A.3).

The slope of the regression between the direct method of estimating LAI and the indirect method was 2.44 (95% CI = ± 0.959) while the slope of the regression between shoot LA and projected shoot profile was 2.56 (95% CI = ± 0.519). The slopes of the two relationships were not significantly different (to be completed when stats complete).

**Discussion**

The LAI-2000 underestimated *M. polymorpha* LAI by a factor of 2.44 which is within the range observed in other studies. A correction factor of 2.63 was measured for Douglas fir (Smith *et al.* 1993) and correction factors from 1.49 to 1.67 were measured for four other conifers (Gower & Norman 1991).

Underestimates by the LAI-2000 appear to be due to the clumping of leaves within shoots. The slope of the regression of shoot LA against projected shoot area (2.56)
was not significantly different from that of direct LAI against indirect LAI. The similarity suggests that shoots are the most important clumping element in the *M. polymorpha* canopy. This was also shown to be the case with the conifers Sitka spruce (Norman & Jarvis 1975), European larch, Red pine, White pine and Norway spruce (Gower and Norman 1991) where aggregation of needles within shoots are the most important clumping elements. In Douglas fir, 26% of the observed clumping was attributed to the non-random arrangement of branches (Smith et al. 1993). However, the similarity between stand-level clumping and shoot-level clumping in *M. polymorpha* suggests a negligible amount of clumping attributable to other non-random features of foliar arrangement.

If shoots are the most important clumping elements in a canopy, then a correction factor based on the shoot LA vs. shoot projected area could reliably correct for underestimates by the gap-fraction method. A shoot-level correction factor is relatively simple to determine when compared with whole tree harvests and site impact is low.

The gap-fraction method of estimating LAI has produced good results with many broad-leaf tree species (Norman and
Campbell 1989, Gower & Norman 1991, Harrington & Fownes 1995) but has proven to be biased in estimates of LAI in conifers where canopy elements are aggregated (Gower & Norman 1991, Smith et al. 1993). We have demonstrated bias in the methodology, as applied with the LAI-2000, for a broad-leaf tree species which exhibits aggregation of canopy elements similar to that seen in conifers. We have further demonstrated that a correction at the shoot-level adequately compensates for the bias, yielding good estimates of LAI with the LAI-2000.
References


Figure A.1. Regression of the natural log of leaf area against the natural log of stem diameter at 1.3 m; $r^2 = 0.85$, $S_{y.x} = 0.48$. 

$LA = 0.028 \times DBH^{2.55}$
Figure A.2. Comparison between LAI derived from allometry and LAI-2000 LAI for ten plots; $r^2 = 0.78$, $S_{y,x} = 0.74$.  

$Y = -1.16 + 2.44 \times X$
Figure A.3. Comparison of leaf area within shoots against the projected shoot profile; $r^2 = 0.85$, $S_{y.x} = 0.27$. 

\[ Y = -0.10 + 2.56 \times X \]

\[ r^2 = 0.85 \]