



Tansley review

Sources of variability in canopy reflectance and the convergent properties of plants

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Contents

Summary	1	V. Functional convergence among optically important traits	13
I. Introduction	2	VI. Conclusions	15
II. Physical properties of incident radiation	3	Acknowledgements	15
III. Sources of variability in vegetation reflectance	4	References	16
IV. The combined effects of multiple traits on whole-canopy reflectance	9		

Summary

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How plants interact with sunlight is central to the existence of life and provides a window to the functioning of ecosystems. Although the basic properties of leaf spectra have been known for decades, interpreting canopy-level spectra is more challenging because leaf-level effects are complicated by a host of stem- and canopy-level traits. Progress has been made through empirical analyses and models, although both methods have been hampered by a series of persistent challenges. Here, I review current understanding of plant spectral properties with respect to sources of uncertainty at leaf to canopy scales. I also discuss the role of evolutionary convergence in plant functioning and the difficulty of identifying individual properties among a suite of interrelated traits. A pattern that emerges suggests a synergy among the scattering effects of leaf-, stem- and canopy-level traits that becomes most apparent in the near-infrared (NIR) region. This explains the widespread and well-known importance of the NIR region in vegetation remote sensing, but presents an interesting paradox that has yet to be fully explored: that we can often gain more insight about the functioning of plants by examining wavelengths that are not used in photosynthesis than by examining those that are.

I. Introduction

The ability to relate information obtained at one scale to patterns and processes that manifest themselves at another is a common theme among all fields of science. In the discipline of terrestrial ecology, methods by which leaf-, plant- and stand-level observations can be related to landscapes, regions and continents have been the subject of much discussion (e.g. Ehleringer & Field, 1993; Enquist *et al.*, 2003). Although a variety of approaches have been proposed, there is widespread agreement that remote sensing holds a central and irreplaceable role. Remote platforms provide the only means of viewing large portions of the Earth's surface at regular intervals and the selective absorption and reflectance of light by plants allow optical sensors to gather tremendous amounts of information relevant to the function of ecosystems. However, the success of this approach depends on our understanding of factors affecting plant spectral properties and our ability to interpret reflectance data from a wide range of ecosystems.

Although the basic structure of vegetation reflectance spectra has been understood for some time (e.g. Gates *et al.*, 1965), the variability that exists among leaves, plants and ecosystems presents serious challenges for efforts to attribute spectral variation to structural or biochemical variables. The earliest attempts to study plants from space were based on the distinct optical properties of live vegetation in the visible and near-infrared (NIR) regions. Whereas reflectance in the visible is typically low because of the absorption properties of pigments, reflectance in the NIR is high because individual leaves and whole plant canopies strongly scatter NIR energy (Gates *et al.*, 1965; Knipling, 1970). Although the functional basis for high NIR scattering remains an active area for research, early work demonstrated that this difference in visible vs NIR reflectance could be significantly related to various properties of plant density or canopy 'greenness' (e.g. Tucker, 1979).

The advent of broad-band Earth-observing satellites, such as Landsat and the advanced very high resolution spectroradiometer (AVHRR), in the 1970s and 1980s resulted in efforts to produce simple vegetation indices, based largely on NIR/visible reflectance ratios, that captured broad variation in dominant vegetation properties (e.g. Gutman, 1991). Subsequent broad-band sensors, including the moderate-resolution imaging spectroradiometer (MODIS), had improved radiometric and geometric characteristics (Justice *et al.*, 1998) as well as a greater number of spectral bands, allowing refinement in the vegetation indices used to infer vegetation condition (Huete *et al.*, 2002). In the nearly four decades since they first became available, data from broad-band instruments have led to an impressive number of regional and global investigations that include characterization of land use and vegetation type (e.g. Running *et al.*, 1995; Hansen *et al.*, 2000), vegetation biomass (e.g. Myneni

et al., 2001), leaf area index (LAI; e.g. Turner *et al.*, 1999; Zheng & Moskal, 2009), light use efficiency (e.g. Hilker *et al.*, 2008), primary productivity (e.g. Potter, 1999; Running *et al.*, 2004), plant water status (e.g. Nishida *et al.*, 2003), wildfire frequency and severity (e.g. Brewer *et al.*, 2005), habitat conservation areas (Wiens *et al.*, 2009), and biophysical variables that influence climate (Schaaf *et al.*, 2002).

Despite these accomplishments, broad-band sensors carry limitations associated with the fact that they sample only portions of the solar spectrum and at bandwidths that are too wide to discern subtle, but important, features related to vegetation composition, biochemistry and physiological activity. For these reasons, a parallel set of investigations have pursued use of imaging spectroscopy, or high spectral resolution remote sensing, with respect to plant traits that can best be estimated using narrow-band features or full spectrum reflectance. This work grew initially from agricultural research that used benchtop spectrometers to estimate protein, fiber and nitrogen (N) contents of vegetable crops and animal feeds (e.g. Thomas & Oerther, 1972; Norris *et al.*, 1976). Subsequent studies sought to refine statistical methods and explored spectral features related to leaf nutrients and biochemical compounds that influence the biogeochemistry of native ecosystems (Wessman *et al.*, 1988; Martin & Aber, 1994; Curran & Kupiec, 1995; Kokaly & Clark, 1999). At the plant level, portable spectrometers are increasingly used for similar purposes, but factors such as leaf structure and stem geometry introduce additional sources of variability (e.g. Yoder & Pettigrew-Crosby, 1995; Milton *et al.*, 2009). Similarly, the ability to deploy spectrometers on aircraft and satellite platforms has emerged as a useful tool for landscape to regional ecological analysis (Ustin *et al.*, 2004) and has led to new plans for future high spectral resolution Earth observation satellites. Nevertheless, such instruments present a variety of new challenges including removal of atmospheric effects (Gao *et al.*, 2009), understanding the influence of canopy structure (e.g. Roberts *et al.*, 2004), and interpreting reflectance spectra from floristically mixed pixels (e.g. Ollinger & Smith, 2005; Plourde *et al.*, 2007).

Although there has been much progress in the use of passive optical remote sensing for vegetation analysis, persistent uncertainties related to sources of variability in vegetation spectral properties still pose challenges. Some of these stem from difficulties in discerning vegetation types that are functionally different, but too similar spectrally to be differentiated with existing instruments (Kokaly *et al.*, 2009). Other challenges involve commonly observed reflectance patterns, particularly in the NIR region, that either cannot easily be explained by current understanding of how plants absorb and reflect light or that can result from numerous combinations of leaf- and canopy-level traits. Given the importance of understanding ecosystem response to

environmental change and the planned development of new space-based remote sensing instruments such as HypSPRI (National Research Council (NRC), 2007), efforts to enhance our ability to interpret vegetation spectral patterns are needed.

In this paper I review current understanding of spectral reflectance patterns in plants with respect to known sources of variability and uncertainties that limit current applications of remote sensing. In doing so, I revisit some of the basic mechanisms governing interactions between plants and incident radiation, and highlight developments spanning > 45 yr of research. I also discuss a persistent challenge in understanding the drivers of plant spectral patterns that requires further examination: the issue of functional convergence among plant traits and the difficulty of assessing the relative importance of individual traits that covary with a suite of plant properties. Treatment of these topics draws from a wide body of literature, use of leaf and canopy radiative transfer models (the PROSPECT and SAIL models: Verhoef, 1984; Jacquemoud & Baret, 1990; Jacquemoud *et al.*, 2000, 2009), and data from recent investigations of canopy spectral properties in forests (Martin *et al.*, 2008; Ollinger *et al.*, 2008).

Research on the spectral properties of plants has produced a greater body of knowledge than can be adequately covered in one short review and many important lines of investigation have necessarily been omitted. Instead, the objective was to provide a review that ties basic physical mechanisms of plant–light interactions to the challenges of understanding variability across leaves, stems and canopies. Although the focus is on reflectance features relevant to passive optical remote sensing platforms, active sensors such as Light Detection and Ranging (LiDAR) and Radio Detection and Ranging (radar) play an increasingly important role in vegetation remote sensing. Ecological applications of these sensors have been reviewed elsewhere and typically focus on detection of the vertical or three-dimensional structure of plant canopies (Lefsky *et al.*, 2002; Treuhaft *et al.*, 2004). Here, treatment of these sensors will focus on cases where their fusion with data from passive optical sensors can improve understanding of canopy spectral properties.

II. Physical properties of incident radiation

Most of the radiation emitted by the sun occurs in the range of 200 to 2500 nm (Fig. 1a), with a peak at *c.* 500 nm and a distribution that approximates the emission spectra of a black body at 5800°K, as described by Planck's law. In the atmosphere, light is scattered by dust, atmospheric molecules and aerosols and is absorbed at various wavelengths by a variety of gases. Whereas much of the incident ultraviolet energy is absorbed by O₂ and O₃, there are few absorbers in the visible portion of the spectrum (400–700 nm), making

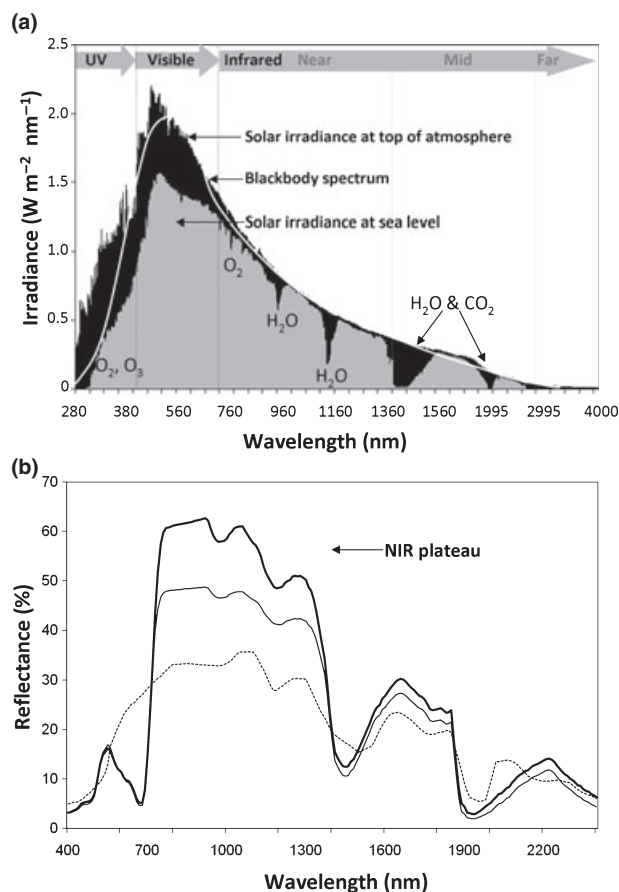


Fig. 1 (a) The solar radiation spectrum above and below the atmosphere, and (b) typical reflectance spectra of (—) crop, (---) tree and (.....) soil surfaces (Gueymard, 2004).

the atmosphere transparent in this region. The dominant absorber in the NIR region is H₂O, which has strong absorption features centered at 1450, 1950 and 2500 nm and weaker features at 980 and 1150 nm. Minor absorption features in the NIR region are caused by CO₂, O₂, N₂O and CH₄. Given the strong and variable influence of the atmosphere, efforts to use aircraft and satellite sensors to estimate vegetation reflectance (e.g. Fig. 1b) must account for atmospheric interference, often using models that estimate atmospheric composition and radiation transfer (e.g. Gao *et al.*, 2009).

Rather than being distributed evenly over the solar spectrum, the energy per quantum of light declines from shorter to longer wavelengths. Roughly half of the energy in incident radiation reaching the Earth's surface is in the visible wavelengths, with the remaining half being in the near- and mid-infrared. This has an important effect on interactions between sunlight and plants and is why, for example, evolution has selected for pigments that absorb narrower, more energetic wavelengths to drive the photochemical reactions of photosynthesis.

III. Sources of variability in vegetation reflectance

Interactions between incident radiation and plants are extremely complex, because of diversity in the size, shape, composition, and arrangement of cells, leaves, stems and plants within ecosystems. However, the biophysical basis for nearly all such interactions can be grouped into one of two categories: absorbance and scattering, with scattering being further subdivided into reflectance and transmittance. Absorbance includes light absorbed by pigments, liquid water and a number of other plant constituents (Blackburn, 1998; Ceccato *et al.*, 2001; Kokaly *et al.*, 2009). Because specific absorption features are caused either by changes in electronic energy states or changes in the vibrational or rotational properties of molecules, absorption features for individual plant compounds tend to occur in discrete portions of the spectrum rather than being distributed over a broader range of wavelengths.

By contrast, scattering occurs whenever solar radiation of any wavelength crosses a boundary between two substances that differ in their refractive index. The difference between the refractive indexes of air (1.0) and liquid water (1.33) causes the well-known illusion of a stick bending when dipped in a pool. Early studies using crops estimated the refractive index of cell walls in a leaf by replacing the intercellular air spaces with various fluids (Knipling, 1970; Gausman *et al.*, 1974; Woolley, 1975). The refractive index of the substance that minimized scattering and reflectance was assumed to be equal to that of the cells. Values obtained using this method varied between 1.4 and 1.5 depending on the degree of leaf hydration, with lower values coming from well-watered leaves.

Although difficult to quantify precisely, the overall degree of scattering in leaves is a function of the number and arrangement of cellular and intercellular surfaces that refract light. With a large enough number of refracting surfaces, the directional properties of light within the leaf become effectively homogenized. For photosynthetically active wavelengths (which largely overlap with visible wavelengths), this has the effect of maximizing absorption by pigments and enhancing overall rates of CO₂ fixation (Evans, 1999; Gutschick, 1999). For NIR wavelengths, where absorbance by leaf constituents is either small (Knipling, 1970; Woolley, 1971; Jacquemoud & Baret, 1990) or altogether absent (Merzlyak *et al.*, 2002), scattering increases the likelihood that photons will exit the leaf in very different directions from the direction of entry. This provides the biophysical basis for high leaf-level reflectance in the NIR region.

1. Leaf and canopy water content

Water is typically the most abundant substance by mass in healthy leaves and its effects on leaf optical properties are

substantial. The influence of leaf water on reflectance includes both direct effects, those caused by the absorption properties of water itself, and indirect effects, those associated with other leaf properties that change with hydration and water stress. As with water absorption in the atmosphere, the direct effects of liquid water in foliage include distinct features at 1450 and 1950 nm, with weaker features at 980 and 1150 nm. The more general rotation-vibration features of water molecules cause additional absorption beginning at *c.* 1400 nm and increasing at longer wavelengths. This causes the characteristic pattern of declining reflectance at wavelengths beyond the maximum values in the NIR plateau (Fig. 1b).

The consistency of direct water absorption features has enabled them to be included in leaf optical models (e.g. Jacquemoud *et al.*, 2000) and has led to the development of simple band ratio indices for characterizing plant water via remote sensing (e.g. the normalized difference water index (NDWI; Gao, 1996) and the plant water index (WI; Peñuelas *et al.*, 1997)). Importantly, field and laboratory measurements of leaf water are often expressed in relative terms as a fraction of leaf weight, whereas leaf- and canopy-level reflectance spectra are influenced by the total amount of water present. To address this problem, several investigators have related spectral indices to estimates of equivalent water thickness (EWT), which can be expressed in units of mass or depth for whole canopies as well as individual leaves (Gao & Goetz, 1995; Ceccato *et al.*, 2001).

Although direct effects of water content on plant spectra are reasonably straightforward, the situation is complicated by indirect effects and plant structural properties that covary with water status. Many, if not most, aspects of plant function are related in some way to changes in water content. As an illustration, Zygielbaum *et al.* (2009) collected leaf spectra from maize (*Zea mays*) plants over a 7-d period during which water stress was induced by withholding water. Relative to a well-watered control group, leaves experiencing water deficits exhibited the expected response of increased reflectance in the mid-infrared (beyond 1400 nm; Section IV.2, Fig. 5). However, similar increases were also observed in the visible and NIR regions, resulting in an overall increase in reflectance across the full range of 400–2400 nm. The response in the visible may be attributed to stress-induced declines in leaf pigments, but the response in the NIR, which lacks strong absorbers of any kind, suggests an indirect effect of drying via changes in leaf structure and scattering. In other cases, variation in EWT has been shown to result from differences in leaf area, leaf density and dry matter content (Serrano *et al.*, 2000; Ceccato *et al.*, 2001). Because these variables can affect reflectance in similar spectral regions, attempts to derive more refined water indices have used radiative transfer models capable of assessing structural properties that covary with, but are not a direct result of, changes in EWT (e.g. Ceccato *et al.*, 2002a,b).

2. Leaf pigments

Leaf pigments, including chlorophyll *a* and *b* (Chl*a* and *b*), carotenoids, anthocyanins and a variety of accessory pigments, have perhaps the most apparent and well-studied effects on leaf optical properties, given their roles in the light-harvesting reactions of photosynthesis and in various aspects of stress avoidance (Govindjee, 2002). The fact that pigments are strong absorbers in the visible region and are abundant in healthy vegetation causes plant reflectance spectra to be generally low and less variable in the visible relative to NIR wavelengths (e.g. Asner *et al.*, 1998; Fig. 1b). Chlorophyll, the major light-harvesting compound in plants, absorbs strongly in the red (650–700 nm) and blue (400–500 nm) regions (Fig. 2), although absorp-

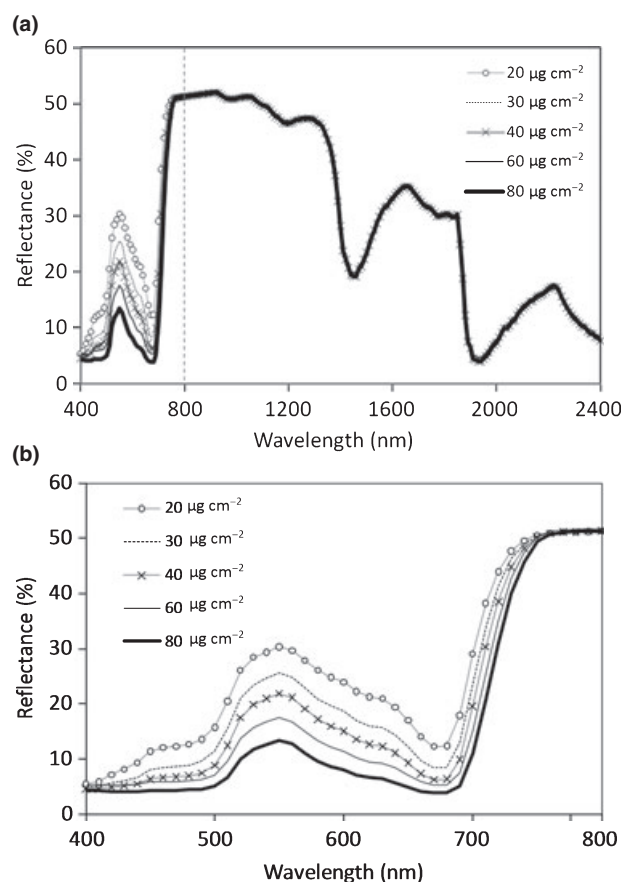


Fig. 2 (a) Reflectance spectra for a range of chlorophyll concentrations simulated with the PROSPECT (Jacquemoud & Baret, 1990) model. Because chlorophyll is a strong absorber in the visible but not in the near-infrared (NIR) region, the model assumes no effect of changes in chlorophyll on the NIR portion of the spectrum. Other model parameters were set using values typical for a deciduous leaf (dry matter = 0.01 g cm⁻², equivalent water thickness (EWT) = 0.012 cm; *N* = 2). (b) Expanded view of the visible region from (a) showing chlorophyll absorption patterns in the blue (c. 400–500 nm) and red (c. 650–700 nm) wavelengths.

tion in the blue by carotenoids often prevents this region from being useful in chlorophyll estimation. Carotenoids, which include the carotenes and xanthophylls, absorb primarily in the blue. Carotenoids play a number of roles in plants, including light harvesting for photosynthesis and, in the case of xanthophylls, dissipating energy to avoid damage by excess light (Demmig-Adams & Adams, 1996). Anthocyanins, often referred to as the ‘stress pigments’, occur in the cytoplasm (rather than in chloroplasts) and are believed to provide protection from stressors such as temperature, excess light, UV radiation and the presence of strong oxidants (Chalker-Scott, 1999; but also see Gould & Quinn, 1999). Anthocyanins absorb in similar wavelengths as chlorophyll, albeit with weaker features in the yellow and red, giving many leaves their autumn colors during senescence (e.g. Feild *et al.*, 2001).

Because of their strong absorbance properties and important physiological roles, considerable effort has been put into estimating pigment concentrations from leaf and canopy reflectance. These include methods using laboratory- and field-based spectrometers (e.g. Sims & Gamon, 2002; Gitelson *et al.*, 2006, 2009) as well as aircraft- and space-based imaging spectrometers (Ustin *et al.*, 2009). The majority of studies have focused on chlorophyll estimation, because of the dominant role of chlorophyll in light harvesting and because spectral overlap makes estimation of other pigments challenging. Nevertheless, methods to characterize carotenoids and anthocyanins have also been explored (Gamon *et al.*, 1990; Gitelson *et al.*, 2006, 2009). Detection of xanthophylls is of particular interest because of their role in dissipation of excess energy during times of stress. The ability to track changes in xanthophyll concentrations through time has given rise to new methods for monitoring changes in photosynthesis and instantaneous light use efficiency (e.g. Gamon *et al.*, 1992, 1997; PRI in Table 1).

Collectively, investigations into pigment reflectance properties have produced a wide variety of spectral detection indices (Table 1), most of which involve some combination of narrow bandwidths in the visible portion of the spectrum. Interestingly, some indices used for chlorophyll detection also make use of reflectance at wavelengths of 800 nm or greater, where the direct effect of pigments is negligible. These include the normalized difference vegetation index (NDVI) and the ratio vegetation index (RVI). Their relationship with chlorophyll concentrations carries the implication that pigment concentrations covary with structural leaf tissue attributes that drive scattering and reflectance in this region. Although progress in understanding pigment effects on plant spectral properties has been substantial, limitations of our present knowledge are highlighted by the wide variety and lack of uniformity of reflectance indices used to estimate pigment concentrations (Table 1).

Table 1 Examples of spectral vegetation indices and their applications

Index	Equation	Application	References
Carter & Miller stress (CMS); Carter stress (CSc and CSd)	$\frac{R_{694}}{R_{760}} \cdot \frac{R_{605}}{R_{760}} \cdot \frac{R_{710}}{R_{760}}$	Chl content	Carter & Miller (1994); Carter (1994)
Datts index (DattsCI)	$\frac{R_{850} - R_{710}}{R_{850} - R_{680}}$	Chl content	Datt (1999)
Difference vegetation index (DVI)	$R_{810} - [(R_{610} + R_{661})/2]$	Canopy Chl density	Broge & Leblanc (2001)
Enhanced vegetation index (EVI) ¹	$\frac{G(RNIR - Rred)}{RNIR + C_1(Rred) - C_2(Rblue) + L}$	Photosynthetic activity	Huete <i>et al.</i> (2002)
Gitelson & Merzlyak chlorophyll index (GM)	$\frac{R_{750}}{R_{700}}$	Chl content	Gitelson & Merzlyak (1994)
Green normalized difference vegetation index (GNDVI)	$\frac{R_{810} - [(R_{510} \pm R_{561})/2]}{R_{810} + [(R_{510} \pm R_{561})/2]}$	Chl content	Gitelson & Merzlyak (1997)
Modified red edge ratio (mSR)	$\frac{R_{750} - R_{445}}{R_{705} + R_{445}}$	Chl content	Sims & Gamon (2002)
Normalized difference vegetation index (NDVI)	$\frac{R_{800} - R_{680}}{R_{800} + R_{680}}$	Chl content and energy absorption	Gamon <i>et al.</i> (1997); Gamon & Surfus (1999)
Normalized difference water index (NDWI)	$\frac{R_{860} - R_{1240}}{R_{860} + R_{1240}}$	Liquid water content of vegetation canopies	Gao (1996)
Photochemical reflectance index (PRI)	$\frac{R_{531} - R_{570}}{R_{531} + R_{570}}$	Carotenoids; xanthophyll cycle	Gamon <i>et al.</i> (1992), (1997)
Pigment-specific normalized difference (PSND)	$\frac{R_{800} - R_{675}}{R_{800} + R_{675}} \cdot \frac{R_{800} - R_{650}}{R_{800} + R_{650}}$	Chla and Chlb content	Blackburn (1998)
Pigment-specific simple ratio (PSSRa, PSSRb and PSSRc)	$\frac{R_{800}}{R_{675}} \cdot \frac{R_{800}}{R_{650}} \cdot \frac{R_{800}}{R_{470}}$	Chla and Chlb content; carotenoids	Blackburn (1998), (1999); Sims & Gamon (2002)
Plant senescence reflectance index (PSRI)	$\frac{R_{680} - R_{500}}{R_{750}}$	Carotenoids; Chl content	Merzlyak <i>et al.</i> (1999); Sims & Gamon (2002)
Ratio analysis of reflectance spectra (RARS _a , RARS _b and RARS _c)	$\frac{R_{675}}{R_{700}} \cdot \frac{R_{675}}{R_{650}} \cdot \frac{R_{760}}{R_{500}}$	Chla and Chlb content; carotenoids	Chappelle <i>et al.</i> (1992); Blackburn (1999)
Ratio vegetation index (RVI)	$\frac{R_{800}}{R_{680}}$	Chl content	Pearson & Miller (1972); Broge & Leblanc (2001); Sims & Gamon (2002)
Red edge NDVI (rNDVI)	$\frac{R_{750} - R_{705}}{R_{750} + R_{705}}$	Chl content	Gitelson & Merzlyak, (1994), Sims & Gamon (2002)
Red/Green Index (RGI)	$\frac{\sum_{i=600}^{700} R_i}{\sum_{i=500}^{600} R_i}$	Anthocyanin	Gamon & Surfus (1999); Sims & Gamon (2002)
Second soil-adjusted vegetation index (SAVI2) ²	$\frac{RNIR}{Rred + (a/b)}$	Canopy Chl density	Broge & Leblanc (2001)
Structure-insensitive pigment index (SIPI)	$\frac{R_{800} - R_{445}}{R_{800} - R_{680}}$	Carotenoids; Chl	Peñuelas <i>et al.</i> (1995); Sims & Gamon (2002)
Water index	$\frac{R_{900}}{R_{970}}$	Canopy water content	Peñuelas <i>et al.</i> (1997)

R, reflectance.

¹EVI variables: *G*, gain factor; *L*, canopy background adjustment factor; *C*_{1,2}, aerosol influence coefficients.

²*a* and *b* in SAVI2 are soil line coefficients (e.g. *a* = 1 and *b* = 0 for bare soil).

Wavelength numbers are in nanometers.

3. Leaf N and nonpigment biochemical constituents

Nonpigment leaf constituents – including N, proteins, lignin and cellulose – influence leaf spectral properties directly through their individual absorption properties, and indirectly through their relationship with leaf structural and biochemical attributes that affect scattering and reflectance. Whereas pigments are the dominant absorbers in the 400–700 nm range, most absorption features caused by nonpigment compounds occur at longer wavelengths and are generally weak, resulting from vibrations and bond stretches of various carbon (C), N, hydrogen and oxygen bonds (e.g. Curran, 1989; Smith *et al.*, 2003; Kokaly *et al.*, 2009).

These features are easiest to discern using dry foliage in laboratory studies (e.g. Kokaly & Clark, 1999), which benefit from the controlled environment and precision of laboratory instruments, and from the absence of water absorption, which can overshadow biochemical absorption features at wavelengths beyond 1400 nm (Kumar *et al.*, 2001).

Despite these challenges, efforts to investigate leaf biochemistry using remote instruments began with the advent of aircraft imaging spectrometers (e.g. Wessman *et al.*, 1988) and have progressed steadily with sensors that have improved spectral and radiometric characteristics (e.g. Matson *et al.*, 1994; Smith *et al.*, 2003; Martin *et al.*, 2008). Particular interest has focused on estimating foliar N

concentrations, given the role of N as a nutrient and the useful information it can convey about a variety of ecosystem processes. Recent efforts have involved characterization of N transformations in soils (e.g. Ollinger *et al.*, 2002), invasion of nonnative tree species (Asner & Vitousek, 2005), forest response to atmospheric N deposition (McNeil *et al.*, 2007) and patterns of productivity and C assimilation (Smith *et al.*, 2002; Ollinger *et al.*, 2008).

Although N itself is a relatively small component of leaf mass, most of the N in leaves is associated with pigments and proteins involved in photosynthesis. The most notable N-containing leaf constituent is Rubisco, which can contain up to 50% of the N in leaves (Elvidge, 1990) and is considered to be the most abundant protein on Earth. Nevertheless, there is still uncertainty surrounding the effects of N on leaf spectra and the degree to which N detection using imaging spectroscopy has been based on direct effects of N-containing compounds or the indirect effect of related leaf traits. Although spectral patterns associated with N-H stretch or C-H stretch features in proteins are often cited as key drivers of the correlation between reflectance spectra and measured N concentrations, some of these features are located in areas that are sensitive to water and leaf or canopy structure. As an example, the most heavily weighted bands in the foliar N calibration by Smith *et al.* (2003) are located either on the shoulders of mid-infrared water absorption features or in the regions of the NIR plateau and red edge inflection point. These latter features are sensitive to structural properties that influence scattering, as will be discussed in the following subsection 'Vegetation architecture'. Similarly, Ollinger *et al.* (2008) found a strong correlation between canopy N concentration (%N) and reflectance across broad portions of the NIR plateau (800–1400 nm) when summarizing a large data set from temperate and boreal forests of North America. This trend was strong enough to dominate overall patterns of shortwave canopy albedo and was probably the result of covariation between %N and some structural trait that influences overall patterns of scattering and reflectance.

Given the interdependence between N, water and leaf structure in regulating various aspects of C assimilation and plant energy regulation, confounding effects that will influence the interpretation of reflectance spectra are to be expected. In many cases, the resulting N detection methods can still be reliable to the extent that these relationships hold up across the conditions for which they are applied. Nevertheless, efforts to tease apart the specific drivers of individual features are needed if existing capabilities are to grow beyond mapping current conditions to modeling and prediction under future scenarios of change.

4. Vegetation architecture

The influence of plant biochemical compounds involves direct effects on light absorption, as well as indirect effects

of associated structural features that affect scattering. Here, plant structural features are explored in greater detail. Although the physical processes that cause scattering are less wavelength-dependent than the processes that cause absorption, the spectral signature of scattering is not manifested uniformly. This is because of the selective effects of absorbers, which determine which wavelengths of scattered radiation can exit the leaf. Because the two dominant absorbers in plants are pigments, which absorb in the visible, and water, which absorbs primarily in the mid infrared (> 1400 nm), the NIR (*c.* 750–1400 nm) represents the region in which leaves are the most optically transparent. As a result, the NIR region is dominated by high reflectance and is influenced by structural properties at the leaf, stem and canopy scales.

Leaf structure Given the large number of cells and cell wall surfaces in leaves (Fig. 3), leaf structural characteristics play an important role in scattering light, and their effects have been studied intensively. Leaf reflectance includes both specular and diffuse components, both of which are influenced primarily by internal leaf surfaces. Cuticular leaf waxes are nearly transparent to visible and infrared radiation, so relatively little incident light is reflected directly from a leaf surface (Knipling, 1970). Leaf reflectance is thus primarily a function of multiple scattering within leaf mesophyll tissues (Baranoski & Rokne, 1997; Slaton *et al.*, 2001), which is influenced by the arrangement of cells within the mesophyll.

Palisade cells (Fig. 3a), for example, can be described as 'light pipes' that help direct light to the interior of cells, ensuring chlorophyll absorption for photosynthesis (Gausman *et al.*, 1969; Vogelmann & Martin, 1993; Knapp & Carter, 1998). Based on this alone, leaves with a higher proportion of spongy mesophyll to palisade mesophyll cells might be expected to scatter more light, resulting in higher NIR reflectivity. However, because NIR absorption by leaf tissues is negligible, this light-channeling function may be limited to visible wavelengths. Further, studies that have examined scattering properties at this scale have determined that the ratio of mesophyll cell surface to intercellular air spaces appears to be the more dominant driver of NIR reflectance (e.g. Knipling, 1970; Woolley, 1971; Nobel *et al.*, 1975; Slaton *et al.*, 2001; Castro & Sanchez-Azofeifa, 2008).

Leaf thickness, geometry and orientation have also been shown to influence leaf reflectance (Knapp & Carter, 1998; Ourcival *et al.*, 1999; Moorthy *et al.*, 2008). For instance, light incident on flat leaves with a thin epidermal layer and long palisade cells generally reflect more NIR light than short, cylindrical needles with thick cell walls and undifferentiated mesophyll (Vogelmann & Martin, 1993; Knapp & Carter, 1998; Johnson *et al.*, 2005). Additional factors such as leaf physiognomy (e.g. bifacial vs unifacial leaves) and orientation can offset or accentuate these differences. For

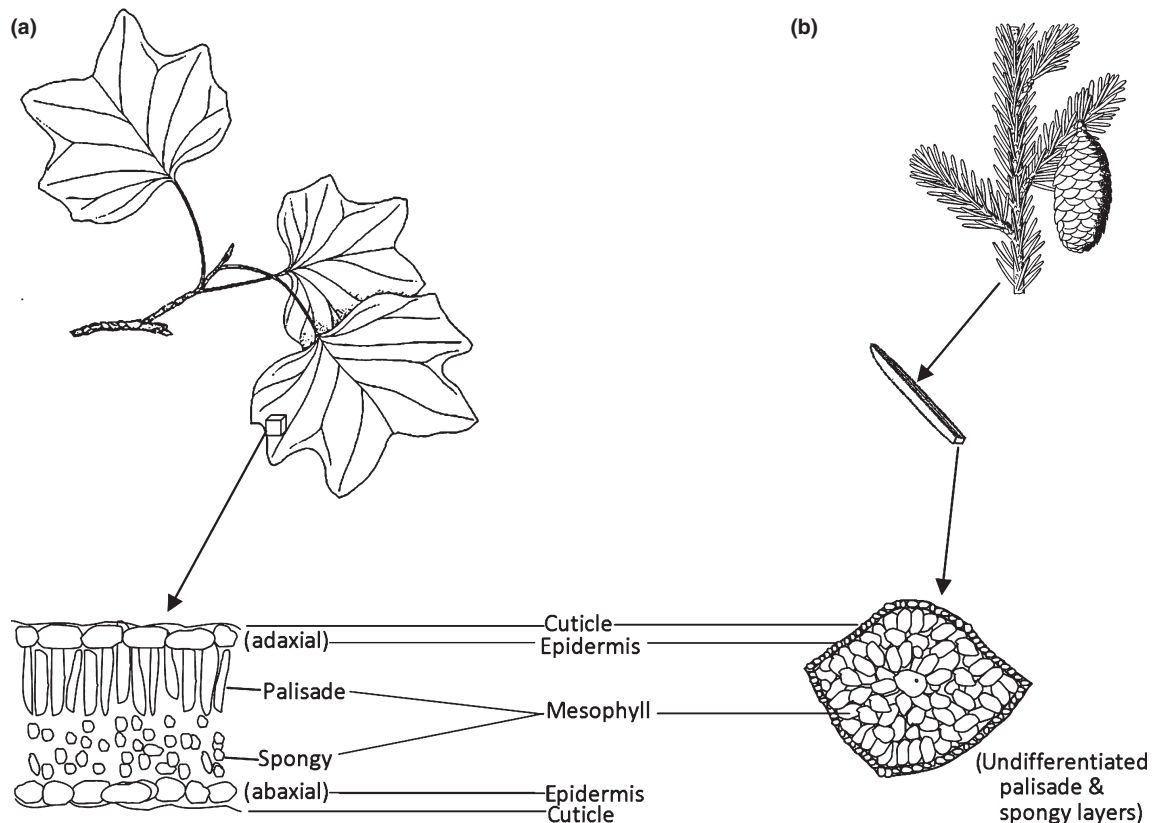


Fig. 3 Schematic representation of leaves with laminar (a) and needle (b) structure and their general cell arrangements. The leaf depicted in (a) is the broadleaf *Liriodendron tulipifera* L. (USDA Natural Resources Conservation Service (NRCS), 2010), although the cross-section shows an internal structure typical of many broadleaf deciduous species. The needleleaf example in (b), *Picea rubens* Sarg. (USDA Natural Resources Conservation Service (NRCS), 2010), displays a more tightly packed cell structure, with undifferentiated palisade and spongy mesophyll layers.

example, the top or face of a bifacial leaf (the adaxial leaf surface) generally has higher NIR reflectance than the back of a leaf (abaxial surface; Woolley, 1971; Hoque & Remus, 1996; Baranoski, 2006). Transmittance, in contrast, is greater across the entire infrared region (*c.* 750–2400 nm) when abaxial, as opposed to adaxial, surfaces are facing the light source (Woolley, 1971; Hoque & Remus, 1996; Baranoski, 2006).

Stem characteristics In addition to structural properties of individual leaves, the number, shape and arrangement of leaves growing along a stem also influence scattering (e.g. Niinemets *et al.*, 2002; Niinemets & Fleck, 2002; Walcroft *et al.*, 2005). The spatial distribution of foliage along a stem describes foliage aggregation, or clumping. Clumping indices have become common for describing the degree of aggregation of foliage (e.g. Chen & Black, 1992). Clumping estimates are based on the size and distribution of gaps in foliage; in forests, this applies both within a shoot and along a stem (Chen & Cihlar, 1995a,b; Chen, 1996). Clumping indices generally range from 0 to 1, and decrease with increasing clumping – the smaller the clumping factor, the more clumped the canopy (Chen, 1996).

The effects of clumped foliage on light scattering are complex, and can vary with light conditions, leaf angle and leaf shape. For example, needles clustered within an evergreen shoot produce self-shading, and tend to reflect less. However, the angular distribution of needles around the stem can affect the level of self-shading – for example, needles at the top of evergreen canopies tend to be more spherically oriented around in order to intercept light from more angles (Cescatti & Zorer, 2003). Regardless, high levels of foliage clumping generally correspond to large numbers of gaps in canopy surfaces, resulting in deeper light penetration and less light interception by foliage. This has been observed in both needleleaf and broadleaf plants (Balocchi & Hutchison, 1986; Niinemets & Fleck, 2002; Niinemets *et al.*, 2004; Walcroft *et al.*, 2005), although the effect of clumping has been considered more important in needleleaf plants (Niinemets *et al.*, 2004).

NIR reflectance is generally lower for conifer crowns than broadleaf crowns, a pattern that has been at least partly explained by the recollision property. The recollision property is the probability that a photon scattered from a leaf in a canopy will interact within the canopy again, increasing its chances of being absorbed (Smolander & Stenberg,

2005). While this property describes much of the within-shoot scattering in conifers, it cannot account for all the variation in NIR reflectance between broadleaf and conifer species. Differences in the direction of scattering, as well as in absorption properties of needles, leaves and woody material have been suggested as additional sources of variation in NIR reflectance between these functional types (Smolander & Stenberg, 2003; Rautiainen & Stenberg, 2005).

Canopy structure Whole-canopy structure can affect patterns of scattering and absorption by, for example, influencing the depth at which photons first encounter foliage and the probability that they will interact with additional leaves after these initial interactions. One of the most widely used descriptors of canopy structure is leaf area index (LAI), which is defined as the ratio of total leaf area to ground area. Although LAI is important to understanding the overall nature of canopies, it aggregates elements of crown shape, canopy density, clumping, gaps and fractional vegetation cover. As a result, LAI alone cannot fully describe the effects of canopy structure on reflectance. Indeed, canopies with similar LAI often have significantly different NIR reflectance, attributed to variation in a multitude of components (e.g. Nagler *et al.*, 2004; Rautiainen *et al.*, 2004; Smolander & Stenberg, 2005).

The effect of whole-canopy structure on reflectance can be partitioned into factors that describe the inner crown structure and those that describe the outer canopy surface (Rautiainen *et al.*, 2008). Shoot and branching architecture influences the inner crown structure, and includes factors such as the heights at which leaves and branches are attached to stems, as well as their lengths, distribution, frequency and angles of inclination or orientation (Niinemets & Lukjanova, 2003; Rautiainen *et al.*, 2008). Leaf orientation in a canopy is characterized through an estimate of leaf angle distribution (LAD). LAD incorporates the gradient between vertically and horizontally inclined leaves within canopies (e.g. King, 1997; Alton & North, 2007; Posada *et al.*, 2009) and can describe the general shape of the crown. Crown shape, together with canopy volume, density and gap fraction, influence the reflectance of the outer canopy surface (Hall *et al.*, 1995; Rautiainen *et al.*, 2004).

In principle, the effects of outer canopy structure on light absorption and scattering are similar to the effects of leaf and stem structure *inside* a crown, generalized over a larger spatial scale. As an example, the directional distribution of photon scattering within a crown has been described by the recollision probability. An implication of this theory is that multiple scattering within the crown allows for a higher probability of photon absorption, and hence lower reflectance (Smolander & Stenberg, 2003; Rautiainen & Stenberg, 2005; Smolander & Stenberg, 2005). Further, scattering of photons within the crown is largely dependent on the orientation of leaves (Ganapol *et al.*, 1999), where

large leaf inclinations (i.e. vertically oriented leaves) permit deeper penetration of light within the canopy (Ellsworth & Reich, 1993). A similar phenomenon has been described for the outer canopy surface of an old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) stand: vertically elongated spaces between dominant trees permit deep penetration of incident radiation, and subsequent scattering and absorption within these spaces have the effect of reducing whole-canopy reflectance (Parker *et al.*, 2004).

Individual components of outer canopy structure such as crown volume, density and shape have also been examined relative to canopy reflectance. For instance, Rautiainen *et al.* (2004) observed that coniferous canopies with the same LAI had lower overall reflectance if their crowns were more conical than ellipsoidal in shape. Additionally, they found that, in stands with smaller canopy closure and lower LAI, scattering appeared to be dominated by reflectance from materials on the ground, whereas in dense stands with high canopy closure and high LAI, scattering from tree crowns was dominated by crown shape (Rautiainen *et al.*, 2004).

These observations suggest the relative importance of individual components of canopy structure on whole-canopy reflectance. Yet some of these components remain challenging to characterize. Leaf orientation, for example, is measured either with a protractor or clinometer, or estimated from photography (Jacquemoud *et al.*, 1995; Close & Beadle, 2006). Because accurate measurements of leaf orientation for whole canopies are challenging and, therefore, rare, canopy LAD is generally set to one of several aggregated functional groups (e.g. spherical, planophile, erectophile or plagiophile; Ganapol *et al.*, 1999) or estimated as a mean leaf inclination angle (Jacquemoud *et al.*, 1995). This has implications for the prediction accuracy of canopy reflectance models, which are typically very sensitive to variation in LAD inputs (e.g. Asner, 1998; Fig. 5). Quantifying errors associated with LAD assumptions is difficult because few studies have the field measurements necessary to accomplish this or to evaluate LAD variation within functional groups. Recent developments in LAD measurement using narrow-beam terrestrial laser scanners (Eitel *et al.*, 2010) could substantially improve this situation.

IV. The combined effects of multiple traits on whole-canopy reflectance

The preceding section considered individual sources of variability in vegetation reflectance, including leaf water content, biochemical constituents and various components of plant structure. In each case, the role of a given factor is governed by physical and biological processes that influence scattering and absorption of light at different wavelengths. At the scale of whole canopies, reflectance patterns represent the integrated effects of all of the above (e.g. Roberts *et al.*, 2004),

often influenced by multiple species and functional groups. Because this is the scale at which most aircraft and satellite remote sensing instrument observations are made, interpreting the data they provide can be challenging.

To date, most of the effort toward interpreting whole-canopy reflectance patterns has involved empirical methods that relate observed reflectance to measured vegetation characteristics or models of plant–light interactions that can be solved or manipulated in a way that helps interpretation of reflectance measurements. While these approaches can be effective under many circumstances, they also have important limitations, especially where various combinations of individual plant properties can yield similar whole-canopy spectra or where multiple spectrally important plant traits covary and cannot be separated statistically.

1. Vegetation indices and other empirical methods

Relationships between plant traits and canopy reflectance features have been derived through the use of multiple regression and other least-squares statistical methods (e.g. Wessman *et al.*, 1988; Martin *et al.*, 2008) and, more commonly, spectral vegetation indices (e.g. Chappelle *et al.*, 1992; Lichtenthaler *et al.*, 1996). Indices from broad-band platforms such as MODIS and Landsat have been widely used for estimating vegetation density and activity at regional to global scales (e.g. Huete *et al.*, 2002; Freitas *et al.*, 2005; Di Bella *et al.*, 2009). However, relative to the number of plant traits they have been used to predict, the number of spectral features in most commonly used reflectance indices is small. As an example, the widely used normalized difference vegetation index (NDVI; Table 1) uses reflectance in just two spectral bands, but has been related to a much larger number of vegetation properties. At the time of writing, an ISI search on 'NDVI' and 'vegetation' yielded > 2500 publications when restricted to journals of ecology, remote sensing and plant science. Among these articles, variation in NDVI has been related to properties such as LAI (e.g. Thenkabail *et al.*, 2000; Houborg & Boegh, 2008), chlorophyll (e.g. Reddy *et al.*, 2001), N stress (e.g. Peñuelas *et al.*, 1994), foliar biomass (e.g. Freitas *et al.*, 2005; Mirik *et al.*, 2005; González-Alonso *et al.*, 2006), fractional vegetation cover (e.g. Rundquist, 2002; Nagler *et al.*, 2004), foliar water potential (e.g. Stimson *et al.*, 2005), and plant primary production (e.g. Tucker & Sellers, 1986; Burke *et al.*, 1991; Paruelo *et al.*, 1997), to name just a few.

That so many vegetation traits have been estimated using such a small number of spectral features presents a conundrum. Either the underlying drivers of reflectance patterns vary across the ecosystems included in various studies, or, more likely, a series of interrelated factors have a collective influence on reflectance, possibly with the degree of importance for each varying across systems. This not a criticism, but it does highlight the need for further progress in identi-

fying specific underlying drivers and for remote sensing instruments that can provide more detailed information about canopy structure and reflectance.

It is also interesting that variation in vegetation indices involving visible and NIR radiation are often driven to a greater extent by variation in NIR reflectance than by variation in visible reflectance. As an illustration, data from Ollinger *et al.* (2008) allow comparison of canopy N in temperate and boreal forests with NIR reflectance, and three commonly used indices: NDVI, RVI and the difference vegetation index (DVI) (Table 1). Across the study sites, reflectance in the NIR was more variable and more strongly related to canopy %N than reflectance in the visible. In fact, canopy %N was more tightly correlated with NIR reflectance on its own than with most of the two-band indices. The contribution of reflectance in the visible was small and, in most cases, added noise to an otherwise strong trend (Fig. 4). Results such as this present another interesting paradox: that the physiological activity of vegetation is often more strongly related to reflectance at wavelengths that are not used in photosynthesis than to those that are. This is, in part, a result of the effectiveness of multi-layered canopies at absorbing visible light, which causes reflectance in this region to be lower and less variable compared with reflectance over other portions of the spectrum. By contrast, scattering and reflectance in the NIR region vary considerably and are driven by factors that appear to covary with plant traits such as photosynthetic capacity, light use efficiency and foliar %N (Green *et al.*, 2002; Kergoat *et al.*, 2008; Ollinger *et al.*, 2008). The nature and potential causes of these associations have only been partially explored and are discussed further in Section V below.

2. Modeling plant–light interactions

Leaf and canopy reflectance models can generally be grouped into two broad classes—descriptive models and physically based models (Asner & Wessman, 1997; Kumar *et al.*, 2001). Descriptive models explain absorption and extinction of light, and include stochastic and ray tracing models, which trace paths of photons through a leaf or canopy to determine patterns of scattering (e.g. Govaerts *et al.*, 1996; Baranoski & Rokne, 1997; Rochdi *et al.*, 2006; Schlerf & Atzberger, 2006; Alton & North, 2007). Physically based models account for absorption and scattering processes based on sensitivities to leaf and/or canopy geometry and biochemistry and thus describe leaves and canopies in terms of their composition, arrangement, geometry, density, and shape (Jacquemoud & Baret, 1990; Li & Strahler, 1992; Dawson *et al.*, 1998; Ganapol *et al.*, 1998). In practice, many models represent a hybridization of these approaches, and all of them incorporate some aspect of radiative transfer theory (Chandrasekhar, 1960).

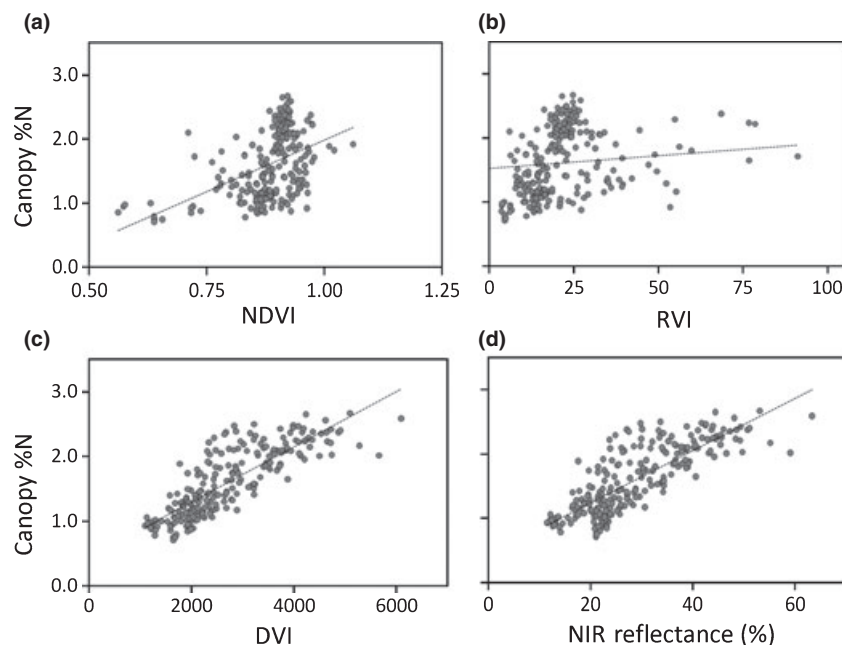


Fig. 4 Relationships between spectral vegetation indices and canopy nitrogen (N) concentration for 232 forested plots from US and Canadian temperate and boreal forests using data from Ollinger *et al.* (2008) and Martin *et al.* (2008). The normalized difference vegetation index (NDVI) (a), ratio vegetation index (RVI) (b) and difference vegetation index (DVI) (c) were calculated by averaging spectra collected by the Airborne Visible/InfraRed Imaging Spectrometer (AVIRIS) in the near-infrared (NIR; c. 840–880 nm) and red (c. 620–670 nm) regions of the spectrum, mimicking the spectral ranges of related bands from MODIS. Only DVI, which represents the difference between reflectance in the NIR and red, correlates with field-measured canopy %N as well as NIR reflectance on its own (d). Vegetation indices were calculated as in Table 1. Regression statistics are as follows: NDVI, $r^2 = 0.21$, $P < 0.0001$, $rmse = 0.46$; RVI, $r^2 = 0.03$, $P = 0.0144$, $rmse = 0.51$; DVI, $r^2 = 0.69$, $P < 0.0001$, $rmse = 0.29$; NIR, $r^2 = 0.64$, $P < 0.0001$, $rmse = 0.30$.

Plant reflectance models are designed and parameterized to capture specific factors that influence light absorption and scattering. Through iterative adjustment of parameters, predictions can be made about their relative effects on patterns of reflectance. Most models can also be calibrated or inverted, in which case reflectance is measured rather than predicted and used to solve for one or more parameters (e.g. Schlerf & Atzberger, 2006; Liang, 2007). Model inversion requires care and involves some means of estimating values for all parameters that are not being retrieved through inversion (Darvishzadeh *et al.*, 2008; Hedley *et al.*, 2009). This can be problematic, given data limitations and the challenges of measuring properties such as leaf angle distribution and intercellular leaf structure. Errors in model structure or prescribed parameter values yield errors in the variables retrieved through inversion. Further, neither forward nor inverse model solutions are necessarily unique (Weiss & Baret, 1999; Darvishzadeh *et al.*, 2008). Different combinations of parameters can produce similar reflectance spectra, confounding an understanding of causal relationships between vegetation characteristics and reflectance.

Fig. 5 illustrates the information obtained from two established radiative transfer models, PROSPECT and SAIL (Verhoef, 1984; Jacquemoud & Baret, 1990; Jacquemoud *et al.*, 2009), which were used to examine the

relative effects of biochemical and structural parameters on visible and NIR reflectance at leaf (PROSPECT) and canopy (SAIL) scales. I conducted a sensitivity analysis using PROSPECT to examine the effects of four parameters that affect leaf-level reflectance: (1) chlorophyll concentration; (2) dry matter content; (3) liquid water content (EWT); and (4) a parameter defining leaf structure (N). The resulting leaf spectra demonstrated the predicted effect of chlorophyll content in the visible portion of the spectra; variability in water content in the mid-infrared portion of the spectrum (> 1400 nm); and variability in dry matter content (e.g. specific leaf weight) and leaf structure, which influence the entire spectrum (Fig. 5a). The model's sensitivity to leaf structure is noteworthy because this parameter is perhaps the most difficult to define and measure. In concept, leaf structure includes variables such as leaf thickness, fraction of intercellular airspace, and epidermal and mesophyll cell dimensions (e.g. Jacquemoud & Baret, 1990; Govaerts *et al.*, 1996; Baranoski & Rokne, 1997; Ganapol *et al.*, 1998, 1999). In the model, these factors are simplified into a single value that serves as an index of the number of air/cell wall interfaces within the mesophyll (Jacquemoud *et al.*, 2009). Although this is conceptually straightforward, it represents a parameterization challenge because there is no easily measured real-world counterpart.

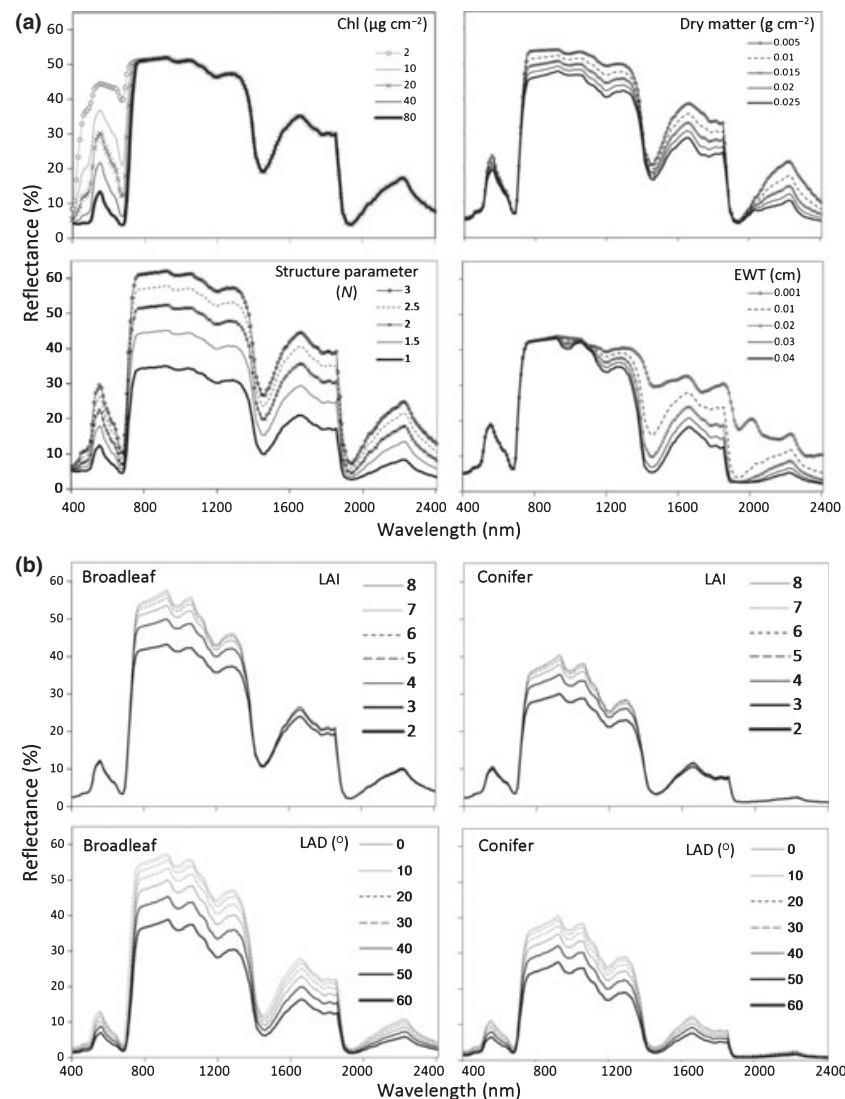


Fig. 5 (a) Leaf reflectance spectra predicted by the PROSPECT model, generated using a range of values for chlorophyll (Chl) concentration, dry matter content, equivalent water thickness (EWT), and the structure parameter N . In each case, parameters not being varied were held constant using typical deciduous broadleaf values (Chl = $40 \mu\text{g cm}^{-2}$; dry matter = 0.01 g cm^{-2} ; EWT = 0.012 cm ; $N = 2$). (b) Variability in canopy-scale reflectance, as estimated by the PROSPECT and SAIL models. Modeled spectra from PROSPECT for a typical deciduous broadleaf (using standard values from Fig. 5a) and a typical evergreen needle (Chl = $20 \mu\text{g cm}^{-2}$; dry matter = 0.02 g cm^{-2} ; EWT = 0.02 cm ; $N = 1$) were used in SAIL to test the effect of varying leaf area index (LAI) and leaf angle distribution (LAD) (values shown are mean leaf angle) on whole-canopy reflectance. For model runs with variable LAI, LAD was held at 20° . Model runs with variable LAD were conducted at LAI = 5. Output from both models was generated using WinSAIL v.1.00.04. USDA, Agricultural Research Service (ARS), Hydrology and Remote Sensing Laboratory, Beltsville, MD, USA.

Spectral variability at the canopy scale was examined with the SAIL model, which was run using leaf-level spectra from PROSPECT representing typical needleleaf evergreen and broadleaf deciduous tree species. For each of these types, the effect of canopy structure was examined by altering values for LAI and LAD. The SAIL model is sensitive to LAI, particularly in the NIR region, although the effect saturates at high LAI values (Fig. 5b). Over the range of values examined, the effect of LAD on NIR reflectance appears to be greater than that of LAI alone, not only in the NIR region,

but across the entire spectrum—for example, canopies with horizontally oriented leaves tend to have higher overall reflectance than those with vertically oriented leaves (Fig. 5b). Because accurate LAD measurements are not generally available this is among the least certain of the canopy modeling parameters (Ganapol *et al.*, 1999).

The challenges of modeling reflectance patterns for complex plant canopies are further evidenced by the difficulty of duplicating field-measured spectra with models. As an example, Coops & Stone (2005) simulated spectral variation

from 400 to 1000 nm in N-deficient *Pinus radiata* needles using the LIBERTY model (Dawson *et al.*, 1998). They identified chlorophyll and moisture content as key parameters to capture the effects of N deficiency. Predicted reflectance varied only in the visible portion of the spectra, consistent with the examples from PROSPECT in Fig. 5. Field-measured spectra, however, showed significant variation in the NIR region as well, where the most N-deficient needles had the lowest NIR reflectance, and the least N-deficient needles had the highest. Although the NIR region is not thought to be affected directly by these variables, they apparently influence, or covary with, other variables that do affect it (e.g. leaf structure, LAD and LAI). Capturing these patterns in models will continue to be a challenge until we gain a clearer understanding of the multiple interdependencies among plant traits.

V. Functional convergence among optically important traits

A challenge to interpreting canopy spectral properties that has emerged throughout this review is the issue of inter-relationships among multiple plant traits that each have an effect on reflectance. That this challenge exists is far from a new idea and, in the ecological and ecophysiological literature, convergence among plant traits has been an active research topic for some time (e.g. Grime, 1977; Mooney & Gulmon, 1979; Wright *et al.*, 2004). All plants must compete for light, water and nutrients, and investments for acquiring any one resource necessarily involve tradeoffs that alter the ability to obtain others. As evolution selects for species that optimize the acquisition and efficient use of all needed resources, nature becomes populated by a limited number of viable combinations of key traits and growth strategies. As an example, different strategies for optimizing leaf-level C gain lead to convergence among traits such as leaf lifespan, leaf mass per unit area (LMA), allocation to defense, N concentrations, photosynthetic capacity and dark respiration, among others (e.g. Mooney & Gulmon, 1979; Reich *et al.*, 1997, 1999; Wright *et al.*, 2004, 2005). Successful combinations of leaf traits also have consequences for canopy and stand properties involving C allocation, wood density, crown geometry, branching architecture, leaf angle distribution and probably others that have yet to be explored.

As should by now be evident, many of the traits subjected to convergence have important effects on how plants absorb, scatter and reflect light. In some cases, this can aid applications of remote sensing in that plant functional types often have distinctive spectral signatures that can be detected using newly available instruments. Ustin & Gamon (2010) even suggest extending the functional type concept to include plant 'optical types' through integration of remote sensing and ecological theory. In other cases, the

ability to tease apart the relative effects of individual traits remains an important goal and a substantial challenge. There are also times when canopy reflectance is itself an important vegetation property, rather than simply providing a method for remotely sensing some other variable. As an example, the relationship between canopy %N and NIR reflectance shown in Fig. 6(a) occurs over a wide enough range of wavelengths and ecosystems to drive an overall trend between %N and shortwave albedo (Ollinger *et al.*, 2008; Hollinger *et al.*, 2010; Fig. 6b). Because vegetation albedo exerts an important influence on climate (e.g. Bonan, 2008), this relationship raises a question of whether factors affecting plant N status also influence climate through altered surface energy exchange. However, because

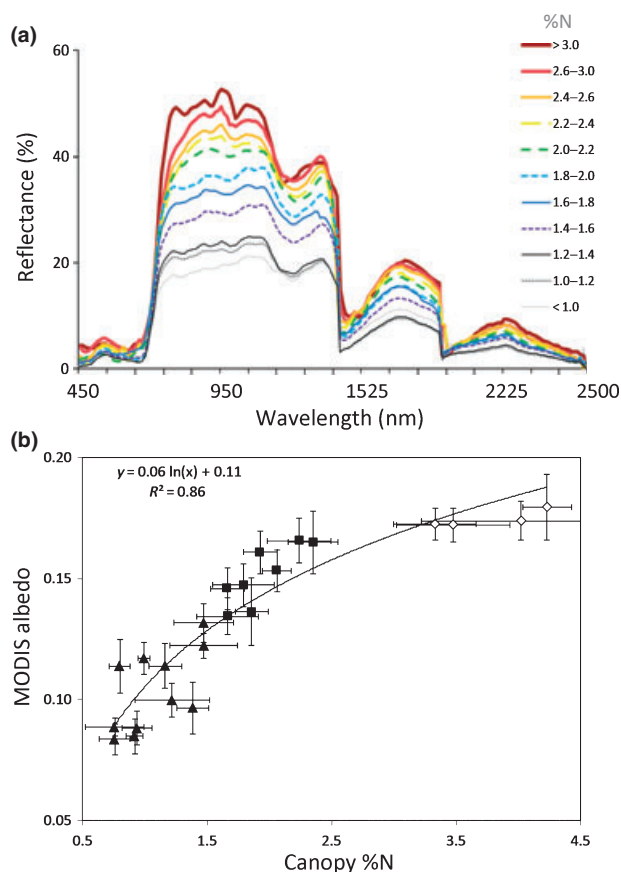


Fig. 6 (a) AVIRIS reflectance spectra from the forested plots in Fig. 4 (Ollinger *et al.*, 2008) plus cropland plots in Hollinger *et al.* (2010) grouped into 11 classes of canopy %N. Variability is most pronounced in the near-infrared (NIR) region, but an increase in reflectance with increasing %N is apparent for most wavelengths above c. 800 nm. This pattern spans a wide enough range of the solar energy spectrum to drive an overall trend between canopy %N and shortwave albedo. This can be seen in (b), which shows canopy %N in relation to growing season albedo from the MODIS instrument (MOD43B; Schaaf *et al.*, 2002) for pixels centered on the eddy flux tower sites examined by Ollinger *et al.* (2008) and Hollinger *et al.* (2010). triangles, forest (evergreen); squares, forest (deciduous); diamonds, cropland.

changes in N availability do not affect all plant traits equally, answering this question requires that specific causal mechanisms be identified. For instance, whereas N-induced changes in leaf-level traits might occur over relatively short time periods, changes in canopy architecture may take years, if they occur at all.

The issues discussed above suggest a need for research on plant trait relationships that emphasize factors affecting reflectance. Multiple lines of evidence suggest that factors such as cellular leaf anatomy, leaf clumping, crown geometry and leaf angle distribution vary predictably with more well-studied variables like photosynthetic capacity and foliar %N, particularly relative to scattering and reflectance in the NIR region. Several such relationships, both established and hypothesized, are shown in Fig. 7. For instance, Hollinger *et al.* (2010) suggested that leaf-level %N should be correlated with anatomical leaf properties that influence scattering. High rates of photosynthesis require both high levels of N-containing enzymes and corresponding changes in leaf anatomy that permit rapid diffusion of CO₂ to the chloroplasts. Among these changes is an increase in the ratio of mesophyll cell surface area exposed to intercellular air spaces per unit leaf area ($A_{mes} : A$; Nobel *et al.*, 1975; Longstreth *et al.*, 1985). Consistent with this idea are results obtained by Slaton *et al.* (2001), who found a strong correlation between NIR leaf reflectance and the $A_{mes} : A$ ratio among a variety of alpine angiosperms. Other related factors such as leaf thickness and leaf density also vary with photosynthetic capacity (Smith *et al.*, 1997) and probably also affect leaf scattering.

Leaf-level associations can influence stem- and canopy-level architecture in ways that accentuate the resulting canopy spectral properties. Leaves adapted to low resource supply (e.g. evergreen needles) tend to have low N concentrations, low rates of CO₂ assimilation and more densely packed cell structures, traits that are both causally and correlatively associated with lower NIR reflectance. Relative to faster growing plants, the limited availability of carbohydrates these leaves produce should limit rates of stem elongation, resulting in leaves that are more densely clustered, or more highly clumped, along the stem. As discussed in Section III, this, too, is a trait that serves to reduce reflectance in the NIR region. Evidence for the association between nutrient availability and leaf clumping was provided by Niinemets *et al.* (2002), who studied Scots pine (*Pinus sylvestris*) growing on sites of varying fertility and found significant inverse relationships between %N and various needle clumping indices, including needle area density and needle number per unit shoot axis length. All of these results suggest stem-level traits that accentuate leaf-level reflectance properties.

Leaf angle is known to play an important role in resource optimization through its effects on light interception, leaf temperature, transpiration and nutrient use efficiency (e.g. Ehleringer & Comstock, 1989; King, 1997; Ackerly,

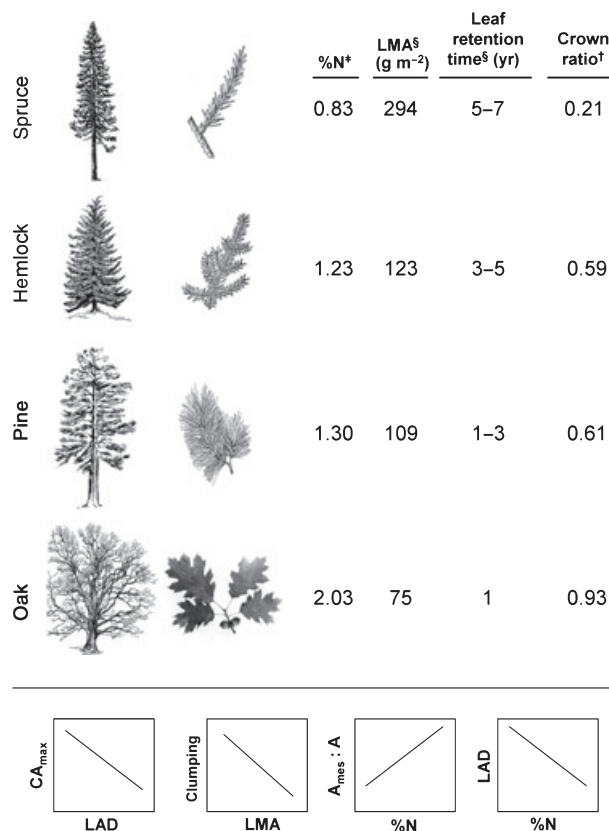


Fig. 7 Examples of convergence among spectrally important plant traits discussed in the text, showing typical values for leaf and canopy traits among several broad groups of tree species. Leaf and tree line drawings are from USDA Natural Resources Conservation Service (NRCS) (2010). Values shown are averages taken from the following sources: [†]NERC foliar chemistry database (2010); [§]Reich *et al.* (1995, 1999); [†]ratio of total crown depth to average crown diameter (Takahashi, 1996; R. A. Hallett, unpublished data). Panels at the bottom show idealized relationships among several other variables that exhibit some degree of convergence and are known to be related to NIR reflectance. Variables are: $A_{mes} : A$, ratio of mesophyll cell surface area exposed to intercellular air spaces per unit leaf area; LMA, leaf mass per unit area; LAD, leaf area distribution (low to high values corresponding to horizontal to vertical foliage, respectively); CA_{max}, canopy photosynthetic capacity; clumping (lower values corresponding to greater foliar clumping along the stem).

1999). It is also widely included in canopy radiative transfer models, which generally predict higher reflectance as leaf orientation shifts from vertical to horizontal (Verhoef, 1984; Asner, 1998; Fig. 5). Yet there have been few attempts to integrate canopy optimization models with models of reflectance, and the degree to which variation in reflectance across native ecosystems is driven by changes in leaf angle distribution is not well understood. This is not surprising, given the difficulties of obtaining accurate LAD measurements and quantified LAD over complex plant canopies. Nevertheless, evidence that does exist indicates pre-

dictable relationships between LAD and other variables included in Fig. 7. A number of studies have observed that optimal use of light within canopies is achieved by varying both leaf angle and leaf N content (e.g. Hollinger, 1996; Posada *et al.*, 2009) and, across species, variation in leaf angle has been related to varying degrees of resource limitation (e.g. King, 1997; Valiente-Banuet *et al.*, 2010). Similarly, N fertilization experiments involving eucalyptus seedlings (*Eucalyptus nitens*; Close & Beadle, 2006), wheat (*Triticum aestivum*; Brooks *et al.*, 2000) and rice (*Oryza sativa* L. Tari *et al.*, 2009) have all demonstrated that leaf angle shifts from more vertical to more horizontal orientation as N nutrition increases.

In addition to leaf- and stem-level traits, plants growing under resource-poor conditions tend to have lower ratios of allocation to wood vs foliage (e.g. Litton *et al.*, 2007), which should constrain lateral branching and crown diameter. Theoretical studies of optimal resource allocation in canopies suggest patterns that are consistent with this and predict that reductions in N supply and other forms of stress should result in narrower, more conical, tree crowns (Cohen & Pastor, 1996). As with the leaf-level effects of stress-adapted species, the effect of this type of crown structure on whole-canopy reflectance is expected to be a decrease in reflectance across the infrared region (Rautiainen *et al.*, 2008).

Collectively, the examples above point toward strong associations among plant traits that affect scattering over scales ranging from cells to canopies. Interestingly, all of the examples discussed suggest a synergy among the effects of individual traits that becomes most apparent in the NIR region; leaf-level traits that produce low NIR reflectance tend to be associated with stem- and canopy-level traits that have a similar influence. This poses a serious challenge for remote detection of specific plant properties, but suggests an emergent property of ecosystems that results from optimization of plant form and function across multiple scales. If so, this puts canopy spectral features among the suite of variables that can be broadly used to define plant function.

VI. Conclusions

In reviewing knowledge about the factors affecting canopy reflectance, several interesting themes have emerged. In attempts to identify specific drivers of reflectance, uncertainties related to scattering presently outweigh uncertainties related to absorbers (pigments, water, etc.). This is perhaps because absorbers influence specific spectral regions and can be measured more easily than structural properties. Factors such as leaf anatomy and leaf angle distribution affect scattering over all wavelengths in ways that are difficult to quantify. This presents a challenge for understanding reflectance in the NIR region, where multiple combinations of interdependent properties can yield similar patterns of reflectance. This does not necessarily restrict our ability to

estimate present-day vegetation attributes, but it does prevent us from predicting changes in reflectance under novel environmental conditions.

Improved understanding of underlying factors affecting canopy reflectance patterns should be aided in the future by several developments in sensor technology and data availability. Planned Earth observation missions such as the HypIRI imaging spectrometer and the DESDynI LiDAR-RaDAR instrument (National Research Council (NRC), 2007) will, for the first time, provide global coverage of vegetation spectral properties and vertical structure. In the USA, the forthcoming National Ecological Observatory Network (NEON) will collect annual aircraft hyperspectral-LiDAR data at higher spatial resolutions for a representative set of ecosystems (Kampe *et al.*, 2010). These efforts will increase by several orders of magnitude the data available to examine vegetation spectral and structural properties over a wide range of ecosystems.

Interpreting data from new aircraft and satellite missions will require complimentary efforts to collect relevant field measurements, especially for structural variables that have historically been difficult to obtain. Here, too, newly available sensors should provide ample opportunities for progress. For example, ground-based LiDAR sensors can provide much greater detail on canopy structural features than can be obtained through conventional methods (e.g. Strahler *et al.*, 2008). Similarly, new approaches for tower-based canopy spectroscopy can provide insights into temporal patterns in reflectance *and* can greatly improve methods for correcting issues of view angle geometry (Hilker *et al.*, 2009).

Finally, realizing the full potential of the above approaches will require an in-depth integration of remote sensing and ecological theory. In the ecological literature, theories of resource optimization have greatly expanded our ability to interpret patterns of plant form and function. Similarly, models that capture the biophysical interactions between plant canopies and incident radiation have advanced our understanding of reflectance. With improved data for model parameterization and validation, integration of these approaches holds enormous potential for future advancements in our understanding of ecosystems.

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