Remote analysis of biological invasion and biogeochemical change

Gregory P. Asner*[†] and Peter M. Vitousek[‡]

*Department of Global Ecology, Carnegie Institution, 260 Panama Street, Stanford, CA 94305; and [‡]Department of Biological Sciences, Stanford University, Stanford, CA 94305

Contributed by Peter M. Vitousek, February 1, 2005

We used airborne imaging spectroscopy and photon transport modeling to determine how biological invasion altered the chemistry of forest canopies across a Hawaiian montane rain forest landscape. The nitrogen-fixing tree *Myrica faya* doubled canopy nitrogen concentrations and water content as it replaced native forest, whereas the understory herb *Hedychium gardnerianum* reduced nitrogen concentrations in the forest overstory and substantially increased aboveground water content. This remote sensing approach indicates the geographic extent, intensity, and biogeochemical impacts of two distinct invaders; its wider application could enhance the role of remote sensing in ecosystem analysis and management.

Hawaii | remote sensing | tropical forest | invasive species | imaging spectroscopy

Human activities move many organisms far from their natural ranges, where some establish populations that invade their new habitat. These biological invasions are widespread, and the breakdown of biogeographic barriers, the blurring of the regional distinctiveness of Earth's biota, that they represent is a significant component of human-caused environmental change (1, 2). Some invaders alter the structure and/or functioning of the ecosystems in which they occur; these do not just compete with or consume organisms in their new habitats, they change the rules of the game under which all organisms exist. Ecosystems of remote oceanic islands and the unique species that they support are particularly vulnerable to alteration by invasion (3).

We report a recently developed application of airborne imaging spectroscopy analyzing ecosystem changes caused by invasion. Remote sensing has been used to map the distribution of some biological invaders (4, 5), but invasions often must be far advanced before they can be detected by conventional remote sensing that relies on canopy emergence and/or dominance by the invader (6). In any case, conventional approaches yield the distribution of the invader, not the ecosystem-level effects of invasion. Our approach uses imaging spectroscopy to evaluate changes in canopy chemistry and other canopy characteristics caused by invasion. Canopy chemistry (particularly nitrogen concentration) is causally connected to and highly correlated with rates of plant productivity and nutrient use efficiency, decomposition, and nutrient availability in soil (7–9). Consequently, changes in canopy chemistry can be used to show not just where invasion occurs, but also whether it has a substantial effect on ecosystem-level biogeochemistry.

Efforts to measure canopy chemistry by remote sensing have been underway for some time (10–15), and have yielded useful empirically based estimates. Recent advances in theory, notably spectroscopic transport models that trace photons through the canopy (16–19), and in the development of airborne sensors with signal-to-noise, stability, and dynamic range performances matching laboratory spectrometers (20, 21) allow for assessment of multiple biogeochemical properties simultaneously across a landscape.

We applied this approach to the invasion by the Canary Islands tree *Myrica faya* into tropical montane forests of Hawaii Volcanoes National Park (HAVO). HAVO is useful for this research because most of the montane forest area of the park is dominated by a single overstory tree species, *Metrosideros polymorpha*, providing a consistent background against which we can evaluate change; and because nitrogen (N) limits forest productivity and causes low foliar N concentrations in this young volcanic landscape (9, 22). *Myrica* is a symbiotic N_2 fixer, a capacity that is lacking in native trees of these young volcanic sites. Its leaves are much richer in N than *Metrosideros*, and invasion by *Myrica* increases N input and availability severalfold, profoundly altering the pathway of ecosystem development in the sites it dominates (1, 23, 24).

Materials and Methods

We used the recently upgraded National Aeronautics and Space Administration Airborne Visible and Infrared Imaging Spectrometer from an ER-2 high-altitude aircraft to measure canopy fractional cover, canopy water content, and leaf N concentrations in a 1,360-hectare area near the summit of Kilauea Volcano in HAVO (Fig. 1) (see *Supporting Text* and Figs. 5–7, which are published as supporting information on the PNAS web site). These remote measurements were complemented by extensive ground-based structural, spectroscopic, and chemical analyses of forest canopies. Native forests in the region are dominated by *Metrosideros*, with the tree fern *Cibotium glaucum* common in the forest understory. Ground-based measurements show that *Metrosideros* forests in this area are 10–20 m tall, with relatively high leaf area index (LAI = 4–6), but low leaf N (0.6–0.8%) and water (H_2O; 45–55%) concentrations. Where it occurs, the *Cibotium* understory is 3–10 m tall; it has low LAI (1–2) but relatively high leaf N (1.2–1.6%) and moderate H_2O (58–67%) concentrations. In contrast, *Myrica* supports very high LAI (6–11) and high leaf N (1.5–1.8%), but moderate leaf H_2O (50–65%) concentrations in the stands it dominates.

Results

Remote analyses of upper-canopy foliar N concentrations correlated strongly with ground-based measurements (Fig. 2*A*, slope = 0.93, r^2 = 0.91), in the 47 image pixels for which we had information. This correlation held up within *Metrosideros*-dominated and *Myrica*-dominated canopies, as well as between them. Similarly, remotely measured canopy water contents correlated highly with ground-based measurements (Fig. 2*B*, slope = 0.90, r^2 = 0.92).

Aircraft-based analyses of the HAVO landscape yielded strong spatial gradients in both leaf N concentration and canopy water content (Fig. 3). Some areas contained both high foliar N and canopy H_2O, whereas others were a mix of high or low values, and still other areas were low in both H_2O and N (Fig. 6). Extensive field observations demonstrated that low canopy H_2O

Abbreviations: HAVO, Hawaii Volcanoes National Park; LAI, leaf area index.

[†] To whom correspondence should be addressed. E-mail: gpa@stanford.edu.

www.pnas.org/cgi/doi/10.1073/pnas.0500823102

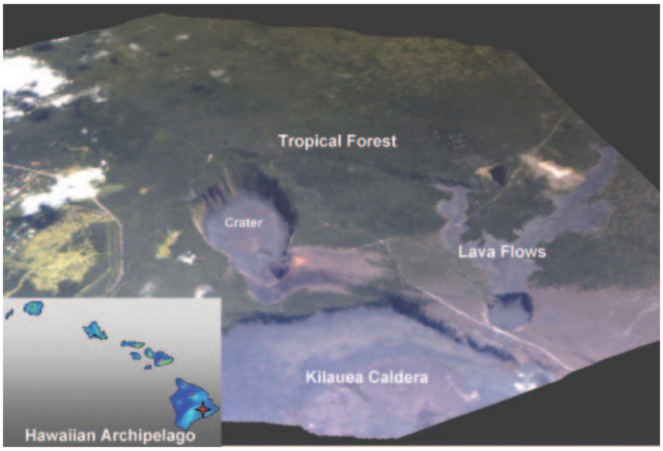

Fig. 1. Southeast flank of Kilauea Volcano in Hawaii Volcanoes National Park, showing recent volcanic activity together with dense tropical forest and its transition to more open woodlands, pastures, and other forms of land use. Although most of this area is under protection by the U.S. Park Service, it has experienced a number of biological invasions.

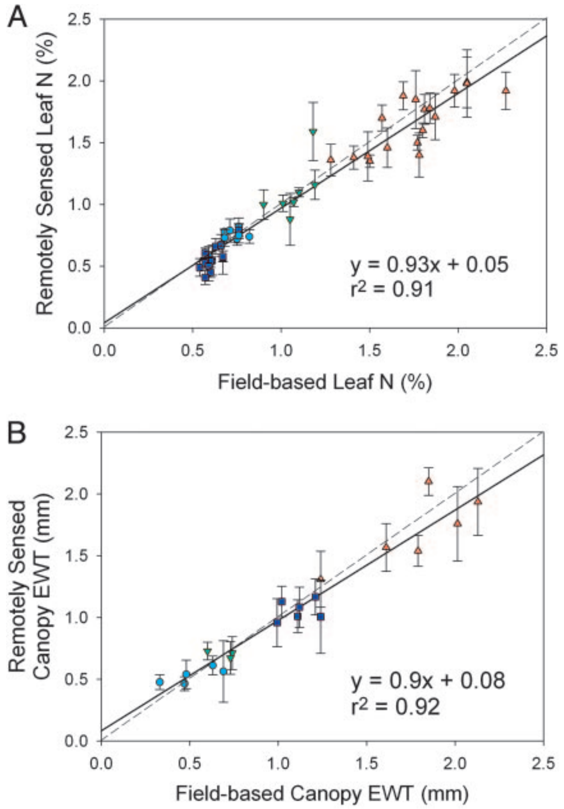

Fig. 2. Comparison of remotely sensed estimates of leaf N concentration and canopy H_2O content with ground-based sampling and laboratory analysis. Areas dominated by *Metrosideros*, *Myrica*, mixed *Metrosideros–Hedychium*, and mixed *Metrosideros–Cibotium* are indicated by cyan, red, blue, and green symbols, respectively. Uncertainty in leaf N estimates increased with mean concentration due to the combined uncertainty in LAI and leaf chemical-optical matching in the model inversions (see supporting information), but absolute errors peaked at only 0.2% leaf N concentration and 0.18 mm of canopy H_2O content.

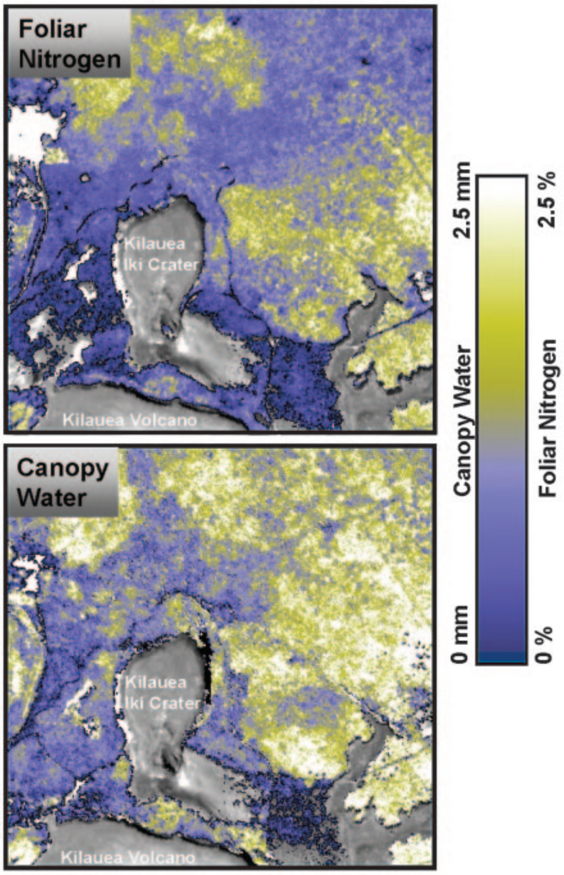

Fig. 3. Leaf N concentrations and canopy H_2O content estimated at 9 × 9 m spatial resolution in a 1,360-hectare area of Hawaii Volcanoes National Park, using airborne high-fidelity imaging spectroscopy and photon transport modeling (also see supporting information).

and leaf N concentrations indicated dominance of native *Metrosideros* trees, whereas high canopy H_2O and leaf N concentrations were associated with well established stands of invasive *Myrica*. Most *Myrica*-dominated stands are surrounded by areas with intermediate foliar N and slightly elevated canopy water content (Fig. 3); in these areas, individual *Myrica* trees are reaching into the canopy but do not yet dominate it, meaning that we are detecting the spread of the invader by its effect on canopy chemistry before it dominates the forest.

We were surprised that the airborne measurements also identified substantial areas with low foliar N but relatively high canopy water content (Fig. 3), and still more surprised to discover that, when we visited those areas, their understories were often dominated by the invasive tall herb *Hedychium gardnerianum* (Kahili ginger). *Hedychium* is known to be a widespread invader of Hawaiian forests, in HAVO and elsewhere (25), but because it colonizes the forest understory, it is invisible to conventional remote sensing techniques. Its canopy differs substantially from those of *Metrosideros* and *Myrica*; although it reaches only 1–2 m in height in the forest understory, it supports relatively high LAI (3–5), and high foliar N (1.8–2.1%) and water (80–93%) concentrations. Because analysis of canopy water content by airborne imaging spectroscopy measures the returning photons that interact with the entire volume of plant tissues in the pixel (see supporting information), it allows the detection of *Hedychium* under the forest canopy. In contrast, airborne imaging spectroscopy is sensitive to foliar N only in the upper canopy, and so the high N content of understory *Hedychium* is undetectable.

In fact, *Metrosideros* stands that have been invaded by *Hedychium* appear to have lower foliar N than uninvaded

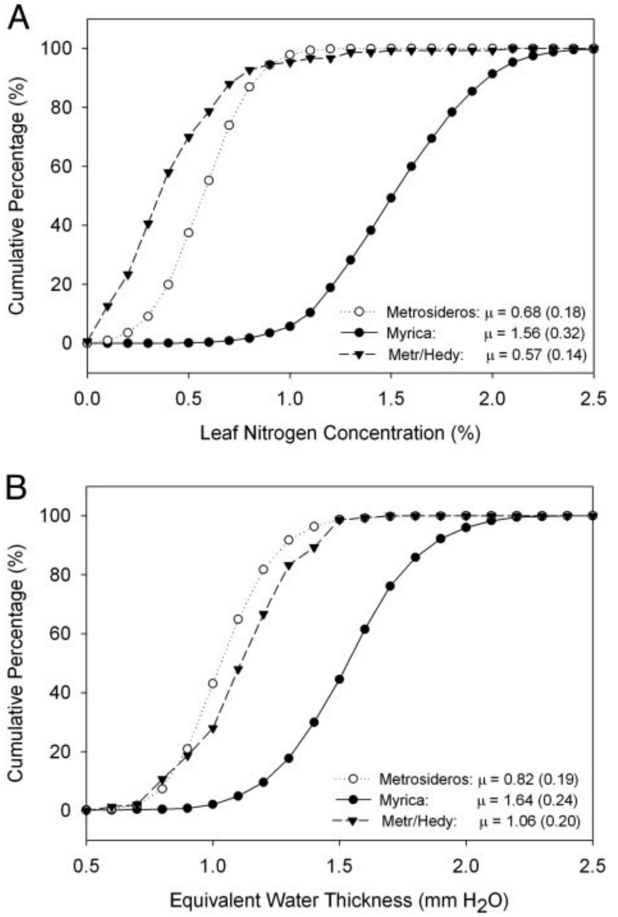

Fig. 4. Cumulative histograms of leaf N concentration and canopy H_2O content values from imaging spectrometer measurements of areas dominated by: native *Metrosideros* forest, invasive N-fixing *Myrica*, and invasive *Hedychium* in *Metrosideros* understory (also see supporting information).

stands, a pattern that we first detected remotely, and later confirmed with ground-based sampling (Fig. 2*A*). We believe that this decrease in foliar N in *Metrosideros* is due to N uptake by nutrient-demanding *Hedychium*; the alternative, that *Hedychium* preferentially invades nutrient-poor sites, is contradicted by observations that its invasion responds strongly and positively to increased nutrient availability (26). In addition to its biogeochemical effects, the dense shade and network of tubers and roots that *Hedychium* forms in invaded sites serves as an effective barrier to the establishment of native plant species (25).

Regional statistics for the *Metrosideros*, *Myrica*, and *Metrosideros–Hedychium* classes demonstrate that invasion significantly alters canopy chemistry at the landscape scale (Fig. 4). Kolmogorov–Smirnov tests showed that all three forest types differed in foliar N distributions ($P < 0.05$). The *Metrosideros–Cibotium* canopy distribution is negatively skewed toward relatively low values (0.68 ± 0.11%), whereas *Myrica* stands have a positively skewed distribution with much higher N concentration values (1.56 ± 0.32%). *Hedychium* invasion is spatially linked to decreased foliar N concentrations of overstory *Metrosideros* (0.51 ± 0.14%). Moreover, *Hedychium* increases aboveground water content by nearly 50% over native *Metrosideros* stands, whereas *Myrica* more than doubles canopy water (Fig. 4).

Classification of the area based on canopy chemistry (Fig. 6) suggests that ≈28% of the landscape is dominated by *Myrica*, and that an additional 23% is undergoing transformation as *Myrica* grows into the canopy. Up to 13% of the remaining *Metrosideros* forest is infested with *Hedychium*, directly altering biogeochemical conditions at the understory level and indirectly at the overstory forest via nutrient competition. Assuming that all current forested areas were once dominated by *Metrosideros*, invasion of *Myrica* has increased canopy N >4-fold locally, and approximately doubled canopy N content over the 1,360-hectare area as a whole.[§]

These observed changes in canopy chemistry are linked to several fundamental changes in ecosystem properties. Higher foliar N in *Myrica* canopies is associated with faster leaf turnover, higher rates of nutrient cycling, faster decomposition, greater N availability, greater fluxes of N-containing trace gases, and ultimately invasion by other nutrient-demanding species (23, 27, 28). For example, nitrification rates in soil increase from near zero in *Metrosideros* stands (−0.04 ± 0.01 mg of N per g of soil per day) to 1.3 ± 2.3 in areas containing *Myrica* saplings, and to 5.2 ± 3.7 in areas dominated by *Myrica* (see supporting information). The biogeochemical consequences of invasion by *Hedychium* have not been evaluated as thoroughly because this invasion's effect on overstory trees had not been identified previously. High-N *Hedychium* foliage decomposes much more rapidly than does *Metrosideros* (29), which could enhance overall rates of nutrient cycling (30), but the decrease in *Metrosideros* foliar N could offset some or all of this effect.

Airborne imaging spectroscopy can provide a unique, spatially detailed understanding of the biogeochemical impacts of different species, including invaders, throughout a forest landscape. Indeed, the chemical, structural, and biological diversity of rain forests in particular requires wholly new remote sensing approaches to understand spatial and temporal variations in nutrient, water, and carbon cycle processes. These airborne observations and techniques cannot substitute for ground-based biogeochemical studies, but they can direct field measurements based on a regional understanding of canopy chemistry.

[§] The increase in N within *Myrica* patches is calculated as a doubling in canopy leaf area (from H_2O content) multiplied by a 2.3-fold increase in leaf N concentration (Fig. 4); to calculate the increase in the area as a whole, the patch-level enrichment is applied to the 46% of the total area that is dominated by *Myrica*. This percentage increase is estimated by classification of the canopy chemistry results, as shown in Fig. 6.

We thank H. Farrington, R. Martin, D. Turner, A. Warner, K. Carlson, K. Lo, A. Chin, M. Meyer, K. Amatangelo, and S. Robinson for assistance with field and laboratory analyses, and C. Field, R. Martin, S. Ollinger, S. Porder, A. Townsend, and S. Ustin for helpful comments on the manuscript. This work was supported by the National Science Foundation Grants DEB-0136957 and DEB-0108492, the National Aeronautics and Space Administration New Investigator Program (NAG5-8709), The Andrew Mellon Foundation, and The Carnegie Institution.

1. Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmanek, M. & Westbrooks, R. (1997) *N. Z. J. Ecol.* **21,** 1–16.
2. Mooney, H. A. & Hobbs, R. J. (2000) *Invasive Species in a Changing World* (Island, Washington, DC).
3. D'Antonio, C. M. & Dudley, T. L. (1995) *Ecol. Stud.* **115,** 103–119.
4. Lass, L. W., Thill, D. C., Shafll, B. & Prather, T. S. (2002) *Weed Sci.* **16,** 426–432.
5. Underwood, E., Ustin, S. & DiPietro, D. (2003) *Remote Sensing Environ.* **86,** 150–161.
6. Hunt, E. R., McMurtrey, J. E., Parker Williams, A. E. & Corp, L. A. (2004) *Weed Sci.* **52,** 492–497.
7. Field, C. & Mooney, H. A. (1986) in *On the Economy of Plant Form and Function*, ed. Givnish, T. J. (Cambridge Univ. Press, Cambridge, U.K.), pp. 25–55.
8. Reich, P. B., Walters, M. B. & Ellsworth, D. S. (1997) *Proc. Natl. Acad. Sci. USA* **94,** 13730–13734.
9. Vitousek, P. M. (2004) *Nutrient Cycling and Limitation: Hawai'i as a Model System* (Princeton Univ. Press, Princeton, NJ).

10. Curran, P. J. (1989) *Remote Sensing Environ.* **30,** 271–278.
11. Matson, P., Johnson, L., Billow, C., Miller, J. & Poo, R. (1994) *Ecol. Appl.* **4,** 280–298.
12. Ollinger, S. V., Smith, M. L., Martin, M. E., Hallett, R. A., Goodale, C. L. & Aber, J. D. (2002) *Ecology* **83,** 339–355.
13. Ustin, S. L., Jacquemoud, S., Zarco-Tejada, P. J. & Asner, G. P. (2004) in *Manual of Remote Sensing: Remote Sensing of Natural Resource Management and Environmental Monitoring*, ed. Ustin, S. L. (Am. Soc. Photogram. Remote Sensing, New York), Vol. 4, pp. 679–730.
14. Wessman, C. A., Aber, J. D., Peterson, D. L. & Melillo, J. M. (1988) *Nature* **335,** 154–156.
15. Ustin, S. L., Roberts, D. A., Gamon, J. A., Asner, G. P. & Green, R. O. (2004) *Bioscience* **54,** 523–534.
16. Asner, G. P., Wessman, C. A. & Schimel, D. S. (1998) *Ecol. Appl.* **8,** 1022–1036.
17. Jacquemoud, S., Baret, F., Andrieu, B., Danson, F. M. & Jaggard, K. (1995) *Remote Sensing Environ.* **52,** 163–172.
18. Jacquemoud, S., Ustin, S. L., Verdebout, J., Schmuck, G., Andreoli, G. & Hosgood, B. (1996) *Remote Sensing Environ.* **56,** 194–202.
19. Zarco-Tejada, P. J., Miller, J. R., Noland, T. L., Mohammed, G. H. & Sampson, P. H. (2001) *IEEE Trans. Geosci. Remote Sensing* **39,** 1491–1507.
20. Green, R. O., Eastwood, M. L., Sarture, C. M., Chrien, T. G., Aronsson, M., Chippendale, B. J., Faust, J. A., Pavri, B. E., Chovit, C. J., Solis, M. S., *et al.* (1998) *Remote Sensing Environ.* **65,** 227–248.
21. Green, R. O. & Pavri, B. E. (2002) in *Proceedings of the 2002 Airborne Earth Science Workshop*, ed. Green, R. O. (Jet Propulsion Laboratory, California Institute of Technology, Pasadena), pp. 1–13.
22. Harrington, R. A., Fownes, J. H. & Vitousek, P. M. (2001) *Ecosystems* **4,** 646–657.
23. Vitousek, P. M. & Walker, L. R. (1989) *Ecol. Monogr.* **59,** 247–265.
24. Walker, L. R. & Vitousek, P. (1991) *Ecology* **72,** 1449–1454.
25. Gardner, D. E. & Davis, C. J. (1982) *The Prospects for Biological Control of Non-Native Plants in Hawaiian National Parks* (Cooperative Parks Studies Unit, Department of Botany, University of Hawaii, Honolulu), pp. 58.
26. Ostertag, R. & Verville, J. H. (2002) *Plant Ecol.* **162,** 77–90.
27. Aplet, G. H. (1990) *Oecologia* **82,** 414–416.
28. Vitousek, P. M., Walker, L. R., Whiteacre, L. D., Mueller-Dombois, D. & Matson, P. A. (1987) *Science* **238,** 802–804.
29. Allison, S. D. & Vitousek, P. M. (2004) *Oecologia* **141,** 612–619.
30. Ehrenfeld, J. G., Kourtev, P. & Huang, W. (2001) *Ecol. Appl.* **11,** 1287–1300.