



Reply to Townsend et al.: Decoupling contributions from canopy structure and leaf optics is critical for remote sensing leaf biochemistry

Townsend et al. (1) agree that we explained that the apparent relationship (2) between foliar nitrogen (%N) and near-infrared (NIR) canopy reflectance was largely attributable to structure (which is in turn caused by variation in fraction of broadleaf canopy). Our conclusion that the observed correlation with %N was spurious (i.e., lacking a causal basis) is, thus, clearly justified: we demonstrated that structure explained the great majority of observed correlation, where the structural influence was derived precisely via reconciling the observed correlation with radiative-transfer theory. What this also suggests is that such correlations, although observed, do not uniquely provide information on canopy biochemical constituents. We, therefore, disagree with the assertion in ref. 1 that we “did not provide an adequate rationale for the inference that %N and other leaf properties cannot be characterized from imaging spectroscopy”; our analysis showed precisely that. Our analysis also led to the conclusion that “NIR and/or SW broadband satellite data cannot be directly linked to leaf-level processes,” and any such link must be indirect and will be a function of structure. This is true for all wavelengths in the interval 423–855 nm (figure 7B and figure S2 in ref. 3), not primarily for the 800- to 850-nm spectral band, as misstated in ref. 1. None of the leaf biochemical constituents can be accurately estimated without accounting for canopy structural effects.

We identified a structural variable, the directional area scattering factor (DASF), which was determined entirely by canopy geometrical properties such as shape and size of the tree crowns, spatial distribution of trees on the ground, within-crown foliage arrangement, and properties of the leaf surfaces. In dense vegetation, this parameter can be directly retrieved from the reflectance spectrum without the use of canopy-reflectance models, prior knowledge, or ancillary information regarding leaf optical properties (3). Equations S4.1–S5.3 in ref. 3 explain the

background physics, but Townsend et al. (1), nonetheless, misinterpret this as “the authors used a single leaf spectrum derived from one PROSPECT simulation.” We clearly demonstrated that DASF provides information critical to accounting for structural contributions to measurements of leaf biochemistry from remote sensing.

Lastly, we do not claim that “links between leaf biochemistry (e.g., %N) and ‘hyperspectral’ reflectance data are obscured by variation in leaf-surface albedo,” as overstated in ref. 1. We emphasized that some radiation is scattered at the surface of leaves and, therefore, contains no information on leaf biochemistry; this presents an additional confounding factor, unless it can be accounted for.

Statistical relationships between leaf biochemistry and canopy reflectance spectra have indeed been repeatedly demonstrated. However, analyses of underlying physical mechanisms that generate the remotely measured signal, which are required to distinguish causality from correlation (4), such as ours, have been lacking thus far. This is absolutely necessary to obtain accurate information on leaf biochemistry from space (5). We agree that analyses including both biologically and physically based approaches will help reveal the subtleties of the empirical relationships.

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1 Townsend PA, Serbin SP, Kruger EL, Gamon JA (2013) Disentangling the contribution of biological and physical properties of leaves and canopies in imaging spectroscopy data. *Proc Natl Acad Sci USA*, 10.1073/pnas.1300952110.

2 Ollinger SV, et al. (2008) Canopy nitrogen, carbon assimilation, and albedo in temperate and boreal forests: Functional relations and potential climate feedbacks. *Proc Natl Acad Sci USA* 105(49):19336–19341.

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4 Fisher JB (2009) Canopy nitrogen and albedo from remote sensing: What exactly are we seeing? *Proc Natl Acad Sci USA* 106(7):E16–E16, author reply E17.

5 Ustin SL (2013) Remote sensing of canopy chemistry. *Proc Natl Acad Sci USA* 110(3):804–805.

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The authors declare no conflict of interest.

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