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Review

Review of optical-based remote sensing for plant trait mapping

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A R T I C L E   I N F O

A B S T R A C T

Plant trait data have been used in various studies related to ecosystem functioning, community ecology, and assessment of ecosystem services. Evidences are that plant scientists agree on a set of key plant traits, which are relatively easy to measure and have a stable and strong predictive response to ecosystem functions. However, the field measurements of plant trait data are still limited to small area, to a certain moment in time and to certain number of species only. Therefore, remote sensing (RS) offers potential to complement or even replace field measurements of some plant traits. It offers instantaneous spatially contiguous information, covers larger areas and in case of satellite observations profits from their revisit capacity.

In this review, we first introduce RS concepts of light–vegetation interactions, RS instruments for vegetation studies, RS methods, and scaling between field and RS observations. Further we discuss in detail current achievements and challenges of optical RS for mapping of key plant traits. We concentrate our discussion on three categorical plant traits (plant growth and life forms, flammability properties and photosynthetic pathways and activity) and on five continuous plant traits (plant height, leaf phenology, leaf mass per area, nitrogen and phosphorous concentration or content). We review existing literature to determine the retrieval accuracy of the continuous plant traits. The relative estimation error using RS ranged between 10% and 45% of measured mean value, i.e. around 10% for plant height of tall canopies, 20% for plant height of short canopies, 15% for plant nitrogen, 25% for plant phosphorus content/concentration, and 45% for leaf mass per area estimates.

The potential of RS to map plant traits is particularly high when traits are related to leaf biochemistry, photosynthetic processes and canopy structure. There are also other plant traits, i.e. leaf chlorophyll content, water content and leaf area index, which can be retrieved from optical RS well and can be of importance for plant scientists.

We underline the need that future assessments of ecosystem functioning using RS should require comprehensive and integrated measurements of various plant traits together with leaf and canopy spectral properties. By doing so, the interplay between plant structural, physiological, biochemical, phenological and spectral properties can be better understood.

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1. Introduction

Plant traits are structural, physiological, biochemical or phenological features, e.g. plant height, photosynthesis rate, nitrogen content or leaf phenology, respectively, which are being increasingly used in ecology research (Cornelissen et al., 2003; Kattge et al., 2011). Due to the fact that groups of plants sharing a similar function within an ecosystem also tend to exhibit similar plant traits, plant traits are used to study the response of plants to various environmental pressures (e.g. changes in climate and land use) and the effect of plants on important ecosystem processes (e.g. biogeochemical cycles) (Díaz and Cabido, 1997; Lavorel and Garnier, 2002). Moreover, they have been successfully used in various studies related to ecosystem functioning (Díaz et al., 2004; Orwin et al., 2010; Wright et al., 2004), community ecology (Kraft et al., 2008), plant response to environmental pressures (de Bello et al., 2006; Garnier et al., 2007), plant invasion (Kurokawa et al., 2010; van Kleunen et al., 2010) and assessment of ecosystem services (Lavorel et al., 2011).

Nowadays there are hundreds of plant traits identified and measured by ecologists (Kattge et al., 2011). Plant trait data are measured at the level of individual plants and further upscaled to canopy properties (Violle et al., 2007) and data are often being compiled in various local (Kleyer et al., 2008; Paula et al., 2009) and global (Kattge et al., 2011) databases. Evidences are that plant scientists agree on a set of key plant traits, which are relatively easy to measure and have a stable and strong predictive response to ecosystem functions at various scales (Cornelissen et al., 2003; Díaz et al., 2004; Wright et al., 2004). Although data on key plant traits can be relatively well obtained from field measurements, the field measurements are still limited to small area, to a certain moment in time and to certain number of species only. Therefore, remote sensing (RS) offers potential to complement or even replace field measurements of some plant traits (Kokaly et al., 2009) at larger areas.

Capabilities to retrieve plant traits and canopy properties from optical RS have evolved hand in hand with the technological development of RS spectroradiometers (Milton et al., 2009). Early RS spectroradiometers providing data of coarser spatial and spectral resolutions have supported mainly vegetation classification into broader functional groups (Ustin and Gamon, 2010) and the development of simple vegetation indices (VIs) that were sensitive to broad variations in canopy properties (Cohen and Goward, 2004; Turner et al., 1999). Next generation of medium spectral and spatial resolution spectroradiometers together with development of radiative transfer models (Liang, 2004) have facilitated quantitative estimation of some plant traits (e.g. chlorophyll content, Dash and Curran, 2004 and water content, Cheng et al., 2006) and canopy properties (e.g. leaf area index, Myeni et al., 2002). Development of high spectral resolution imaging spectroradiometers encouraged even more the quantitative estimation of plant traits related to physiology and biochemistry. Plant pigments are the most studied traits (Blackburn, 2007; Ustin et al., 2009) and among them chlorophylls a and b (C_{ab}) have received most attention (Haboudane et al., 2002; le Maire et al., 2004; Malenovský et al., 2013; Schlerf et al., 2010; Zarco-Tejada et al., 2004), whereas carotenoids (Gitelson, 2002; Hernández-Clemente et al., 2012) and anthocyanins (Gitelson et al., 2006) have been studied less. Other biochemical traits retrieved from optical RS data are plant macronutrients (N, P, K, Mg, Ca) (Mutanga et al., 2004; Pimstein et al., 2011) and there is clear dominance of N and P related studies (both traits discussed in details later). Furthermore, leaf water content (Clevers et al., 2010; Colombo et al., 2008), leaf mass per area (discussed in details later), lignin and cellulose (Kokaly et al., 2009) or polyphenols (Skidmore et al., 2010) can be potentially retrieved from optical spectral data too.

Advantages of using RS are its capability to provide spatially contiguous and – for certain observations – high revisit frequency at the typical length scale of the trait processes observed. Moreover, it offers different sampling scheme to trait mapping, determined by combination of pixel size, spatial extent and revisit time of RS observations, than in situ measurements. The major challenge in quantitative RS of plant traits plays the canopy structure. It affects interpretation of canopy reflectance and has negative impact on the retrieval accuracy of biochemical traits (Knyazikhin et al., 2012; le Maire et al., 2008). Therefore approaches accounting for integral effects of canopy structure (Knyazikhin et al., 2012) or measurements of canopy structure itself (van Leeuwen and Nieuwenhuis, 2010) have recently gained more attention.

The potential of RS data for ecological applications is large, however, we see that successful integration of RS observations and ecological applications still requires bridging gaps in the perception of traits importance, scientific terminology (Schaepman-Strub et al., 2006; Violle et al., 2007) and scaling among leaf, plant and canopy levels (Malenovský et al., 2007; Messier et al., 2010). In this review, we want to demonstrate the potential of RS for estimating individual plant traits as defined by ecologists and therefore strengthen links between plant ecology and remote sensing research communities. First, we introduce RS concepts of light–vegetation interactions, RS instruments for vegetation studies, RS methods, and scaling between field and RS observations. Further, we discuss in detail current achievements and challenges when using optical RS to estimate key plant traits. We used Cornelissen et al. (2003) as baseline reference for key traits. These included plant growth and life forms, flammability properties, photosynthetic pathways and activity, plant height, leaf lifespan and phenology, specific leaf area, leaf nitrogen and phosphorous. Regenerative (e.g. seed mass) and belowground (e.g. rooting depth) traits are deliberately excluded, since they cannot be estimated using direct measurements from optical RS. We put emphasis on optical, passive RS, but mention active RS (laser scanning and microwave radar) to trait mapping whenever appropriate.

2. Remote sensing of vegetation

2.1. Light-vegetation interactions

Interactions between incident radiation and canopy elements are extremely complex and are described by three main physical mechanisms: absorption reflection, and transmission. The solar reflected radiation in the optical domain (i.e. between 380 and 2500 nm) is commonly used in vegetation studies, because most of the diagnostic absorption features of green vegetation are located in this part of the spectrum (Kokaly et al., 2009; Ustin et al., 2009). Reflectance of vegetation canopies depends on radiative properties of leaves, other non-photosynthetic canopy elements and their spatial organization. Leaf reflectance spectra are mainly characterized by (i) strong and well described absorption of foliar photosynthetic pigments, dominated by chlorophylls, in the visible region (400–700 nm, VIS), (ii) leaf structure in the near infrared region (700–1300 nm, NIR), and (iii) prevailing water and protein absorptions (as well as other biochemicals) in the shortwave infrared region (1300–2500 nm, SWIR). Mechanisms influencing leaf reflectance are well understood (Kumar et al., 2001), but interpretation of canopy level reflectance remains challenging due to multiple light interactions between canopy elements and background (Disney et al., 2006; Ross, 1981; Widlowski et al., 2004). The key factor influencing canopy reflectance is the canopy structure (Disney et al., 2006; Rautiainen et al., 2004). The most widely used descriptor of a canopy structure in RS studies is leaf area index (LAI) (Fernandes et al., 2004; Turner et al., 1999). LAI alone cannot fully describe the effects of the canopy structure. There are many other leaf level traits (e.g. ratio of mesophyll cell surface to intercellular air spaces, leaf thickness) and canopy properties (e.g. leaves orientation in a canopy characterized by leaf angle distribution, leaves aggregation characterized by clumping index) that strongly influence remotely sensed canopy reflectance. Lack of field measurements and complex interplay among structural leaf traits and canopy properties prevents to decouple their individual effects on RS reflectance data. Furthermore, presence of background and understory components (Eriksson et al., 2006), presence of non-photosynthetic elements (Verrelst et al., 2010), and varying observation geometries (Lobell et al., 2002) also influence canopy reflectance. Therefore RS methods try to minimize these confounding effects (Knyazikhin et al., 2012) and enhance the sensitivity of reflectance data towards a trait or a property of interest (Haboudane et al., 2002; Verstraete and Pinty, 1996). Alternatively, combined retrieval schemes are optimizes to use spectral, spatial and directional domains simultaneously (Laurent et al., 2011b; Schaepman, 2007).

2.2. Remote sensing instruments

Environmental studies can nowadays benefit from a large variety of RS data provided by different passive and active RS systems. We first discuss optical, passive RS systems, because they are being prevailingly used to study vegetation properties. Optical spectroradiometers on satellite-, airborne- and ground-based platforms represent a trade-off among spatial, spectral and temporal resolutions. Spectroradiometers onboard satellite platforms acquire data of regional to global coverage with spatial resolution of tens to hundreds metres and revisit time typically between 2 and 16 days. From the advent of broad-band, multispectral and coarse spatial resolution spectroradiometers (e.g. advanced very high resolution spectroradiometer AVHRR onboard NOAA) in the 1970s and 80s we have moved towards spectroradiometers of increasing resolutions. Currently operational satellite-based spectroradiometers suitable for vegetation monitoring are of moderate spectral and spatial resolutions

(e.g. moderate resolution imaging spectroradiometers MODIS onboard Aqua and Terra, the recently terminated Envisat mission with MERIS, and Enhanced Thematic Mapper ETM+ onboard Landsat). New advanced data for systematic, long-term observation of the Earth systems will be provided from 2013 onwards by the prospective future ESA Sentinel missions (Malenovský et al., 2012).

The major disadvantage of satellite-based multispectral spectroradiometers is that they sample the electromagnetic spectrum only with a few spectral bands. Therefore imaging spectroscopy has emerged to overcome spectral limitations of multispectral systems (Goetz, 2009; Schaepman, 2009). Imaging spectroscopy (often referred as hyperspectral RS) acquire data of unprecedented radiometric quality and high spectral resolution – typically the number of overlapping narrow spectral bands exceeds one hundred, providing therefore almost contiguous spectral information (Schaepman, 2009). Spaceborne imaging spectrometers are still only sparsely available (Hyperion on EO1 and CHRIS on PROBA platforms). Most of the existing imaging spectroradiometers are therefore operated on airborne platforms, which enables acquiring data at a very high spatial resolution (the ground pixel size is usually less than a few metres). A great advantage of airborne RS is high versatility to meet user requirements on target selection, spatial and spectral resolutions, and acquisition date. Additionally, it allows combining imaging spectroradiometers with other type of RS instruments (Asner et al., 2012). One drawback of is reduced multi-temporal feasibility due to costs and logistics.

Mounting an imaging (or non-imaging) spectroradiometer on ground-based constructions (proximal sensing) certainly increases the temporal frequency, which is ideal to study diurnal changes in vegetation activity, but limits the spatial coverage to very small areas or individual plants only (Ač et al., 2009).

Comprehensive overviews of currently operational and future satellite multispectral and airborne imaging spectroradiometers and their specifications are published elsewhere (Ayanu et al., 2012; Grace et al., 2007; Malenovský et al., 2009; Schaepman, 2009).

Other RS systems like multi-directional and active RS systems, which have supported studies of vegetation structue (Widlowski et al., 2004), are introduced only briefly. Multi-directional optical systems (e.g. CHRIS on the PROBA platform) provide observations of the same target from multiple viewing directions over a short timeframe provides. This measurement setup captures the anisotropy of reflected solar radiation in different wavelengths, which conveys information about canopy structure (Chopping, 2008; Widlowski et al., 2004).

Laser scanners (often referred as lidars) emit and record backscattered signal in the optical part of the electromagnetic spectrum (0.01–10 μm) and measure runtime from the instrument to the ground surface and back. There are two types of laser scanners: discrete return systems that record either single or multiple backscatter echoes and full waveform systems that record the entire backscatter signal from a return (Mallet and Bretar, 2009; Wulder et al., 2012). Up to date vegetation structural properties derived from laser scanning include vegetation height (see Section 3.4 for detailed discussion), canopy volume, leaf area index, gap fraction and vegetation profiles (Lefsky, 2002; Lindberg et al., 2012; van Leeuwen and Nieuwenhuis, 2010). Recent development has advanced towards a multispectral full waveform system, which provide additional information on the 3D distribution of plant physiological properties (Hakala et al., 2012).

Imaging synthetic aperture radars (SAR) emit and record backscattered signal at one or more polarizations in the microwave part of the electromagnetic spectrum (cm to multiple m). Their greatest advantage over the optical instruments is of being able to acquire images independently of cloud cover. However, challenges

remain to interpret radar data from very dense or moist canopies, where backscatter signal saturates (Mitchard et al., 2009). The major application domain of radar data is to estimate vegetation height and biomass (partly reviewed by Koch (2010) and Patenaude et al. (2005)). This will be strongly supported by the future ESA radar mission BIOMASS (le Toan et al., 2011).

Studies whereby data from optical spectroradiometers, laser scanners and radar are combined are becoming more common and promising for complex vegetation studies (Asner et al., 2012; Cartus et al., 2012; Hyde et al., 2006; Montesano et al., 2013).

2.3. Remote sensing methods

Plant traits and canopy properties may be assessed qualitatively or quantitatively from RS data. Qualitative methods – classification techniques use a set of decision rules assigning image pixels with similar spectral properties into discrete thematic vegetation classes (Xie et al., 2008). Qualitative methods used to interpret optical RS data can be divided into two broad groups: empirical and physical methods (or combination of both) (Liang, 2004). Empirical methods build on statistical relationships established between limited number of field trait observations and RS data using regression techniques (Ferwerda and Skidmore, 2007; Smith et al., 2002). The sensitivity of RS data towards traits or properties of interests is often enhanced by calculating VIs (Chen et al., 2010; le Maire et al., 2004; Turner et al., 1999) or spectral transformations in case of contiguous hyperspectral data (Schlerf et al., 2010). By nature, empirical methods are computationally fast and effectively summarize local data, but they lack cause-effect relationships. Consequently, predictive statistical relationships often suffer from lack of robustness and transferability as they are usually site, species and time specific (Colombo et al., 2003; Grossman et al., 1996).

Limitations of empirical methods can be partly overcome by using physical RS methods. These methods are based on radiative transfer models (RTMs), which simulate light absorption and scattering inside vegetation canopies accounting for leaf biochemical composition and canopy structural properties (Gastellu-Etchegorry et al., 2004; Jacquemoud et al., 2009; Rautiainen et al., 2010; Verhoef and Bach, 2007). The role of coupled soil-leaf-canopy RTMs (Jacquemoud et al., 2009) in RS is two-fold. First, they help to study the effects of additional perturbing factors (soil background, non-photosynthetic materials and observation geometry) on canopy

reflectance. Second, they enable direct estimation of leaf traits and canopy properties that are directly involved in the radiative transfer by using inversion techniques (Baret and Buis, 2008). Further, when combined with atmospheric RTMs, they hold the promise to estimate many leaf traits and canopy properties simultaneously (Laurent et al., 2011a). Some traits and properties can be estimated with high accuracy and fidelity, e.g. leaf chlorophyll content (Sampson et al., 2003; Zarco-Tejada et al., 2004), leaf water content (Clevers et al., 2008; Colombo et al., 2008) and leaf area index (Myneni et al., 2002; Schlerf et al., 2005). Still, other canopy structural properties (e.g. leaf aggregation, leaf angle distribution) present a substantial challenge for RTMs parameterization and interpretation from RS data (Ollinger, 2011). The major drawback of the physical methods is that different combinations of RTM input parameters may produce the same reflectance spectra, which makes estimation of canopy properties from RS data ambiguous (Baret and Buis, 2008; Combal et al., 2003).

2.4. Scaling and terminology

Spatial scale of in situ measured plant traits and RS data often disagrees. Here we want to demonstrate how to match scaling terminology used in ecology and RS (Fig. 1). An ultimate requirement for RS of plant traits shall be to match the spatial scales of trait with RS data. We exemplify this using a key plant trait – nitrogen (N) and demonstrate simple scaling of field measurements from leaf to canopy level and overlap it with scaling approaches applied to RS data (Table 1). Quantitative traits such as N are usually measured at the level of individual leaves of dominant plant species and expressed either as concentration (mass fraction per unit dry leaf mass) or content (mass fraction per unit leaf area) (here we refer to the terminology introduced by Datt (1998)). Assuming the mass ratio hypothesis (Grime, 1998), the leaf level measurements can be further upscaled to the community (canopy) level by calculating a weighted mean using relative abundances of the most dominant species (Lavorel et al., 2008). This community weighted mean of a leaf trait is not directly comparable with RS, unless a physical scaling using leaf-canopy RTMs is applied to interpret RS data (Malenovský et al., 2007). If the community weighted mean is multiplied by biomass or LAI, one obtains a canopy integrated value (i.e. canopy property) expressed per unit surface area (Table 1), which can be directly compatible with remotely sensed canopy reflectance. Ultimately,

Ecological hierachy	LEAF	INDIVIDUAL	POPULATION / CUMMUNITY	ECOSYSTEM	BIOME	BIOSPHERE
Physiological & ecosystem processes	Evapotransp. Photosynthesis		Succession, decomposition			Biogeochem. cycles
		Phenology dynamic and productivity				
				Carbon sequestration		
RS scales	Leaf					
		Canopy				
		UP- / DOWN-SCALING		Landscape		
Typical spatial coverage of RS data	Local (< 10^2 km^2)					
			Regional (< 10^2 - 10^6 km^2)			
				Global (> 10^6 km^2)		
Proximal Airborne Satellite spectroradiom. (pixel size)	FieldSpec (non-imaging)					
		CASI, HyMap, AISA, APEX (< 10m)				
		Landsat ETM+, Sentinel-2 MSI (10-60 m)				
			Aqua/Terra MODIS, Envisat MERIS (250-1000 m)			
			SPOT VGT, NOAA AVHRR (> 1 km)			

Fig. 1. Link between ecological and remote sensing spatial scales with examples of typical remote sensing spectroradiometers operational at variety of spatial scales.

Table 1
Example of scaling of leaf nitrogen concentration and content from the leaf to the canopy level.

Trait	Leaf trait of a species i	Leaf trait of a community	Canopy trait of a community ($\sim$property)
N concentration	N_i	$N_{CWM} = SUM(N_i \times F_i)$	N_{CWM} [mg g^{-1}] $\times$ BIO [g m^{-2}]
[units]	[mg g^{-1} of leaf mass]	[mg g^{-1} of leaf mass]	[mg m^{-2} of surface area]
N content	N_i	$N_{CWM} = SUM(N_i \times F_i)$	N_{CWM} [mg m^{-2}] $\times$ LAI [m^2 m^{-2}]
[units]	[mg cm^{-2} of leaf area]	[mg m^{-2} of leaf area]	[mg m^{-2} of surface area]
			RS up/downscaling (Malenovský et al., 2007) $\leftrightarrow$
Reflectance data	Laboratory or proximal sensing	RS data combined with RTM upscaling	RS data (optionally combined with up/downscaling)

N_i – nitrogen concentration or content of a species i, CWM – community weighted mean, F_i – relative abundance of species i, BIO – biomass, LAI – leaf area index, RTM – radiative transfer model.

RS spectroradiometers measure a mixed signal reflected from entire plants (including woody and dry elements) and soil background. Information content originating from the green vegetation fraction can be enhanced by downslcaing techniques – spectral unmixing or data fusion (Malenovský et al., 2007). However, interpretation of RS data in areas with fractional vegetation cover below 30% remains extremely difficult (Okin et al., 2001) and largely non-conclusive.

3. Remote sensing of plant traits

In the following sections we will introduce individual plant traits and possible RS solutions (summarized in Table 2), including strengths and drawbacks of currently available RS methods. In order to support our discussion about RS of plant traits we compiled a database of reviewed scientific articles (Appendix S1 in the online supplementary material). We reviewed scientific papers about RS of leaf mass per area (LMA), nitrogen (N) and phosphorus (P) concentration or content. These are three frequently used traits in plant ecology analysis with strong potential to be derived from RS data. We also discuss plant growth and life forms, plant flammability properties, plant photosynthetic pathway and photosynthesis, plant or canopy height, leaf lifespan and phenology. From the reviewed articles (Appendix S1) we extracted two accuracy indicators: coefficient of determination (R^2) and relative root mean square error (RMSE) to evaluate the accuracy of RS methods estimating N, P and LMA (Fig. 2).

3.1. Plant growth and plant life forms

Plant growth form and plant life form classifications (Cornelissen et al., 2003) are considered as one of many existing plant functional classification schemes (Ustin and Gamon, 2010). There is no comprehensive assessment of plant growth forms or plant life forms as defined in Cornelissen et al. (2003) using RS. But current moderate resolution RS spectroradiometers (e.g. MODIS, MERIS) have been providing global data for land cover classifications, where vegetation is classified into broader functional classes (Arino et al., 2008; Bartholomé and Belward, 2005; Friedl et al., 2010). Existing global vegetation classifications are by definition closer to plant growth forms than to plant life forms, because they determine the vegetation classes based on canopy phenology and structure. Additionally, local studies demonstrated capabilities of RS to map specific plant growth forms or even individual species. Martin et al. (1998) determined forest species composition using maximum likelihood classification. Kokaly et al. (2003) mapped vegetation types in Yellowstone national park using continuum removal. Hamada et al. (2007) detected an invasive Tamarisk shrub species in riparian vegetation using hierarchical clustering. Kalacska et al. (2007) discriminated between forest lianas and their host trees in tropical forest. Underwood et al. (2006) and Hestir et al. (2008) mapped invasive aquatic vegetation using spectral mixture

analysis. The common feature of RS data used in the above mentioned studies is the pixel size smaller than 20 m.

The overall accuracy of the global land cover classifications varies between 68% and 75% (Friedl et al., 2010; Mayaux et al., 2006), whereas the accuracy of local RS studies varies between 65% and 95% and for some cases it drops below 50% (Underwood et al., 2006). Despite improving spectral and spatial resolution of RS instruments, it seems that RS reaches certain limits in accuracy and number of vegetation classes that can be distinguished. This is due to large variability within and among species, which decreases spectral separability among plant growth forms (Ustin and Gamon, 2010), as well as limited increase in dimensionality of RS data with increasing number of spectral bands (Schimel et al., 2013).
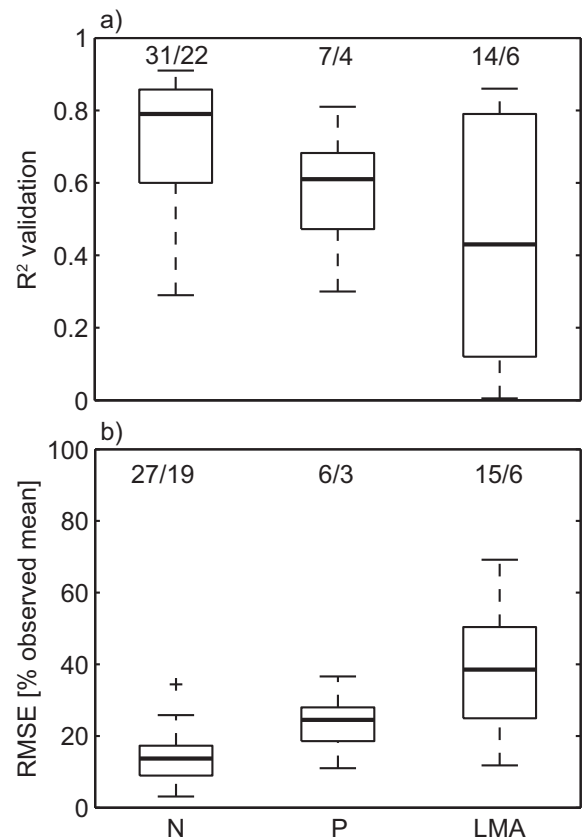
Fig. 2. Performance of remote sensing methods evaluated by (a) the coefficient of determination R^2 and (b) the relative root mean square error RMSE for the estimation of nitrogen, phosphorus concentration and content and leaf mass per area from various type of remote sensing data. (Legend: Central line in a box is median, box height is the interquartile range (i.e. 50% of the data) and whiskers represent minimum and maximum unless the observed values exceed 1.5 of the interquartile range in that case they are marked as outliers (crosses). Number (in format of x/y) above each box indicates number of reported accuracy indicators (x) and corresponding number of scientific articles (y) they were extracted from.)

Table 2

Link between plant traits as described by Cornelissen et al. (2003) and possible remote sensing counterparts.

Plant traits from Cornelissen et al. (2003) [typical units]	Trait definition	RS methods	RS references	Operational scale					LOSU[a]
				Leaf	Individual	Pop./Com.	Ecosystem	Biome	
Plant growth form [categories]	Determined by canopy structure and height	Global land cover classification, where several growth forms can be combined in one class	(Arino et al., 2008; Bartholomé and Belward, 2005; Friedl et al., 2010)				*	*	4
		Direct detection of some specific plant growth forms:							
		Shrubs	(Chopping et al., 2006; Hamada et al., 2007)		*	*	*	*	3
		Trees	(Kokaly et al., 2003; Martin et al., 1998)		*	*	*	*	4
		Lianas	(Kalacska et al., 2007; Sánchez-Azofeifa et al., 2009)	*	*				1–2
		Aquatic vegetation	(Hestir et al., 2008; Underwood et al., 2006)		*	*			2
Plant life form [categories]	Determined by position of perenating tissue to the ground surface	Not available	Not available						
Plant flammability (combined trait) [categories]	Combination of six traits determining how easily a plant produces flames	Not available But RS can asses vegetation fire properties:	Not available						
		Canopy moisture content	(Chuvieco et al., 2002; Koetz et al., 2004)		*		*		3
		Proportion between dead and live biomass	(Erdody and Moskal, 2010; Jia et al., 2006)		*		*		3
Photosynthetic pathway [categories]	C3, C4, CAM metabolism	Chlorophyll b/a ratio	(Siebke and Ball, 2009)	*					1–2
		Canopy structure	(Irisarri et al., 2009)		*	*			1
		Multi-temporal satellite RS detecting asynchronous seasonality of C3 and C4 species	(Davidson and Csillag, 2001; Foody and Dash, 2007)				*	*	2–3
Clonality [categories]	Ability to reproduce vegetatively	Not available	Not available						
Spinescence [categories]	Presence, type, size and density of spines	Not available	Not available						
Plant/canopy height [m]	Distance between ground and the upper boundary of the main photosynthetic tissue	Directly derived from laser scanning data	(Holmgren et al., 2003; Næsset et al., 2004; Kaartinen et al., 2012; Straatsma and Middelkoop, 2007)		*	*	*		4–5
		Indirectly related to leaf area index	(Chopping et al., 2008; van Wijk and Williams, 2005)			*	*		2
Leaf lifespan [months]	Period when an individual leaf is physiologically active	See leaf phenology	Not available						
Leaf phenology [months]	Number of months per year when canopy is green	For plant periodically changing leaves the length of growing season is derived from Satellite multi-temporal data	(Reed et al., 1994; White et al., 2009)				*	*	4
		Proximal phenological cameras	(Richardson et al., 2009)		*	*			4

Leaf trait	Definition	RS estimation method	References					LOSU[a]
Leaf size [m²]	One-sided surface area	Not available But for entire plant communities it can be linked to leaf area index	Not available (Chen et al., 2002; Fernandes et al., 2004; Garrigues et al., 2008)		*	*	*	4
Specific leaf area [m² kg⁻¹]	One-sided area of a fresh leaf divided by its dry mass	Directly estimated as leaf mass per area (1/SLA) from RTM inversion Related to leaf water content that can be estimated from RTM inversion or empirical methods	(Fourty and Baret, 1998; Riaño et al., 2005; Vohland et al., 2010) (Clevers et al., 2008; Colombo et al., 2008)	*	* *	* *	*	2–3 3–4
Leaf dry matter content [mg g⁻¹]	Dry mass of leaf divided by its fresh mass	Empirical methods estimating individual components such as lignin or cellulose Related to specific leaf area (see above)	(Kokaly et al., 2009; Serrano et al., 2002)	*	*	*		2
Leaf nitrogen concentration/content [mg g⁻¹/mg m⁻²]		Directly estimated using empirical RS methods Indirectly related to chlorophyll content that can be estimated using RTM inversion	(Martin et al., 2008; Oppelt and Mauser, 2004; Serrano et al., 2002) (Dash and Curran, 2004; Zarco-Tejada et al., 2004)	*	* *	* *	*	3 4–5
Leaf phosphorus concentration/content [mg g⁻¹/mg m⁻²]		Directly estimated using empirical RS methods	(Mutanga and Kumar, 2007; Porder et al., 2005)	*	*	*		2–3
Leaf physical strength [N]	Leaf resistance to fracture	Not available	Not available					

[a] LOSU (level of scientific understanding) indicates the fidelity of RS methods and RS-based products used in vegetation studies. It represents a weighted average of scores for the number of reported studies and obtained accuracy of RS methods (1 is low, 2 is low-medium, 3 is medium, 4 is medium-high, and 5 is high level of the scientific understanding).

3.2. Plant flammability properties

Individual components of the flammability trait are twig and leaf dry matter content, degree of ramification, leaf size, presence of standing litter, oils and waxes (Cornelissen et al., 2003). RS cannot quantify individual components of the flammability trait, but it can be used to assess combustibility of entire plant communities, which is driven by the amount of dry biomass and canopy structure. RS data have been used to support fire risk assessment and served as basis for fire monitoring schemes at the landscape level (Arroyo et al., 2008). Optical RS data have been used to derive vegetation properties such as the proportion between live and dead biomass (Jia et al., 2006) and fuel moisture content (ratio between water and dry leaf mass) (Chuvieco et al., 2002; Koetz et al., 2004). Both are relevant attributes for classification of fuel types (Arroyo et al., 2008; Lasaponara and Lanorte, 2007). The major limitation of passive optical RS for fire risk assessment is its inability to (i) estimate vegetation height, which is critical for fuel type discrimination, and (ii) to penetrate deeper into multi-layered canopies and therefore cannot provide information about understory, which plays an important role for fire spreading (Arroyo et al., 2008). Using active radar RS systems (Saatchi et al., 2007) and the fusion of optical RS data with laser scanning (Erdody and Moskal, 2010; Mutlu et al., 2008) or radar data (Treuhaft et al., 2004) represent a promising approach for fire risk assessment in terms of precise canopy structure and biomass mapping.

3.3. Plant photosynthetic pathway and photosynthesis

Spatial distribution of the plant photosynthetic pathway, i.e. C3, C4 and CAM metabolism, is relevant for simulating global carbon budget, because C4 plants tend to benefit from increasing temperature and atmospheric CO_2 (Ehleringer et al., 1997; Still et al., 2003). C3 and C4 leaves differ in internal leaf structure and biochemical composition (Hatch, 1987) and therefore a possibility of spectral discrimination between C3 and C4 plants exists. Siebke and Ball (2009) discriminated C3 and C4 grass species using a simple ratio between leaf reflectance at 696–709 and 545–567 nm that was sensitive to various concentrations of chlorophyll a and b. Irisarri et al. (2009) found that proximal reflectance can distinguish between a pure plantation of C3 and C4 grass species. However, observed spectral differences can be partly attributed to differences in leaf orientation, because C3 species in the study of Irisarri et al. (2009) had more erect leaves than C4 species. Airborne or satellite based RS studies used multi-temporal RS observations that captured asynchronous seasonality of C3 and C4 grass species (Davidson and Csillag, 2001; Foody and Dash, 2007) and could explain about 60% of the variability in C3/C4 grassland species composition.

Complementary to RS based mapping of plant photosynthetic pathways, we can profit from intensive and ongoing research of RS of global plant photosynthesis known as gross primary productivity (GPP) (Coops et al., 2010; Grace et al., 2007; Hilker et al., 2008b). The most widely applied approach of GPP modelling is based on the light use efficiency concept of Monteith (1972), which calculates GPP as the product of two plant growth limiting factors: the amount of absorbed photosynthetic active radiation (APAR) between 400 and 700 nm and plant light use efficiency (LUE) converting APAR into biomass (Field et al., 1995; Hilker et al., 2008b).

APAR is approximated by unitless fraction expressing how much of incoming photosynthetic active radiation is absorbed by vegetation (fAPAR). FAPAR was recognized as one of the essential climate variables by FAO Global Terrestrial Observing System (Gobron and Verstraete, 2009) and it is being currently estimated from global satellite RS data. The simplest empirical solutions relate fAPAR to the vegetation greenness using NDVI (Myneni and Williams, 1994) and EVI (Xiao et al., 2004) indices. EVI tends to outperform NDVI in denser canopies, where NDVI saturates (Huete et al., 2002). Empirical retrievals of fAPAR are sensitive to perturbing effects of soil background, observing geometry and atmospheric conditions (Fensholt et al., 2004). Alternatively, many operational RS-based fAPAR algorithms rely nowadays on physically based approaches using RTMs (Baret et al., 2007; Gobron et al., 2000; Myneni et al., 2002). Recent comparative studies (D'Odorico et al., 2013; Martínez et al., 2013; McCallum et al., 2010), however, found inconsistencies among fAPAR products. The largest discrepancies were reported for coniferous forests (D'Odorico et al., 2013; McCallum et al., 2010), which is mainly attributed to simplified representation of canopy structure in existing RTMs.

Possibility of LUE estimation from RS increased only in the past decade because of the development of fine spectral resolution instruments. We concentrate our discussion on direct RS approaches, which quantify LUE by measuring subtle changes in leaf and canopy reflectance resulting from two photoprotective mechanisms: non-photochemical quenching and chlorophyll fluorescence (Grace et al., 2007). Non-photochemical quenching dissipates the excess energy into heat by inducing changes in the xantophyll pigment cycle. Different composition of xantophyll pigments results into changes of leaf reflectance at 531 nm, which lead to the formulation of the photochemical reflectance index (PRI) (Gamon et al., 1992; Peñuelas et al., 1995). PRI exponentially increases with increasing LUE and is able to explain about 42% of LUE variability at the leaf level and 59% at the canopy level (Garbulsky et al., 2011). According to Garbulsky et al. (2011) PRI seems to perform better at the canopy level, but some studies argued that the PRI-LUE relationship is negatively affected by the canopy structure, soil background and observation geometry (Barton and North, 2001; Hernández-Clemente et al., 2011; Hilker et al., 2008a). Moreover, PRI values vary between species with the same photosynthetic capacity (Guo and Trotter, 2004). Therefore the use of PRI as the LUE proxy in complex canopies needs to be further investigated.

Sun induced chlorophyll fluorescence (SiF) is recently being explored as an indicator of LUE and actual photosynthesis (Damm et al., 2010; Malenovský et al., 2009; Meroni et al., 2009). SiF is a flux of photons that were not used for photosynthesis, but re-emitted at 685 nm and 740 nm (Buschmann, 2007). This adds a weak ($\leq 3\%$), but detectable, signal to the remotely sensed leaf and canopy reflectance (Meroni et al., 2009; Moya et al., 2004). SiF was first estimated using proximal reflectance data by analysing double-peak reflectance feature between 690 and 710 nm (Zarco-Tejada et al., 2003) or the narrow oxygen absorptions – Fraunhofer lines (Meroni and Colombo, 2006). The later principle was recently applied on airborne and satellite RS data. Zarco-Tejada et al. (2009) estimated SiF of individual trees under water stress using RS data of very high spatial (15 cm) and spectral (1 nm) resolutions. Joiner et al. (2011) and Guanter et al. (2012) presented the first global map of plant steady state SiF as monthly averages in $2° \times 2°$ grid derived from Fourier Transform Spectrometer (FTS) on board of the Greenhouse gases Observing SATellite (GOSAT). Despite the recent evidence of SiF retrievals from optical RS data, the operational approaches will require rigorous spectral calibrations and atmospheric corrections (Guanter et al., 2007) and to fully understand the effects of environmental variables on SiF (Malenovský et al., 2009).

3.4. Plant height

Plant height is an important trait associated with plant competitive abilities. Laser scanning has emerged to be the most

accurate RS technology for the measurement of plant and canopy height (Danson et al., 2009; Lefsky, 2002; van Leeuwen and Nieuwenhuis, 2010). Discrete return laser scanning have been successfully used for height estimation mainly of tall canopies such as boreal coniferous (Hopkinson et al., 2004; Næsset et al., 2004), temperate deciduous (Brandtberg et al., 2003) or tropical (Clark et al., 2004) forests. Less often it has been used in smaller canopies, such as shrubs (Glenn et al., 2011), crops (Davenport et al., 2000) or grasslands (Straatsma and Middelkoop, 2007). The best absolute accuracies achieved in tree height estimation from airborne discrete return laser scanners are between 0.5 and 1.0 m irrespective to a tree height (Kaartinen et al., 2012). According to Næsset et al. (2004) the accuracy in height estimation from discrete return laser scanning is higher for individual trees (relative RMSE of $5 \pm 2.5\%$) than for forest canopies (relative RMSE of $7 \pm 2.5\%$). Generally, a relative error of height estimation in tall forest canopies is usually less than 10% of the measured mean canopy height (Kaartinen et al., 2012; Næsset et al., 2004), while for lower canopies it reaches up to 20% (Davenport et al., 2000; Kaartinen et al., 2012).

Canopy height estimation using discrete return laser scanning faces three major issues. First is the determination of the terrain elevation, which is difficult in very low or too dense canopies, where emitted signal cannot penetrate to the ground (Falkowski et al., 2008; Lefsky, 2002). Second is the accurate detection of the uppermost canopy layer, which depends on the sampling pulse density (Jakubowski et al., 2013; Magnusson et al., 2007). Tree height accuracy decreases with decreasing sampling pulse density, but remains relatively constant and high until the densities drops below 1 pulse/m^2 (Jakubowski et al., 2013). The last issue is related to the selection of an extraction method. A recent international comparison revealed large variability among 14 extractions methods (RMSE varied between 0.5 and 4.5 m) to estimate height of individual coniferous trees (Kaartinen et al., 2012).

Full waveform lasers (Mallet and Bretar, 2009) provide certainly better insight into the 3D vegetation structure (Lindberg et al., 2012), but they do not necessarily yield more accurate plant and canopy height estimates than discrete return systems. Benefits of full waveform systems are improved detection of the ground surface elevation in denser canopies and possibly more accurate height estimates for plants underneath the main canopy layer.

3.5. Lifespan and phenology

Leaf lifespan (longevity) and phenology (seasonal timing) are closely related to plant nutrition conservation and competitive strategies and are influenced by local meteorological, topographic and soil variations (Dahlgren et al., 2007). It is beyond the capabilities of RS to measure leaf lifespan of evergreen species. But for plant communities that periodically change their foliar apparatus, time series of RS data provide an effective means of extracting land surface phenology (LSP) indicators including start, end, duration and maximum peak of the vegetation season (Liang and Schwartz, 2009; Reed et al., 1994). Considering strictly the definition of leaf phenology by Cornelissen et al. (2003) then the length of the vegetation season is the equivalent RS proxy of leaf phenology. It is important to realize that LSP indicators are related, but not identical, to field observed plant phenology indicators such as budburst, leaf unfolding, flowering (Liang and Schwartz, 2009).

Typical temporal and spatial resolutions of RS data used for LSP analysis are biweekly composites of VIs of global spatial extent and a pixel size ranging from 0.25 to 8 km (e.g. MODIS land products (Huete et al., 2002), AVHRR NDVI time series (Tucker et al., 2005)). The estimation of the LSP indicators from the satellite RS is influenced by four factors: (i) temporal resolution (Kross et al.,

2011), (ii) missing or noisy data due to clouds or snow cover (Delbart et al., 2006), (iii) magnitude of the seasonal amplitude in vegetation greenness to override other sources of variation (e.g. earlier greening of understory), and (iv) a method extracting the phenology indicators (de Beurs and Henebry, 2010; White et al., 2009). White et al. (2009) demonstrated that different extraction methods (e.g. global and local threshold values, inflection points in time series curves) applied on NDVI time series can yield differences up to 60 ± 20 days in the estimation of the start of the vegetation season. This suggests that there is no agreement on a single, globally appropriate extraction method of LSP (Schwartz and Hanes, 2010; White et al., 2009).

Consistent and long time series of RS data enable analyzing inter-annual variability in vegetation trends (de Jong et al., 2012) and land surface phenology (White et al., 2009) (see Remote Sensing special issue on monitoring global vegetation with AVHRR NDVI3g Data (1981–2011); http://www.mdpi.com/journal/remotesensing/special_issues/monitoring_global). Particular attention has been drawn on high latitude regions (Delbart et al., 2006), where climatic changes have been pronounced. Prolongation of the vegetation season has been revealed in Europe (Stöckli and Vidale, 2004) and globally (Julien and Sobrino, 2009) in 1980s and 90s, but the extent and quantification of these changes are still under discussion.

3.6. Specific leaf area and leaf dry matter content

Plant scientists consider leaf dry matter content (LDMC in mg g^{-1}) and specific leaf area (SLA in m^2 g^{-1}) as two separate traits. LDMC negatively correlates with SLA (Garnier et al., 2001; Shipley and Vu, 2002; Vile et al., 2005) and both traits are related to plant growth rate and leaf resistance to physical damage. We want to clarify first that some RS studies use terms "leaf dry matter content" or "dry matter content" when actually referring to leaf mass per area (LMA) – the inverse ratio of SLA (Riaño et al., 2005; Schaepman et al., 2004; Vohland et al., 2010).

LMA can be retrieved from RS data using empirical, as well as physical methods, because LMA is an input into leaf RTM (Jacquemoud et al., 2009). Despite this fact, only a few RS studies specifically targeted LMA estimation from proximal or remote sensing data achieving rather inconsistent results. Based on our literature review (Appendix S1) and Fig. 2, we can conclude that LMA can be retrieved with low to moderately good accuracy. The average R^2 between RS-estimated and measured LMA was equal to 0.45 ± 0.34 and the average relative RMSE was equal to $45 \pm 30\%$. Higher estimation accuracies were achieved for the canopy integrated estimates (i.e. LMA $\times$ LAI) than for leaf-level estimates (Schaepman et al., 2004; Vohland et al., 2010). Physically based retrieval methods dominate and we found little agreement among empirical methods on the best spectral wavelengths for LMA estimation. Interestingly, Wang et al. (2011) found that the most optimal spectral bands for LMA estimation are located at 1649 and 1722 nm, but almost identical bands were used to estimate phosphorus content of wheat canopies (Pimstein et al., 2011). Question remains whether these studies observed direct variations in LMA and P, or whether both traits correlate with another canopy property, which influences the reflectance in 1650–1720 nm. Only a few studies attempted to estimate single leaf dry matter components such as cellulose or lignin using empirical methods. For example, Zagolski et al. (1996) could explain around 60% of lignin and cellulose variability in a pine forest, Serrano et al. (2002) could explain up to 80% of lignin variability in chaparral communities.

SWIR wavelengths are most important for LMA estimation (Asner et al., 2011; Kokaly et al., 2009), but they are also strongly influenced by water absorption (Riaño et al., 2005). The masking effect of water and canopy structure decreases the accuracy of LMA

estimates from optical RS. Therefore a water removal algorithm is required or one could estimate leaf water content instead, because it is a complementary measure of LMA and can be retrieved with higher accuracy than LMA using RTM inversion (Clevers et al., 2008; Colombo et al., 2008).

3.7. Leaf and canopy nitrogen

Nitrogen (N) is an important component in proteins, nucleic acids and chlorophylls and therefore strongly linked to plant photosynthesis (Reich et al., 1995) and gross primary productivity (LeBauer and Treseder, 2008; Smith et al., 2002). Currently the best way to estimate N from optical RS is by means of empirical methods, because physically based retrievals are not well established. The only leaf RTM having N as an input is the LIBERTY model (Dawson et al., 1999). This model is not often used among the RS research community, which prefers using a simpler model–PROSPECT (Jacquemoud et al., 1996). Though there were attempts to incorporate N into PROSPECT, they were abandoned due to its strong covariance with other N containing compounds leading to inconsistent results (Jacquemoud et al., 1996; Kokaly et al., 2009). Among many empirical approaches, several VIs were proposed specifically to estimate leaf N and they were mainly established for crops (Chen et al., 2010; Tian et al., 2011). Also band selection techniques, such as stepwise or partial least square regressions, were successfully applied on transformed reflectance spectra (Smith et al., 2003; Yoder and Pettigrew-Crosby, 1995). Based on our literature review (Appendix S1) and Fig. 2, we can conclude that empirical RS methods can retrieve N with high accuracy. The average R^2 between RS-estimated and measured N was equal to 0.72 ± 0.16 and the average relative RMSE was equal to $15 \pm 7\%$.

Wavelengths that were frequently reported as important for N estimation are summarized in Fig. 3. These wavelengths can be integrated into three broad spectral regions: (i) red-edge region (680–780 nm) that is characterized by low reflectance in red due to strong C_{ab} absorption and high reflectance in NIR due to leaf internal scattering, (ii) NIR region around 1200 nm that is associated also with water absorption, and (iii) SWIR region where three main protein absorption features are located around 1680 nm, 2050 nm and 2170 nm (Kumar et al., 2001). Recent work of Knyazikhin et al. (2012) showed that a positive correlation between N and NIR reflectance, which was previously found in some temperate and boreal forests (Ollinger et al., 2008), is

actually a result of canopy structure effects. They emphasized that quantification of biochemical traits from NIR in general is strongly influenced by radiation scattering processes, which have to be accounted for in order to achieve correct results.

Moreover, we bring evidence that a moderately strong correlation between leaf N and C_{ab} exists across different species (Table 3 and Appendix S2). The average Pearson correlation coefficient is equal to 0.65 ± 0.15, and it varies between 0.4 and 0.9 for individual species. This finding supports our hypothesis that remotely sensed C_{ab} can be potentially used as an operational approach to estimate N. Many C_{ab} sensitive VIs (Sims and Gamon, 2002), simple spectral models (Gitelson et al., 2006) and spectral transformations (Kokaly and Clark, 1999) have been developed and tested to estimate C_{ab} from the leaf reflectance data. Their robustness and upscaling to the canopy level have been thoroughly tested using RTM (Haboudane et al., 2002; le Maire et al., 2004). Additionally, physical RS methods using RTM enable direct estimation of C_{ab} (Jacquemoud et al., 2009). This is particularly an advantage in structurally complex canopies such as conifers (Malenovský et al., 2013; Zarco-Tejada et al., 2004), where simple empirical methods often fail. When using RS-based C_{ab} as proxy of N, one has to keep in mind that the positive N–C_{ab} relationship is species specific (Hallik et al., 2009; Appendix S2) and therefore more suitable for communities with lower species diversity.

3.8. Leaf and canopy phosphorus

Leaf phosphorus (P) is an indicator of plant growth rate and nutrient quality. We found only limited number of studies that estimated P from RS data (Appendix S1). Only Porder et al. (2005) used airborne RS to estimate canopy P concentration of broadleaf tropical forest. The rest of the reviewed studies used airborne-based or proximal sensing to estimate P concentration in structurally homogeneous canopies, such as crops and grasslands. Based on results of our literature review (Appendix SA1) and Fig. 2, we can conclude that P can be retrieved from optical RS with lower accuracies than N. The average R^2 between RS-estimated and measured P was equal to 0.57 ± 0.16 and the average relative RMSE was equal to $23 \pm 7\%$. In all cases empirical retrieval methods were used. The selection of spectral bands used in regression models was inconsistent among the reviewed studies, which can be mainly attributed to the low P concentration in leaves (less than 1% of dry leaf mass) and the absence of pronounced P absorption features. NIR and SWIR spectral bands were often included in the regression models,
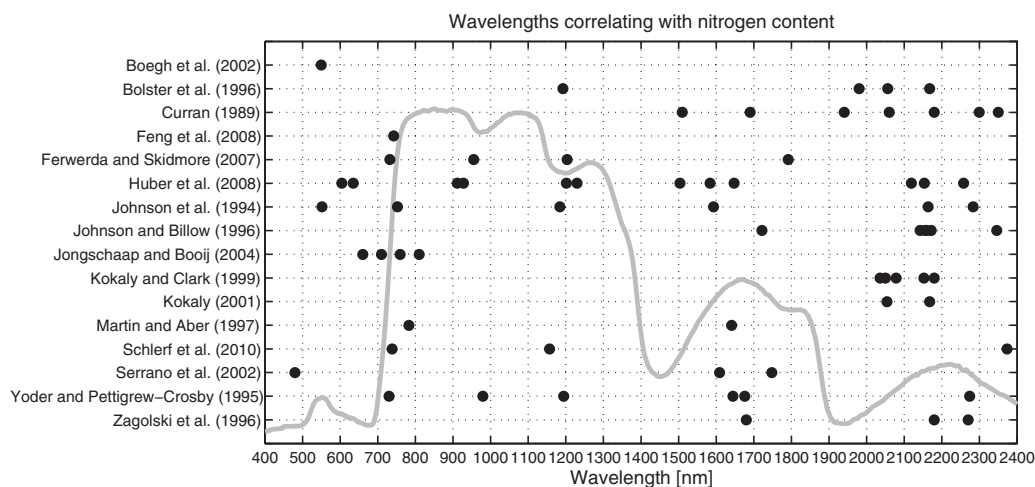
Fig. 3. Overview of spectral wavelengths used in scientific literature for estimation of nitrogen concentration and content in green and dry plant leaves. Each dot represents a reported spectral wavelength. A typical reflectance response of green vegetation (grey line) is plotted for clarity (Bolster et al., 1996; Curran, 1989; Feng et al., 2008; Huber et al., 2008; Johnson and Billow, 1996; Jongschaap and Booij, 2004; Kokaly, 2001; Martin and Aber, 1997).

Table 3
Pearson's correlation coefficient (R) between measured leaf chlorophyll and leaf nitrogen concentration and content as reported for some plant species in literature and from our own field measurements. The number of stars in the superscript indicates the statistical significance of the reported correlations (****$p \leq 0.001$, ***$p \leq 0.01$, **$p \leq 0.05$, *$p \leq 0.1$, in case the statistical significance was not reported the R value is without a superscript).

Species name (no. of observations)	R	Units		Reference
		C_{ab}	N	
Trees				
Larix decidua (18)	0.60***	$\mu g\,cm^{-2}$	$mg\,cm^{-2}$	(Appendix S2)
Populus tremula (19)	0.71****	$g\,m^{-2}$	$g\,m^{-2}$	(Hallik et al., 2009)
Tilia cordata (20)	0.75****	$g\,m^{-2}$	$g\,m^{-2}$	(Hallik et al., 2009)
Acer macrophyllum (80)	0.65	$mg\,g^{-1}$	$mg\,g^{-1}$	(Yoder and Pettigrew-Crosby, 1995)
Picea abies (78)	0.37***	$mg\,g^{-1}$	%	(Schlerf et al., 2010)
Fagus sylvatica (70) and Quercus spp. (75)	0.81****	$\mu g\,cm^{-2}$	$mg\,g^{-1}$	(le Maire et al., 2008)
Tsuga heterophylla (11), Pinus ponderosa (6), Pseudotsuga menzeisii (3), Juniperus occidentalis (3)	0.60***	$mg\,cm^{-2}$	$mg\,cm^{-2}$	(Johnson et al., 1994)
Tropical forest species (n.a.)	0.70–0.84	–	–	(Asner and Vitousek, 2005)
Shrubs				
Juniperus nana (11)	0.70*	$\mu g\,cm^{-2}$	$mg\,cm^{-2}$	(Appendix S2)
Vaccinium myrtillus (14)	0.51*	$\mu g\,cm^{-2}$	$mg\,cm^{-2}$	(Appendix S2)
Gossypium hirsutum (18)	0.68	$mmol\,m^{-2}$	$mmol\,m^{-2}$	(Evans, 1989)
Graminoides				
Dactylis glomerata (13)	0.78***	$\mu g\,cm^{-2}$	$mg\,cm^{-2}$	(Appendix S2)
Dactylis glomerate (32)	0.38**	$g\,m^{-2}$	$g\,m^{-2}$	(Hallik et al., 2009)
Kobresia myosuroides (14)	0.47**	$\mu g\,cm^{-2}$	$mg\,cm^{-2}$	(Appendix S2)
Festuca violacea (6)	0.74*	$\mu g\,cm^{-2}$	$mg\,cm^{-2}$	(Appendix S2)
Bromus erectus (18)	0.42***	$\mu g\,cm^{-2}$	$mg\,cm^{-2}$	(Appendix S2)
Phleum pratense (33)	0.64****	$g\,m^{-2}$	$g\,m^{-2}$	(Hallik et al., 2009)
Forbs/herbs				
Laserpitium latifolium (14)	0.65*	$\mu g\,cm^{-2}$	$mg\,cm^{-2}$	(Appendix S2)
Rhinanthus alectorolophus (28)	0.84****	$\mu g\,cm^{-2}$	$mg\,cm^{-2}$	(Appendix S2)
Crepis pyrenaica (15)	0.84****	$\mu g\,cm^{-2}$	$mg\,cm^{-2}$	(Appendix S2)
Leonthodon hispidus (20)	0.47*	$\mu g\,cm^{-2}$	$mg\,cm^{-2}$	(Appendix S2)
Centaurea scabiosa (15)	0.81****	$\mu g\,cm^{-2}$	$mg\,cm^{-2}$	(Appendix S2)
Gentiana luthea (14)	0.61*	$\mu g\,cm^{-2}$	$mg\,cm^{-2}$	(Appendix S2)
Plantago media (15)	0.57*	$\mu g\,cm^{-2}$	$mg\,cm^{-2}$	(Appendix S2)
Cirsium arvense (9)	0.75**	$g\,m^{-2}$	$g\,m^{-2}$	(Hallik et al., 2009)
Phaseolus vulgaris (21)	0.84	$mmol\,m^{-2}$	$mmol\,m^{-2}$	(Evans, 1989)
Spinacia oleracea (12)	0.96	$mmol\,m^{-2}$	$mmol\,m^{-2}$	(Evans, 1989)
Alocasia macrorrhiza (15)	0.50	$mmol\,m^{-2}$	$mmol\,m^{-2}$	(Evans, 1989)
Crops				
Triticum spp. (21)	0.86****	$g\,cm^{-2}$	$g\,m^{-2}$	(Boegh et al., 2002)
Triticum spp. (123)	0.50**	$mg\,g^{-1}$	%	(Oppelt and Mauser, 2004)
Triticum aestivum (51)	0.89	$mmol\,m^{-2}$	$mmol\,m^{-2}$	(Evans, 1989)

but these bands are strongly influenced by water absorption and canopy structure. When the effect of leaf water content was suppressed by applying a water removal technique (Schlerf et al., 2010), the accuracy of the P prediction in savana grasslands from proximal sensing increased (Ramoelo et al., 2011). We have not found any VI that is specifically designed for P estimation and previously designed indices for C_{ab} or N estimation did not perform satisfactorily (Pimstein et al., 2011). Similar to nitrogen, the biomass weighted canopy P concentration can be retrieved with higher accuracy than leaf-level concentration (Pimstein et al., 2011).

4. Concluding remarks

In this review, we provided an extensive summary of RS data at different spectral, spatial and temporal resolutions, and RS methods for the estimation of key plant traits as defined by Cornelissen et al. (2003). Main conclusions and future outlooks for the individual traits are listed as follows:

- Classification of plant growth and plant life forms cannot be entirely reproduced by RS. Global RS-based land cover classification schemes classify vegetation to broad classes, which are by definition closer to plant growth forms. Their classification accuracy is around 70%. High resolution RS facilitate local classifications of some plant growth forms or even individual species, but the classification accuracy vary between 50 and 95%. Combination of optical RS with multi-directional RS or laser scanning can improve existing plant classifications by increasing the separability among vegetation types.

- Plant flammability as a combined trait cannot be quantified using optical RS observations. However, when combining optical passive and active RS then the combustibility of entire plant communities can be well assessed. RS data are currently being used to quantify fire properties such as moisture content, plant height and the proportion between live and dead biomass. These are valuable input data for fire models and fuel classification schemes.

- Use of optical RS for mapping C3 and C4 photosynthetic pathways remains rare. Instead, RS data has been widely exploited for spatio-temporal mapping of plant photosynthetic activity using proxies of fraction of absorbed photosynthetic radiation and light use efficiency. Direct estimation of light use efficiency by means of chlorophyll fluorescence has emerged as a very promising approach. Though major challenges in RS of chlorophyll fluorescence are currently being investigated, recent results already demonstrated that large scale mapping of chlorophyll fluorescence from RS is possible.

- Plant height can be directly and most accurately estimated from active laser scanning data. The relative error of height estimation from discrete return laser systems is usually bellow 10% in tall

forest canopies and increases up to 20% in lower canopies. Full waveform lasers do not necessarily provide improvement in absolute height estimation, but they certainly offer better insight into the 3D vegetation structure. Understanding the effects of canopy structure on reflectance is a major challenge in RS of vegetation.

- Multi-temporal satellite RS can deliver relevant land surface phenological indicators, such as start, end, maximum peak and duration of the vegetation season for plant communities periodically changing their foliage. Recent comparative studies suggested that there is no agreement on a single, globally appropriate method to extract land surface phenology. There is critical need to effectively validate RS-based phenology indicators and therefore field data are required across global biomes. Future studies should attempt to employ data from active RS systems to separate asynchronous phenology of understory and the main canopy. Moreover, the future chlorophyll fluorescence observations from space can provide an accurate identification of the photosynthesis onset and offset.

- Specific leaf area or its inverse ratio leaf mass per area can be estimated from the optical RS data using empirical, as well as physical methods. Despite this possibility, the retrieval accuracy substantially varied and it was the lowest among the reviewed plant biochemical traits. Inconsistencies are mainly due to confounding effects of water present in the plant tissue and the atmosphere. An algorithm that significantly suppresses the absorption effect of water or improvements in atmospheric corrections is prerequisite for an accurate retrieval of leaf mass per area from optical RS.

- Nitrogen can be estimated from optical RS using empirical methods achieving the highest accuracies among the reviewed plant biochemical traits. The highest uncertainty was observed in coniferous canopies, which is due to their complex canopy structure. Therefore there is an urgent need for improved RS methods accounting and correcting for canopy structure effects. We supported the hypothesis that RS of chlorophyll content can be used as an operational proxy for N estimation, since moderately strong relationship between nitrogen and chlorophyll exists. Moreover, the future multi-temporal observations of chlorophyll fluorescence might also improve N retrieval methods.

- Finally, phosphorus can be estimated from optical RS using empirical methods only. The achieved accuracies are moderately good, but lower than for nitrogen. Due to low concentration of P in leaves and confounding effects of canopy structure and water content we do not expect that operational large scale mapping of P from RS will be achievable in a near future.

In addition, the applicability of RS methods goes beyond the traits discussed in this review. Several well-established and thoughtfully validated RS-based traits can support or even extend the collection of current key plant traits used in ecology. Those are mainly leaf/canopy chlorophyll and water content, LAI, fAPAR and fractional vegetation cover.

We see an urgent need to address in a more comprehensive fashion the effects of vegetation structure in interpretation of RS data. Therefore advanced measurements of traits such as the volume of intracellular air spaces, leaf thickness, leaf angle distribution, proportion of non-photosynthetic biomass within canopy light acclimation are required. Generally, more coherent collection of field trait data together with proximal and remote sensing observations will be required to develop robust scaling schemes and support airborne and satellite based RS methods of trait estimation. Such an interdisciplinary cooperation resulted recently in a novel concept of "optical traits", i.e. assessing combined effects of vegetation physiological, structural and

phenological properties on reflectance measurements (Ustin and Gamon, 2010).

The most important advantage of using RS is its ability to provide spatially explicit and continuous maps of relevant traits repeatedly during the vegetation season. If combined with eco-physiological models that are designed having the current and future capabilities of RS data in mind, substantial progress will be achieved in spatio-temporal mapping of ecosystem functioning.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecocom.2013.06.003.

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