LETTER

# Reply to Ollinger et al.: Remote sensing of leaf nitrogen and emergent ecosystem properties

Various physical, chemical, and physiological processes, including canopy structure, impact surface reflectance. Remote sensing aims to derive ecosystem properties and their functional relationships, given these impacts. Ollinger et al. (1) do not distinguish between the forward and inverse problems in radiative transfer and, hence, misrepresent our results (2). The authors also suggest our conclusions are based on a subset of data from ref. 3, which is not the case.

Remote sensing instruments do not measure canopy properties, only photons that enter the canopy, interact with foliage, woody material, and ground, and escape toward the sensor. Fundamental laws of light interaction with matter describe this process and provide causal mechanisms to explain observations. We report an explicit relationship between radiation measured by an optical sensor, canopy structural properties, and leaf optics (Eq. S6.1 in ref. 2) and demonstrate its validity over a wide range of forests (*SI Text 7* and figure 6 in ref. 2). The relationship was derived from well-established principles of light interaction with leaves and radiative-transfer theory. Our conclusions are based on this result, not on "[u]sing a subset of data from ref. ([3])." We used data from ref. 3 to: (*i*) reproduce Ollinger et al.'s result (figure 3 in ref. 2); (*ii*) analyze their methodology; (*iii*) demonstrate flaws in their interpretation (figure 2 in ref. 2); and (*iv*) formulate the inverse problem of inferring leaf-scattering properties from satellite data.

We demonstrate that the link between near-infrared reflectance (NIR) and foliar nitrogen (%N) is both indirect and a function of structure (across the entire shortwave domain). In situ %N, too, is a function of structure because foliar nitrogen in ref. 3 was "determined as the mean of mass-based foliar %N over all species in each plot (weighted by the relative abundance of each)." In both cases we found canopy structure dominated variations in NIR reflectance with %N, resulting in spurious correlation (2). We therefore disagree with Ollinger et al. (1, 3) that the observed NIR vs. %N relationship alone adequately justifies its use in remote sensing: reflectance data must be corrected for canopy structure effects to extract information about %N and other chemical constituents. Furthermore, we identified the directional area scattering factor (DASF) as a means to achieve this correction. DASF is a purely structural term, directly obtainable from canopy reflectance spectra, and does not "rely on an assumption that a useful link between nitrogen and reflectance requires a direct, biochemical mechanism" (1). Our report does not per se rule out indirect connections between nitrogen availability and structure, but it does allow the direct relationship between leaf nitrogen and remote sensing signals to be elucidated without needing such an assumption.

Although biological mechanisms certainly shape complex linkages between ecosystem components, canopy radiative response is the only source of information about ecosystem properties from remote sensing, and follows physical laws governing radiation transport. Our analysis explains the observed behavior entirely through application of these laws, but Ollinger et al. (1) appeal to more complex and as yet unspecified ecological and evolutionary mechanisms to explain their observations: Ockham's razor (4) surely applies. Physically based approaches must underlie remote sensing analysis of ecosystem properties and functional relationships between their components (5).

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The authors declare no conflict of interest.

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