LETTER

Disentangling the contribution of biological and physical properties of leaves and canopies in imaging spectroscopy data

We agree with Knyazikhin et al. (1), who reported in a recent issue of PNAS that relationships between foliar nitrogen (%N) and near-infrared (NIR) canopy albedo appeared to be indirect and explained largely by differences in leaf and canopy structure, primarily between conifer and broadleaf species. We disagree, however, with the conclusion that %N–NIR correlations are necessarily spurious. On the contrary, they are consistent with ample evidence that canopy architecture and leaf structural and chemical and optical properties tend to covary among plant functional types (2–4), and we can exploit this tendency for the purposes of prediction and mapping. We are also troubled by certain sweeping and somewhat misleading generalizations, such as the purported implications of the authors' findings for all imaging spectroscopy. The analyses focused primarily on 800- to 850-nm albedo, and, thus, it is unclear whether the results are applicable to narrow-waveband (e.g., 10 nm) and full-spectrum (e.g., 400–2500 nm) studies, especially because the signature of leaf-level variation in foliar nutrients, such as nitrogen, is most prominent in shortwave infrared regions (>1,100 nm) that were not addressed by the authors (2, 3).

Knyazikhin et al. (1) addressed the need to disentangle contributions of canopy structural and leaf optical properties in canopy reflectance spectra (5), but they did not provide an adequate rationale for the inference that %N and other leaf properties cannot be characterized from imaging spectroscopy. Rather, in our opinion,

the paper by Knyazikhin et al. illustrated that the biology and physics of leaves and canopies cannot be evaluated in isolation and, correspondingly, that we need to better understand why certain spectroscopic methods work, given that they are not fully reconciled by existing radiative-transfer models. More extensive simulations over broader wavelength ranges are required, using improved parameterization of leaf structural, physiological, and optical properties. For instance, the authors used a single leaf spectrum derived from one PROSPECT simulation, but, as they acknowledged, leaf albedo varies substantially among species, including those in the study, and that variation is related to physiology, biochemistry, and internal leaf structure (2, 3). Use of species-specific simulations of leaf spectra could potentially lead to significant changes in the authors' findings across the full 400- to 2,500-nm spectrum. Thus, a reasonable inference drawn from Knyazikhin et al. (1) and previous work (5) is that canopy structure is a potentially confounding factor in analyzing vegetation reflectance spectra, not that "NIR and/or SW broadband satellite data cannot be directly linked to leaf-level processes."

Finally, Knyazikhin et al. (1) argue that links between leaf biochemistry (e.g., %N) and "hyperspectral" reflectance data are obscured by variation in leaf-surface albedo, which seems inconsistent with a sizeable and growing body of empirical evidence (2, 3). Statistically robust relationships between leaf or canopy biochemistry and

imaging spectroscopy, within and across a diverse range of species, have repeatedly been demonstrated, albeit for reasons that we are currently unable to fully represent within radiative-transfer models. In any case, progress in remote sensing requires integration of both biologically and physically based approaches, and better linkages between the two will improve our ability to remotely detect biologically meaningful leaf optical properties.

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1 Knyazikhin Y, et al. (2013) Hyperspectral remote sensing of foliar nitrogen content. *Proc Natl Acad Sci USA* 110(3):E185–E192.
2 Kokaly RF, Asner GP, Ollinger SV, Martin ME, Wessman CA (2009) Characterizing canopy biochemistry from imaging spectroscopy and its application to ecosystem studies. *Remote Sens Environ* 113(S1):S78–S91.
3 Ollinger SV (2011) Sources of variability in canopy reflectance and the convergent properties of plants. *New Phytol* 189(2):375–394.
4 Wright IJ, et al. (2004) The worldwide leaf economics spectrum. *Nature* 428(6985):821–827.
5 Lewis P, Disney M (2007) Spectral invariants and scattering across multiple scales from within-leaf to canopy. *Remote Sens Environ* 109(2):196–206.