Supporting Text

Supporting Methods

Airborne Remote Sensing. We developed an approach to quantify the biophysical and chemical properties of tropical forest canopies using a spectroscopic photon transport model and airborne imaging spectroscopy. Imaging spectroscopy is the measurement of solar radiation reflected from the Earth's surface in contiguous, narrow spectral channels spanning the wavelength region from 350 to 2,500 nm. The National Aeronautics and Space Administration (NASA) Airborne Visible and Infrared Imaging Spectrometer (AVIRIS) (1) has been recently upgraded with improved foreoptics and electronics, and is now one of the few "high fidelity" sensors in existence. "High fidelity" distinguishes those instruments providing measurements with signal-to-noise, stability, and dynamic range performance matching laboratory spectrometers. AVIRIS acquires optical radiance data in 224 channels from 350 to 2,500 nm with 10-nm full width at half maximum (FWHM) spectral resolution. In October 2001, AVIRIS data were collected over Hawaii Island by an ER-2 (U-2) aircraft modified to fly at an altitude of ~10 km above sea level. Surface elevations within AVIRIS flight measurement area of Hawaii Volcanoes National Park (HAVO) ranged from 1,060 to 1,140 m, resulting in an average image pixel size of 9 m.

The aircraft global positioning system (GPS) provided a preliminary geo-correction of the AVIRIS data. Further geo-rectification was performed using USGS digital orthophotoquad maps and geographic information system (GIS) coverages provided by the State of Hawaii (www.state.hi.us). The undulating terrain introduced non-linear effects on the geometric quality of the data. These effects were compensated for by nonlinear rubber sheeting of the imagery to reference GIS layers (2). The AVIRIS data were corrected to apparent surface reflectance to minimize the effects of water vapor and other atmospheric constituents. This step was performed by using the ACORN code (ImSpec LLC, Pasadena, CA), which uses MODTRAN-4 radiative transfer modeling to estimate atmospheric water vapor on a pixel-by-pixel basis.

Photon Transport Modeling. We used a photon transport inverse modeling approach with the airborne imaging spectrometer measurements to estimate total canopy water content and upper canopy leaf nitrogen (N) concentration throughout the tropical forest. This physically based model is a hybrid system of algorithms designed to maximize the observational accuracy of the spectroscopic measurements to these two unique canopy chemical variables (3). The model simulates spectroscopic reflectance signatures at the pixel level based on the scale-dependent characteristics of forest canopies, from molecules of water to forest canopy gap fraction. The basis and overall approach are described below. The core physical equations used in the model are detailed in *Model Description*.

The reflectance spectroscopy of tropical forest canopies [$R(\lambda)$] is driven by a hierarchy of scale-dependent factors:

$$R(\lambda) = f(\rho_{tissue}, \tau_{tissue}, \text{LAI, LAD, intercrown gap fraction}, \theta_s, \phi_s, \theta_v, \phi_v), \quad (1)$$

where ρ_{tissue} and τ_{tissue} are the reflectance and transmittance properties of plant tissues, LAI is the canopy leaf area index, LAD is the canopy leaf angle distribution, θ_s and ϕ_s are the solar zenith and azimuth angles, and θ_v and ϕ_v are the sensor viewing zenith and azimuth angles.

In tropical forest canopies, tissue reflectance (ρ) and transmittance (τ) is dominated by foliage, and foliar spectra are controlled by another suite of variables:

$$[\rho(\lambda),\tau(\lambda)]_{foliage} = f(EWT_L, \text{pigments, nitrogen, cellulose, lignin, SLA}), \quad (2)$$

where leaf equivalent water thickness (EWT_L) is the mass of water per unit leaf area. EWT_L dominates in the wavelength region 700-2,500 nm but with wavelength-specific intensities (4). Pigments are dominated by chlorophyll a and b, carotenoids, and anthocyanin. Cellulose and lignin are the two dominant carbon constituents affecting the optical properties of foliage. In tropical forest foliage, absorption features associated with

lignin and cellulose (5) are masked by water absorptions throughout the 700- to 2,500-nm spectral region (6). Pigments have variable absorptions only in the 400- to 690-nm range, and specific leaf area (SLA) is of background importance throughout the spectrum (*4*). Nitrogen is primarily bound in proteins and chlorophyll. Nitrogen displays a moderate correlation with chlorophyll a+b, which has fundamental absorptions centered at 460-480 nm and 650-670 nm (5); protein-nitrogen has additional absorptions centered on 1,510-1,790 nm, but this region is also partly obscured by water absorption and is partially affected by variations in leaf structure and thickness. Nonetheless, a combination of the chlorophyll and protein-N absorption features provides the strongest spectral correlations with leaf N concentration (see *Model Description*).

Leaf-level reflectance and transmittance properties (Eq. **2**) are modified by canopy structural properties including LAI, LAD, and crown dimensions (Eq. **1**). The amount of foliage present in the canopy strongly affects near-infrared (700-1,300 nm) reflectance at the top of the canopy. Spectroscopic reflectance properties in these wavelengths regions are thus tightly linked to both the water concentration of the foliage and the amount of foliage in the canopy. In particular, the 980- and 1,180-nm regions are highly sensitive to changes in total canopy water content ($EWT_L \times LAI$), and the effective penetration depth of photons measured by the aircraft sensor is a function of the convolved effects of leaf EWT and LAI. Recent studies show that measures of canopy water content are sensitive to LAI values of 8-12 (7), encompassing the range of values measured for all vegetation types globally (8).

Leaf N concentrations are expressed in the 400- to 690-nm and 1,510- to 1,790-nm wavelength regions. Photons in these spectral ranges are readily absorbed by green vegetation, and thus the effective penetration depth of the measured reflectance is only the uppermost portion of the canopy (1-1.5 LAI units). As a result, the canopy structural variables listed in Eq. **1** have relatively little impact on observed variations in canopy chlorophyll and/or nitrogen in densely foliated forest environments (6).

The difference in canopy water and leaf N expression in the spectrum provides a fundamental limitation to the type of variables that can be estimated from remotely measured spectroscopic data. The near-infrared is most sensitive to changes in canopy water content, whereas leaf biochemical variation is expressed only in the visible and shortwave-infrared. The differences in spectral-chemical relationships between water and N serve to constrain the physically based method by which canopy water content and leaf N concentration are estimated using photon transport model inversion techniques, as described below.

Model Inversion. Numerical inversion of Eqs. **1** and **2** has been detailed (9, 10). However, this approach also requires knowledge of the structural and chemical sources of variance in spectroscopic measurements of vegetation canopies and ecosystems. When viewed from above in the visible spectral range (400-700 nm) or the shortwave-infrared (1,500-2,500 nm), mature tropical forest canopies appear as dark clusters of foliage organized in crowns with spatially varying sizes and gaps. When gaps in tropical forests are not shaded, the middle- and understory vegetation may become evident from nadir-looking sensors. When gaps are in shade, this portion of the canopy is considered nearly null space in the spectroscopic observations (11). When viewed in the near-infrared spectral region (700-1,300 nm), tropical forests are very bright and vegetation within gaps are usually relatively well illuminated, so shadowing is often less important in this spectral region.

We estimated canopy water content by numerical inversion of Eqs. **1** and **2** using the near-infrared wavelength range of 880-1,290 nm after spectral continuum removal (12). For the canopy water estimates, model parameters with low variance were held constant, whereas the most dynamic parameters remained unconstrained. Intercrown gaps are less important in the near-infrared due to the intense scattering of light, so this parameter was set to a range of 0-20% (based on ref. 13). Leaf angle distribution was assumed random over the area of a typical remote sensing pixel, and both viewing and solar geometry were known at the time of imaging (Eq. **1**). Of all factors in Eqs. **1** and **2**, only EWT_L and LAI are of major importance in the 880- to 1,290-nm range, and thus the model was inverted

for a simultaneous retrieval of EWT_L and canopy LAI. These two variables cannot be uniquely estimated using this approach, as they have a convolved effect on these near-infared features (14). However, their product is unique, and thus can be solved as canopy equivalent water thickness (EWT_c) in units of mm H_2O per pixel. Uncertainty in canopy gap fraction was propagated to the final EWT_c by iterative inversion with randomly selected gap fractions of 0-25%, providing EWT_c estimates with standard deviations.

Upper canopy leaf N concentration was estimated in a three-step model inversion using only the visible (450-690 nm) and the shortwave-infrared (1,500-2,400 nm) wavelength regions. Again, leaf angle distribution was assumed random over the area of a typical remote sensing pixel, and both viewing and solar geometry were known (Eq. **1**). In the first step, the 2,000- to 2,400-nm range was used to estimate canopy fractional cover, as developed in ref. 15 and demonstrated in ref. 16. In the second step, the gap parameter (Eq. **1**) was fixed to the value estimated in the first step. Within the overall canopy photon transport model inversion, estimates of leaf chlorophyll and N concentration relied on both a leaf optical submodel PROSPECT (4) and a leaf optical-chemical look-up table (3), detailed in *Model Description*. Leaf chlorophyll concentration was estimated by inversion of PROSPECT using only the 450- to 690-nm wavelength region. With this estimate of chlorophyll concentration, along with randomly selected inputs of water and lignin+cellulose, full spectral range (400-2,500 nm) leaf reflectance and transmittance spectra were then forward-modeled using PROSPECT. These modeled spectra were then matched to a large database of leaf spectra collected throughout Hawaii and Amazônia using the 450- to 690-nm and 1,510- to 1,790-nm portions of the modeled spectrum that contain the primary nitrogen absorptions (5). The look-up table spectrum that best matched the PROSPECT spectrum was used to estimate total leaf N concentration. This ensemble of steps was carried out iteratively while randomly selecting canopy LAI values in the 1-1.5 range, the average penetration depth of photons in the visible and shortwave-infrared spectral regions (*6*). The result was leaf N concentration with standard deviations depicting uncertainty caused by LAI variability and optical-chemical matching.

Model Description. *Photon Transport at the Canopy Scale.* The pixel-scale, photon transport in vegetation is divided into three major parts: (*i*) radiation that is not scattered by vegetative tissues, (*ii*) singly scattered radiation, and (*iii*) radiation that undergoes multiple scattering:

$$\rho_{canopy}(\Omega'\Omega) = \rho_{unscat}(\Omega'\Omega)) + \rho_{\sin gsc}(\Omega'\Omega)) + \rho_{multsc}(\Omega'\Omega), \quad (3)$$

where Ω' represents the geometry of illumination in both zenith (μ' = cos(θ')) and azimuth (ϕ') directions, and Ω represents the observer's geometric position in zenith (μ = cos(θ)) and azimuth (ϕ) directions. In the following sections, Eq. **1** is broken down into components describing the transfer of incoming radiation between plant parts (e.g., foliage, wood, litter), the soil/litter surface, and the atmosphere.

Photon Scattering by Plant Tissues. The spectral and angular distribution of scattered flux at the tissue (e.g., leaf) level is described by the scattering phase function for a single-sided tissue element. When incident radiation from a direction The spectral and angular distribution of scattered flux at the tissue (e.g., leaf) level is described by the scattering phase function for a single-sided tissue element. When incident radiation from a direction Ω' strikes an infinitesimally small tissue area $d\sigma_T$ whose orientation is Ω_T, and if the intensity of that radiation is $I(\Omega')$, then the amount of radiant energy contained in the solid angle about Ω' that interacts with the tissue element within an interval of time (dt) is:

$$dE'_T = I(\Omega') \,|\cos\Omega_T\Omega'|\, d\sigma_T d\Omega' dt \quad (4)$$

where $\cos\Omega_T\Omega' = \cos\theta'\cos\theta_T + \sin\theta'\sin\theta_T\cos(\phi' - \phi_T)$. A fraction of this incident energy is scattered, and the remainder is absorbed. The tissue scattering phase function is: raction of this incident energy is scattered, and the remainder is absorbed. The tissue scattering phase function is:

$$f(\Omega,\Omega';\Omega_T)d\Omega = \frac{dE_{T\omega}}{dE_T^{'}} \tag{5}$$

where the numerator represents the amount of energy scattered into a solid angle about the direction Ω. Tissue scattering phase functions are modeled as Lambertian distributions for each side of the tissue element. The equation for bi-Lambertian scattering by each tissue element is:

$$f(\Omega',\Omega;\Omega_T) = \begin{matrix}(r_T \mid \cos\Omega_T\Omega \mid)/\pi; & (\cos\Omega_T\Omega)(\cos\Omega_T\Omega') < 0 \\ (t_T \mid \cos\Omega_T\Omega \mid)/\pi; & (\cos\Omega_T\Omega)(\cos\Omega_T\Omega') > 0\end{matrix} \tag{6}$$

Here, r_T is the scattered energy due to reflection, and t_T is the energy via transmission. Wood tissue has a τ_T equal to zero because wood does not transmit photons.

Hemispherical reflectance and transmittance spectra (r_T, t_T; Eq. **6**) are simulated using a leaf model (e.g., PROSPECT; ref. 4) combined with a leaf chemical-optical look-up table. PROSPECT uses specific absorption coefficients and concentrations of chlorophyll (a+b), lignin+cellulose, and water to simulate tissue hemispherical reflectance and transmittance (r_T, t_T). Chlorophyll a+b displays absorption potentials only in the visible spectral range (400-690 nm), whereas water absorbs differentially across the 700-2,500 nm region (5). Lignin and cellulose absorptions are most pronounced in the 1500-2300 nm range, although they are readily masked by water (6). The leaf model is thus embedded within the canopy photon transport model, simulating tissue-level spectral properties, resulting from variations in chlorophyll, water, and lignin+cellulose, that are then propagated to the canopy and pixel scale as described below.

Total chlorophyll is often highly correlated with percentage leaf N concentration of crops and annual plants ($r^2 > 0.7$; ref. 17), thus it is often used as a remote sensing proxy for leaf N concentration using the absorption and reflectance signatures in the 400-690 nm range (18). However, our experience in tropical forests suggests that pigments are somewhat decoupled from nutrient concentrations ($r^2 = 0.5$-0.7), and thus chlorophyll estimation alone is not always sufficient for estimating leaf N concentration. Fortunately,

protein-nitrogen has strong absorptions in the 1,510- to 1,790-nm region (Fig. 5). As a result, we developed a tropical forest look-up table for foliar optics based on the spectral properties of leaves in the 400- to 690-nm and 1,510- to 1,790-nm wavelength regions, along with leaf chlorophyll and total N concentrations. The look-up table contains leaves from 129 tropical forest trees and understory plants, with chlorophyll and N ranges of 19-72 $\mu g \cdot cm^{-2}$ and 0.4-3.3%, respectively. In the forward modeling mode, combinations of total chlorophyll per area and N concentration are prescribed, and the closest matching combination of chlorophyll and total N is used to select the paired reflectance and transmittance spectrum of the leaf (r_T, t_T in Eq. **6**).

Single Photon Scattering by a Canopy. The canopy photon transport model uses the formulation outlined in ref. 19 to exactly express photon single scattering in a canopy:

$$\rho_{\sin scat}(\Omega',\Omega) = \frac{\Gamma(\Omega',\Omega)}{|\mu'|\,\mu} \int_P \Im'(p)\Im(p)dp \tag{7}$$

where the gamma function (Γ) is the area scattering phase function, $\Im$' is the direct solar radiation transmission, and $\Im$ is the transmission of scattered radiation. This process is integrated over the canopy plant area index (P), which is the sum of leaf (LAI), wood (WAI), and standing litter (LittAI) area indices (6). An important part of this formulation for single photon scattering is that the so-called hotspot or retro-solar effect (when $\Omega' = \Omega$) is accounted for explicitly.

The area scattering phase function (Γ) is well known in canopy radiative transfer work (e.g., ref. 20) and is given as

$$\Gamma(\Omega',\Omega) = \frac{1}{2\pi} \int_{2\pi} f(\Omega',\Omega;\Omega_T)\, g_T(\Omega_T) |\cos\Omega_T\Omega'| d\Omega_T \tag{8}$$

where f(Ω',Ω;Ω_T) is the tissue scattering function (Eq. **6**), and $g_T(\Omega_T)$ is the tissue orientation distribution with respect to the upward facing hemisphere. A random azimuthal orientation is assumed for plant tissues, thus the orientation distribution function for each tissue type can be stated in terms of normal zenith angle only (q_T). deWit (21) offered several leaf inclination distribution functions useful for plant canopy photon transport modeling:

Planophile: $g_T(\theta_T) = 2/\pi\,(1+cos2\theta_T)$; tissues mostly horizontal

Erectophile: $g_T(\theta_T) = 2/\pi\,(1-cos2\theta_T)$; tissues mostly vertical

Plagiophile: $g_T(\theta_T) = 2/\pi\,(1+cos4\theta_T)$; tissues mostly inclined at 45^o

Uniform: $g_T(\theta_T) = 2/p$; random tissue orientation

The direct solar radiation tranmission $\mathfrak{I}$'' and scattered solar radiation transmission $\mathfrak{T}$ are given by (19):

$$\mathfrak{I}'(p) = e^{\left(-\frac{G(\Omega')}{|\mu'|}P\right)} \qquad \mathfrak{I}(p) = e^{\left(-\frac{G(\Omega)}{\mu}\frac{V_2(\Omega'\Omega,P)}{V(\Omega,P)}P\right)} \tag{9}$$

where

$$\frac{V_2(\Omega'\Omega,P)}{V(\Omega,P)} = \left(1-\frac{4}{3\pi}\right)\frac{P}{P_i} \qquad if\ P < P_i$$

$$= 1-\frac{4}{3\pi}\frac{P_i}{P} \qquad if\ P \geq P_i$$

Importantly, Pi = 2rΛ/Geo(Ω'Ω), Λ is tissue area density (m^2/m^3), r is the radius of the sun-flecks on the illuminated tissue, and Geo(Ω'Ω) is a function describing the geometry:

mbda]/Geo(Ω'Ω), Λ is tissue area density (m^2/m^3), r is the radius of the sun-flecks on the illuminated tissue, and Geo(Ω'Ω) is a function describing the geometry:

$$Geo(\Omega',\Omega) = \sqrt{\tan(\theta')^2 + \tan(\theta)^2 - 2\tan(\theta')\tan(\theta)\cos(\phi'-\phi)} \quad (10)$$

The *G*-function describes the total tissue area that is projected in a specific direction (Ω_X) by a unit canopy area, and this canopy area has a distribution function of tissue normal orientation which is identified by $g_T(z,\Omega_T)$, where *z* is the depth from the top of the canopy:

$$G(z,\Omega_X) = \frac{1}{2\pi}\int_0^{2\pi}\int_0^{1} g_T(z,\Omega_T)\,|\cos\Omega_T\Omega_X\,|\,d\Omega_T \quad (11)$$

For some tissue orientations, the *G*-function can be solved analytically. For instance, random, vertical, and horizontal orientations produce *G* values of 0.5, $2/\pi\sqrt{1-\mu_T^2}$, and μ_T, respectively.

Photons Unscattered Until Reaching the Soil/Litter Surface

Photons that travel through the vegetation canopy without interception and which collide with the soil or litter surface are modeled according to ref. 22, but modified to allow for multiple types of tissues such as foliage and wood:

$$\rho_{unscat}(\Omega'\Omega) = \rho_{surface}\Im'(P)\Im(P) = \rho_{surface}\, e^{\left[-\left(\frac{G(\Omega')}{|\mu u'|}+\frac{G(\Omega)\,V_2(\Omega'\Omega,P)}{\mu\quad V(\Omega,P)}\right)P\right]} \quad (12)$$

Surface soil and litter hemispherical reflectance is an input to the model, and is contained in databases constructed by Asner (6). In forested environments, the effects of soil reflectance variability on top-of-canopy reflectance are minor (6), and thus they are prescribed simply by random selection based on forest type (3).

Photons Multiply Scattered in the Canopy. One of the most computationally expensive components of a physical model of photon transport is the treatment of multiple scattering by plant tissues. Several models have been developed to solve the multiple scattering component of the radiative transfer equation (e.g., refs. 20 and 23). These models simulate photon scattering in many "streams," often 48 or 96 in the unit sphere. This makes for a computationally demanding algorithm that can be difficult to employ when simulating many spectral bands or many pixels. Iaquinta and Pinty (22) present a reasonable alternative in which multiple scattering is assumed to occur equally in angles exiting the canopy; it preserves much of the interaction depicted in the more computationally demanding models:

$$\rho_{multsc}(\Omega') = \frac{1}{|\mu'|} \int_{0 \to 1} I^M(\mu') \mu' d\mu' \tag{13}$$

where I^M represents the source term within the canopy that consists of upward-traveling photons from the soil surface, singly scattered photons from all directions, and multiply scattered photons from all directions. This approximation is reasonable for nadir-viewing remote sensing instruments.

Pixel-Level Canopy Reflectance Spectroscopy. Previous sections describe radiation transport in one dimension, a theoretical slab of infinitesimally small scatters of multiple plant tissue types. Several 3D radiative transfer models have been developed (20), allowing for the representation of multiple canopies and in-homogeneous canopy coverage. These 3D models are computationally expensive, which limits their inversion using numerical optimization techniques.

We circumvent the 3D problem by estimating fractional cover using the shortwave-infrared (SWIR) spectral region from 2,000 to 2,400 nm (15). Lateral mixing of canopy and background materials is approximately linear when this region of the spectrum is normalized to remove the albedo component of the observed reflectance (6). In doing so,

the fractional closed (F^{v}_{closed}) and open (F_{open}) canopy cover can be estimated directly from the data (16). The pixel-level reflectance is then summed:

$$\rho_{pixel}(\Omega'\Omega) = \left[\rho^{v}_{closed}(\Omega'\Omega) \cdot F^{v}_{closed}\right] + \left[\rho_{open}(\Omega'\Omega) \cdot F_{open}\right] \quad (14)$$

where the reflectance of the closed canopy (ρ^{v}_{closed}) is calculated by using Eqs. **1**-**13**:

$$\rho_{closed}(\Omega'\Omega) = \rho_{unscat}(\Omega'\Omega)) + \rho_{\sin gsc}(\Omega'\Omega)) + \rho_{multsc}(\Omega'\Omega) \quad (15)$$

and the shaded canopy reflectance is estimated by Eq. **12**.

Field Studies. *Remote Sensing Validation.* We carried out field studies to evaluate the canopy H_2O and leaf N results derived from inversion of the photon transport model with the airborne spectroscopy data. This was executed in two complementary ways. Spatially intensive measurements were made on three transects of up to 1.9 km for systematic sampling of foliar H_2O and N. Within a 10 × 10 m area centered every 25 m on each transect, the dominant over- and understory vascular plants were noted. Upper-canopy, sunlit foliage was then collected from overstory species using a slingshot, whereas understory species were sampled by hand. Leaves were kept cool in polyethylene bags until fresh weights could be determined (3-4 h). The foliage was then dried at 60-70ºC for at least 72 h, weighed again, and then ground for N analysis by using block digestion and colorimetric autoanalysis (Alpkem, Los Angeles). Foliar H_2O was calculated in units of equivalent water thickness (EWT_L) by fresh to dry weight difference and division by leaf area. Leaf area was measured with an optical scanning leaf area meter.

A second, spatially extensive sampling approach was used to further evaluate the information content in the spectroscopic image results. The leaf N and canopy H_2O images from the airborne imaging spectroscopy were classified into four broad categories: (*i*) low canopy H_2O, low leaf N; (*ii*) high canopy H_2O, low leaf N; (*iii*) low canopy H_2O, high leaf N; and (*iv*) high canopy H_2O, high leaf N (Fig. 6). Partitioning was

established by using histograms of the remote sensing results, which led to high H_2O threshold of >1.2 mm per pixel and high N determinations of >1.1% per pixel. A thematic map was developed from these thresholds, which was then used to guide a spatially extensive sampling effort throughout the region. Initial sample points were randomly selected in each image class and entered into the GPS for foliage collection in the field. However, access in some areas was limited by geologic features (e.g., lava tubes), in which case a sample was collected as close to the initial point as possible. At each sampling point, dominant species were identified and foliage was collected for water and N concentration, as described above. At a subset of these points, canopy LAI was measured with a plant canopy analyzer (LAI-2000, Licor, Lincoln, NE) using the protocol detailed in ref. 24. These LAI measurements were multiplied by EWT_L to estimate EWT_C, the total water content of the canopy. When both under- and overstory plants were present, total EWT_C was calculated as the sum of leaf-level EWT_L values multiplied by the LAI of each canopy (i): $EWT_C = \Sigma[EWT_L(i) \times LAI(i)]$.

High-resolution GPS data were collected at all sampling points for colocation of field data with airborne spectroscopic measurements. A Leica GS-50+ survey-grade GPS with Racal L-band, multiple bounce filtering, and postdifferential correction was used to estimate our position in the forest to average uncertainties of 2 m. Remaining uncertainty in the location of the field data collections was accommodated by taking the 2 × 2 pixel (18 × 18 m) average of the airborne spectroscopy results at each sampling point.

Soil Properties. We quantified differences in net nitrification (NO_3) and mineralization (NH_4) rates along a 1.1-km transect containing intact *Metrosideros*, mixed *Metrosideros*/*Myrica*, and dense *Myrica* stands. Samples were collected every 25 m, and dominant species were noted. Field-moist soils (> 50 g per sample) were placed in polyethylene bags and kept cool for transport to the laboratory in HAVO. NO_3 and NH_4 were extracted from fresh soil by using 2 M KCl and a colorimetric autoanalyzer (Alpkem). Soils were incubated at ≈25ºC for 10 days, and reextracted for NO_3 and NH_4. Net nitrification and mineralization were calculated by differencing assay results from the

beginning and end of the incubation period (Fig. 7). Additional details on this method are provided by Vitousek and Walker (25).

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