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Review of optical-based remote sensing for plant trait mapping

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Review of optical-based remote sensing for plant trait mapping

Abstract

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.

Disciplines

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1 **Title: Review of optical-based remote sensing for plant trait mapping.**

2

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21 Plant trait data have been used in various studies related to ecosystem functioning, community
22 ecology, and assessment of ecosystem services. Evidences are that plant scientists agree on a
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36 nitrogen and phosphorous concentration or content). We review existing literature to
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38 using RS ranged between 10% and 45% of measured mean value, i.e. around 10% for plant
39 height of tall canopies, 20% for plant height of short canopies, 15% for plant nitrogen, 25%
40 for plant phosphorus content/concentration, and 45% for leaf mass per area estimates.

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42 biochemistry, photosynthetic processes and canopy structure. There are also other plant traits,
43 i.e. leaf chlorophyll content, water content and leaf area index, which can be retrieved from
44 optical RS well and can be of importance for plant scientists.

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46 require comprehensive and integrated measurements of various plant traits together with leaf
47 and canopy spectral properties. By doing so, the interplay between plant structural,
48 physiological, biochemical, phenological and spectral properties can be better understood.

49

50

51 **Keywords**

52 Plant traits; Remote sensing; Plant Ecology; Accuracy; Scaling

53 **1. Introduction**

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

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

77 Capabilities to retrieve plant traits and canopy properties from optical RS have evolved
78 hand in hand with the technological development of RS spectroradiometers (Milton et al.,

79 2009). Early RS spectroradiometers providing data of coarser spatial and spectral resolutions
80 have supported mainly vegetation classification into broader functional groups (Ustin and
81 Gamon, 2010) and the development of simple vegetation indices (VIs) that were sensitive to
82 broad variations in canopy properties (Cohen and Goward, 2004; Turner et al., 1999). Next
83 generation of medium spectral and spatial resolution spectroradiometers together with
84 development of radiative transfer models (Liang, 2004) have facilitated quantitative
85 estimation of some plant traits (e.g. chlorophyll content (Dash and Curran, 2004) and water
86 content (Cheng et al., 2006)) and canopy properties (e.g. leaf area index (Myneni et al.,
87 2002)). Development of high spectral resolution imaging spectroradiometers encouraged even
88 more the quantitative estimation of plant traits related to physiology and biochemistry. Plant
89 pigments are the most studied traits (Blackburn, 2007; Ustin et al., 2009) and among them
90 chlorophylls a and b (C_{ab}) have received most attention (Haboudane et al., 2002; le Maire et
91 al., 2004; Malenovsky et al., 2013; Schlerf et al., 2010; Zarco-Tejada et al., 2004), whereas
92 carotenoids (Gitelson, 2002; Hernández-Clemente et al., 2012) and anthocyanins (Gitelson et
93 al., 2006) have been studied less. Other biochemical traits retrieved from optical RS data are
94 plant macronutrients (N, P, K, Mg, Ca) (Mutanga et al., 2004; Pimstein et al., 2011) and there
95 is clear dominance of N and P related studies (both traits discussed in details later).
96 Furthermore, leaf water content (Clevers et al., 2010; Colombo et al., 2008), leaf mass per
97 area (discussed in details later), lignin and cellulose (Kokaly et al., 2009) or polyphenols
98 (Skidmore et al., 2010) can be potentially retrieved from optical spectral data too.

99 Advantages of using RS are its capability to provide spatially contiguous and – for certain
100 observations – high revisit frequency at the typical length scale of the trait processes
101 observed. Moreover, it offers different sampling scheme to trait mapping, determined by
102 combination of pixel size, spatial extent and revisit time of RS observations, than in-situ
103 measurements. The major challenge in quantitative RS of plant traits plays the canopy
104 structure. It affects interpretation of canopy reflectance and has negative impact on the

105 retrieval accuracy of biochemical traits (Knyazikhin et al., 2012; le Maire et al., 2008).
106 Therefore approaches accounting for integral effects of canopy structure (Knyazikhin et al.,
107 2012) or measurements of canopy structure itself (van Leeuwen and Nieuwenhuis, 2010) have
108 recently gained more attention.

109 The potential of RS data for ecological applications is large, however, we see that
110 successful integration of RS observations and ecological applications still requires bridging
111 gaps in the perception of traits importance, scientific terminology (Schaepman-Strub et al.,
112 2006; Violle et al., 2007) and scaling among leaf, plant and canopy levels (Malenovsky et al.,
113 2007; Messier et al., 2010). In this review, we want to demonstrate the potential of RS for
114 estimating individual plant traits as defined by ecologists and therefore strengthen links
115 between plant ecology and remote sensing research communities. First, we introduce RS
116 concepts of light – vegetation interactions, RS instruments for vegetation studies, RS
117 methods, and scaling between field and RS observations. Further, we discuss in detail current
118 achievements and challenges when using optical RS to estimate key plant traits. We used
119 Cornelissen et al. (2003) as baseline reference for key traits. These included plant growth and
120 life forms, flammability properties, photosynthetic pathways and activity, plant height, leaf
121 lifespan and phenology, specific leaf area, leaf nitrogen and phosphorous. Regenerative (e.g.
122 seed mass) and belowground (e.g. rooting depth) traits are deliberately excluded, since they
123 cannot be estimated using direct measurements from optical RS. We put emphasis on optical,
124 passive RS, but mention active RS (laser scanning and microwave radar) to trait mapping
125 whenever appropriate.

126

127 **2. Remote sensing of vegetation**

128 **2.1. Light-vegetation interactions**

129 Interactions between incident radiation and canopy elements are extremely complex and are
130 described by three main physical mechanisms: absorption reflection, and transmission. The

131 solar reflected radiation in the optical domain (i.e. between 380 and 2500 nm) is commonly
132 used in vegetation studies, because most of the diagnostic absorption features of green
133 vegetation are located in this part of the spectrum (Kokaly et al., 2009; Ustin et al., 2009).
134 Reflectance of vegetation canopies depends on radiative properties of leaves, other non-
135 photosynthetic canopy elements and their spatial organisation. Leaf reflectance spectra are
136 mainly characterized by i) strong and well described absorption of foliar photosynthetic
137 pigments, dominated by chlorophylls, in the visible region (400 – 700 nm, VIS), ii) leaf
138 structure in the near infrared region (700 – 1300 nm, NIR), and iii) prevailing water and
139 protein absorptions (as well as other biochemicals) in the shortwave infrared region (1300 –
140 2500 nm, SWIR). Mechanisms influencing leaf reflectance are well understood (Kumar et al.,
141 2001), but interpretation of canopy level reflectance remains challenging due to multiple light
142 interactions between canopy elements and background (Disney et al., 2006; Ross, 1981;
143 Widlowski et al., 2004). The key factor influencing canopy reflectance is the canopy structure
144 (Disney et al., 2006; Rautiainen et al., 2004). The most widely used descriptor of a canopy
145 structure in RS studies is leaf area index (LAI) (Fernandes et al., 2004; Turner et al., 1999).
146 LAI alone cannot fully describe the effects of the canopy structure. There are many other leaf
147 level traits (e.g. ratio of mesophyll cell surface to intercellular air spaces, leaf thickness) and
148 canopy properties (e.g. leaves orientation in a canopy characterized by leaf angle distribution,
149 leaves aggregation characterized by clumping index) that strongly influence remotely sensed
150 canopy reflectance. Lack of field measurements and complex interplay among structural leaf
151 traits and canopy properties prevents to decouple their individual effects on RS reflectance
152 data. Furthermore, presence of background and understory components (Eriksson et al.,
153 2006), presence of non-photosynthetic elements (Verrelst et al., 2010), and varying
154 observation geometries (Lobell et al., 2002) also influence canopy reflectance. Therefore RS
155 methods try to minimize these confounding effects (Knyazikhin et al., 2012) and enhance the
156 sensitivity of reflectance data towards a trait or a property of interest (Haboudane et al., 2002;

157 Verstraete and Pinty, 1996). Alternatively, combined retrieval schemes are optimized to use
158 spectral, spatial and directional domains simultaneously (Laurent et al., 2011b; Schaepman,
159 2007).

160

161 **2.2. Remote sensing instruments**

162 Environmental studies can nowadays benefit from a large variety of RS data provided by
163 different passive and active RS systems. We first discuss optical, passive RS systems, because
164 they are being prevalently used to study vegetation properties. Optical spectroradiometers on
165 satellite-, airborne- and ground-based platforms represent a trade-off among spatial, spectral
166 and temporal resolutions. Spectroradiometers onboard satellite platforms acquire data of
167 regional to global coverage with spatial resolution of tens to hundreds meters and revisit time
168 typically between 2 and 16 days. From the advent of broad-band, multispectral and coarse
169 spatial resolution spectroradiometers (e.g. advanced very high resolution spectroradiometer
170 AVHRR onboard NOAA) in the 1970's and 80's we have moved towards spectroradiometers
171 of increasing resolutions. Currently operational satellite-based spectroradiometers suitable for
172 vegetation monitoring are of moderate spectral and spatial resolutions (e.g. moderate
173 resolution imaging spectroradiometers MODIS onboard Aqua and Terra, the recently
174 terminated Envisat mission with MERIS, and Enhanced Thematic Mapper ETM+ onboard
175 Landsat). New advanced data for systematic, long-term observation of the Earth systems will
176 be provided from 2013 onwards by the prospective future ESA Sentinel missions
177 (Malenovský et al., 2012).

178 The major disadvantage of satellite-based multispectral spectroradiometers is that they
179 sample the electromagnetic spectrum only with a few spectral bands. Therefore imaging
180 spectroscopy has emerged to overcome spectral limitations of multispectral systems (Goetz,
181 2009; Schaepman, 2009). Imaging spectroscopy (often referred as hyperspectral RS) acquire
182 data of unprecedented radiometric quality and high spectral resolution – typically the number

183 of overlapping narrow spectral bands exceeds one hundred, providing therefore almost
184 contiguous spectral information (Schaepman, 2009). Spaceborne imaging spectrometers are
185 still only sparsely available (Hyperion on EO1 and CHRIS on PROBA platforms). Most of
186 the existing imaging spectroradiometers are therefore operated on airborne platforms, which
187 enables acquiring data at a very high spatial resolution (the ground pixel size is usually less
188 than a few meters). A great advantage of airborne RS is high versatility to meet user
189 requirements on target selection, spatial and spectral resolutions, and acquisition date.
190 Additionally, it allows combining imaging spectroradiometers with other type of RS
191 instruments (Asner et al., 2012). One drawback of is reduced multi-temporal feasibility due to
192 costs and logistics.

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

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

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

207 Laser scanners (often referred as lidars) emit and record backscattered signal in the optical
208 part of the electromagnetic spectrum (0.01 – 10 μm) and measure runtime from the instrument

209 to the ground surface and back. There are two types of laser scanners: discrete return systems
210 that record either single or multiple backscatter echoes and full waveform systems that record
211 the entire backscatter signal from a return (Mallet and Bretar, 2009; Wulder et al., 2012). Up
212 to date vegetation structural properties derived from laser scanning include vegetation height
213 (see section 3.4 for detailed discussion), canopy volume, leaf area index, gap fraction and
214 vegetation profiles (Lefsky, 2002; Lindberg et al., 2012; van Leeuwen and Nieuwenhuis,
215 2010). Recent development have advanced towards a multispectral full waveform system,
216 which provide additional information on the 3D distribution of plant physiological properties
217 (Hakala et al., 2012).

218 Imaging synthetic aperture radars (SAR) emit and record backscattered signal at one or
219 more polarizations in the microwave part of the electromagnetic spectrum (cm to multiple m).
220 Their greatest advantage over the optical instruments is of being able to acquire images
221 independently of cloud cover. However, challenges remain to interpret radar data from very
222 dense or moist canopies, where backscatter signal saturates (Mitchard et al., 2009). The major
223 application domain of radar data is to estimate vegetation height and biomass (partly reviewed
224 by Koch et al. (2010) and Patenaude et al. (2005)). This will be strongly supported by the
225 future ESA radar mission BIOMASS (le Toan et al., 2011).

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

229

230 **2.3. Remote sensing methods**

231 Plant traits and canopy properties may be assessed qualitatively or quantitatively from RS
232 data. Qualitative methods – classification techniques use a set of decision rules assigning
233 image pixels with similar spectral properties into discrete thematic vegetation classes (Xie et
234 al., 2008). Qualitative methods used to interpret optical RS data can be divided into two broad

235 groups: empirical and physical methods (or combination of both) (Liang, 2004). Empirical
236 methods build on statistical relationships established between limited number of field trait
237 observations and RS data using regression techniques (Ferwerda and Skidmore, 2007; Smith
238 et al., 2002). The sensitivity of RS data towards traits or properties of interests is often
239 enhanced by calculating VIs (Chen et al., 2010; le Maire et al., 2004; Turner et al., 1999) or
240 spectral transformations in case of contiguous hyperspectral data (Schlerf et al., 2010). By
241 nature, empirical methods are computationally fast and effectively summarize local data, but
242 they lack cause-effect relationships. Consequently, predictive statistical relationships often
243 suffer from lack of robustness and transferability as they are usually site, species and time
244 specific (Colombo et al., 2003; Grossman et al., 1996).

245 Limitations of empirical methods can be partly overcome by using physical RS methods.
246 These methods are based on radiative transfer models (RTMs), which simulate light
247 absorption and scattering inside vegetation canopies accounting for leaf biochemical
248 composition and canopy structural properties (Gastellu-Etchegorry et al., 2004; Jacquemoud
249 et al., 2009; Rautiainen et al., 2010; Verhoef and Bach, 2007). The role of coupled soil-leaf-
250 canopy RTMs (Jacquemoud et al., 2009) in RS is two-fold. First, they help to study the effects
251 of additional perturbing factors (soil background, non-photosynthetic materials and
252 observation geometry) on canopy reflectance. Second, they enable direct estimation of leaf
253 traits and canopy properties that are directly involved in the radiative transfer by using
254 inversion techniques (Baret and Buis, 2008). Further, when combined with atmospheric
255 RTMs, they hold the promise to estimate many leaf traits and canopy properties
256 simultaneously (Laurent et al., 2011a). Some traits and properties can be estimated with high
257 accuracy and fidelity, e.g. leaf chlorophyll content (Sampson et al., 2003; Zarco-Tejada et al.,
258 2004), leaf water content (Clevers et al., 2008; Colombo et al., 2008) and leaf area index
259 (Myneni et al., 2002; Schlerf et al., 2005). Still, other canopy structural properties (e.g. leaf
260 aggregation, leaf angle distribution) present a substantial challenge for RTMs

261 parameterization and interpretation from RS data (Ollinger, 2011). The major drawback of the
262 physical methods is that different combinations of RTM input parameters may produce the
263 same reflectance spectra, which makes estimation of canopy properties from RS data
264 ambiguous (Baret and Buis, 2008; Combal et al., 2003).

265

266 [Fig. 1. and Table 1 about here]

267

268 **2.4. Scaling and terminology**

269 Spatial scale of in-situ measured plant traits and RS data often disagrees. Here we want to
270 demonstrate how to match scaling terminology used in ecology and RS (Fig. 1). An ultimate
271 requirement for RS of plant traits shall be to match the spatial scales of trait with RS data. We
272 exemplify this using a key plant trait – nitrogen (N) and demonstrated simple scaling of field
273 measurements from leaf to canopy level and overlap it with scaling approaches applied to RS
274 data (Table 1). Quantitative traits such as N are usually measured at the level of individual
275 leaves of dominant plant species and expressed either as concentration (mass fraction per unit
276 dry leaf mass) or content (mass fraction per unit leaf area) (here we refer to the terminology
277 introduced by Datt (1998)). Assuming the mass ratio hypothesis (Grime, 1998), the leaf level
278 measurements can be further upscaled to the community (canopy) level by calculating a
279 weighted mean using relative abundances of the most dominant species (Lavorel et al., 2008).
280 This community weighted mean of a leaf trait is not directly comparable with RS, unless a
281 physical scaling using leaf-canopy RTMs is applied to interpret RS data (Malenovský et al.,
282 2007). If the community weighted mean is multiplied by biomass or LAI, one obtains a
283 canopy integrated value (i.e. canopy property) expressed per unit surface area (Table 1),
284 which can be directly compatible with remotely sensed canopy reflectance. Ultimately, RS
285 spectroradiometers measure a mixed signal reflected from entire plants (including woody and
286 dry elements) and soil background. Information content originating from the green vegetation

287 fraction can be enhanced by downsampling techniques – spectral unmixing or data fusion
288 (Malenovsky et al., 2007). However, interpretation of RS data in areas with fractional
289 vegetation cover below 30% remains extremely difficult (Okin et al., 2001) and largely non-
290 conclusive.

291

292 **3. Remote sensing of plant traits**

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

305

306 [Table 2 and Fig. 2. about here]

307

308 **3.1. Plant growth and plant life forms**

309 Plant growth form and plant life form classifications (Cornelissen et al., 2003) are considered
310 as one of many existing plant functional classification schemes (Ustin and Gamon, 2010).

311 There is no comprehensive assessment of plant growth forms or plant life forms as defined in
312 Cornelissen et al. (2003) using RS. But current moderate resolution RS spectroradiometers

313 (e.g. MODIS, MERIS) have been providing global data for land cover classifications, where
314 vegetation is classified into broader functional classes (Arino et al., 2008; Bartholomé and
315 Belward, 2005; Friedl et al., 2010). Existing global vegetation classifications are by definition
316 closer to plant growth forms than to plant life forms, because they determine the vegetation
317 classes based on canopy phenology and structure. Additionally, local studies demonstrated
318 capabilities of RS to map specific plant growth forms or even individual species. Martin et al.
319 (1998) determined forest species composition using maximum likelihood classification.
320 Kokaly et al. (2003) mapped vegetation types in Yellowstone national park using continuum
321 removal. Hamada et al. (2007) detected an invasive Tamarisk shrub species in riparian
322 vegetation using hierarchical clustering. Kalacska et al. (2007) discriminated between forest
323 lianas and their host trees in tropical forest. Underwood et al. (2006) and Hestir et al. (2008)
324 mapped invasive aquatic vegetation using spectral mixture analysis. The common feature of
325 RS data used in the above mentioned studies is the pixel size smaller than 20 meters.

326 The overall accuracy of the global land cover classifications varies between 68% and 75%
327 (Friedl et al., 2010; Mayaux et al., 2006), whereas the accuracy of local RS studies varies
328 between 65% and 95% and for some cases it drops below 50% (Underwood et al., 2006).
329 Despite improving spectral and spatial resolution of RS instruments, it seems that RS reaches
330 certain limits in accuracy and number of vegetation classes that can be distinguished. This is
331 due to large variability within and among species, which decreases spectral separability
332 among plant growth forms (Ustin and Gamon, 2010), as well as limited increase in
333 dimensionality of RS data with increasing number of spectral bands (Schimel et al., 2013).

334

335 **3.2. Plant flammability properties**

336 Individual components of the flammability trait are twig and leaf dry matter content, degree of
337 ramification, leaf size, presence of standing litter, oils and waxes (Cornelissen et al., 2003).
338 RS cannot quantify individual components of the flammability trait, but it can be used to

339 assess combustibility of entire plant communities, which is driven by the amount of dry
340 biomass and canopy structure. RS data have been used to support fire risk assessment and
341 served as basis for fire monitoring schemes at the landscape level (Arroyo et al., 2008).
342 Optical RS data have been used to derive vegetation properties such as the proportion
343 between live and dead biomass (Jia et al., 2006) and fuel moisture content (ratio between
344 water and dry leaf mass) (Chuvienco et al., 2002; Koetz et al., 2004). Both are relevant
345 attributes for classification of fuel types (Arroyo et al., 2008; Lasaponara and Lanorte, 2007).
346 The major limitation of passive optical RS for fire risk assessment is its inability to i) estimate
347 vegetation height, which is critical for fuel type discrimination, and ii) to penetrate deeper into
348 multi-layered canopies and therefore cannot provide information about understory, which
349 plays an important role for fire spreading (Arroyo et al., 2008). Using active radar RS systems
350 (Saatchi et al., 2007) and the fusion of optical RS data with laser scanning (Erdody and
351 Moskal, 2010; Mutlu et al., 2008) or radar data (Treuhaft et al., 2004) represent a promising
352 approach for fire risk assessment in terms of precise canopy structure and biomass mapping.

353

354 **3.3. Plant photosynthetic pathway and photosynthesis**

355 Spatial distribution of the plant photosynthetic pathway, i.e. C₃, C₄ and CAM metabolism, is
356 relevant for simulating global carbon budget, because C₄ plants tend to benefit from
357 increasing temperature and atmospheric CO₂ (Ehleringer et al., 1997; Still et al., 2003). C₃
358 and C₄ leaves differ in internal leaf structure and biochemical composition (Hatch, 1987) and
359 therefore a possibility of spectral discrimination between C₃ and C₄ plants exists. Siebke and
360 Ball (2009) discriminated C₃ and C₄ grass species using a simple ratio between leaf
361 reflectance at 696–709 and 545–567 nm that was sensitive to various concentrations of
362 chlorophyll a and b. Irisarri et al. (2009) found that proximal reflectance can distinguish
363 between a pure plantation of C₃ and C₄ grass species. However, observed spectral differences
364 can be partly attributed to differences in leaf orientation, because C₃ species in the study of

365 Irisarri et al. (2009) had more erect leaves than C4 species. Airborne or satellite based RS
366 studies used multi-temporal RS observations that captured asynchronous seasonality of C3
367 and C4 grass species (Davidson and Csilag, 2001; Foody and Dash, 2007) and could explain
368 about 60% of the variability in C3/C4 grassland species composition.

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

377 APAR is approximated by unitless fraction expressing how much of incoming
378 photosynthetic active radiation is absorbed by vegetation (fAPAR). FAPAR was recognized
379 as one of the essential climate variables by FAO Global Terrestrial Observing System
380 (Gobron and Verstraete, 2009) and it is being currently estimated from global satellite RS
381 data. The simplest empirical solutions relate fAPAR to the vegetation greenness using NDVI
382 (Myneni and Williams, 1994) and EVI (Xiao et al., 2004) indices. EVI tends to outperform
383 NDVI in denser canopies, where NDVI saturates (Huete et al., 2002). Empirical retrievals of
384 fAPAR are sensitive to perturbing effects of soil background, observing geometry and
385 atmospheric conditions (Fensholt et al., 2004). Alternatively, many operational RS-based
386 fAPAR algorithms rely nowadays on physically-based approaches using RTMs (Baret et al.,
387 2007; Gobron et al., 2000; Myneni et al., 2002). Recent comparative studies (D'Odorico et al.,
388 2013; Martínez et al., 2013; McCallum et al., 2010), however, found inconsistencies among
389 fAPAR products. The largest discrepancies were reported for coniferous forests (D'Odorico et

390 al., 2013; McCallum et al., 2010), which is mainly attributed to simplified representation of
391 canopy structure in existing RTMs.

392 Possibility of LUE estimation from RS increased only in the past decade because of the
393 development of fine spectral resolution instruments. We concentrate our discussion on direct
394 RS approaches, which quantify LUE by measuring subtle changes in leaf and canopy
395 reflectance resulting from two photoprotective mechanisms: non-photochemical quenching
396 and chlorophyll fluorescence (Grace et al., 2007). Non-photochemical quenching dissipates
397 the excess energy into heat by inducing changes in the xanthophyll pigment cycle. Different
398 composition of xanthophyll pigments results into changes of leaf reflectance at 531 nm, which
399 lead to the formulation of the photochemical reflectance index (PRI) (Gamon et al., 1992;
400 Peñuelas et al., 1995). PRI exponentially increases with increasing LUE and is able to explain
401 about 42% of LUE variability at the leaf level and 59% at the canopy level (Garbulsky et al.,
402 2011). According to Garbulsky et al. (2011) PRI seems to perform better at the canopy level,
403 but some studies argued that the PRI-LUE relationship is negatively affected by the canopy
404 structure, soil background and observation geometry (Barton and North, 2001; Hernández-
405 Clemente et al., 2011; Hilker et al., 2008a). Moreover, PRI values vary between species with
406 the same photosynthetic capacity (Guo and Trotter, 2004). Therefore the use of PRI as the
407 LUE proxy in complex canopies needs to be further investigated.

408 Sun induced chlorophyll fluorescence (SiF) is recently being explored as an indicator of
409 LUE and actual photosynthesis (Damm et al., 2010; Malenovský et al., 2009; Meroni et al.,
410 2009). SiF is a flux of photons that were not used for photosynthesis, but re-emitted at 685 nm
411 and 740 nm (Buschmann, 2007). This adds a weak ($\leq 3\%$), but detectable, signal to the
412 remotely sensed leaf and canopy reflectance (Meroni et al., 2009; Moya et al., 2004). SiF was
413 first estimated using proximal reflectance data by analysing double-peak reflectance feature
414 between 690 and 710 nm (Zarco-Tejada et al., 2003) or the narrow oxygen absorptions –
415 Fraunhofer lines (Meroni and Colombo, 2006). The later principle was recently applied on

416 airborne and satellite RS data. Zarco-Tejada et al. (2009) estimated SiF of individual trees
417 under water stress using RS data of very high spatial (15 cm) and spectral (1 nm) resolutions.
418 Joiner et al. (2011) and Guanter et al. (2012) presented the first global map of plant steady
419 state SiF as monthly averages in 2° x 2° grid derived from Fourier Transform Spectrometer
420 (FTS) on board of the Greenhouse gases Observing SATellite (GOSAT). Despite the recent
421 evidence of SiF retrievals from optical RS data, the operational approaches will require
422 rigorous spectral calibrations and atmospheric corrections (Guanter et al., 2007) and to fully
423 understand the effects of environmental variables on SiF (Malenovsky et al., 2009).

424

425 **3.4. Plant height**

426 Plant height is an important trait associated with plant competitive abilities. Laser scanning
427 has emerged to be the most accurate RS technology for the measurement of plant and canopy
428 height (Danson et al., 2009; Lefsky, 2002; van Leeuwen and Nieuwenhuis, 2010). Discrete
429 return laser scanning have been successfully used for height estimation mainly of tall canopies
430 such as boreal coniferous (Hopkinson et al., 2004; Næsset et al., 2004), temperate deciduous
431 (Brandtberg et al., 2003) or tropical (Clark et al., 2004) forests. Less often it has been used in
432 smaller canopies, such as shrubs (Glenn et al., 2011), crops (Davenport et al., 2000) or
433 grasslands (Straatsma and Middelkoop, 2007). The best absolute accuracies achieved in tree
434 height estimation from airborne discrete return laser scanners are between 0.5 and 1.0 m
435 irrespective to a tree height (Kaartinen et al., 2012). According to Næsset et al. (2004) the
436 accuracy in height estimation from discrete return laser scanning is higher for individual trees
437 (relative RMSE of 5±2.5%) than for forest canopies (relative RMSE of 7±2.5%). Generally, a
438 relative error of height estimation in tall forest canopies is usually less than 10% of the
439 measured mean canopy height (Kaartinen et al., 2012; Næsset et al., 2004), while for lower
440 canopies it reaches up to 20% (Davenport et al., 2000; Kaartinen et al., 2012)..

441 Canopy height estimation using discrete return laser scanning faces three major issues.
442 First is the determination of the terrain elevation, which is difficult in very low or too dense
443 canopies, where emitted signal cannot penetrate to the ground (Falkowski et al., 2008; Lefsky,
444 2002). Second is the accurate detection of the uppermost canopy layer, which depends on the
445 sampling pulse density (Jakubowski et al., 2013; Magnusson et al., 2007). Tree height
446 accuracy decreases with decreasing sampling pulse density, but remains relatively constant
447 and high until the densities drops below 1 pulse/m² (Jakubowski et al., 2013). The last issue is
448 related to the selection of an extraction method. A recent international comparison revealed
449 large variability among 14 extractions methods (RMSE varied between 0.5 and 4.5 m) to
450 estimate height of individual coniferous trees (Kaartinen et al., 2012).

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

456

457 **3.5. Lifespan and phenology**

458 Leaf lifespan (longevity) and phenology (seasonal timing) are closely related to plant nutrition
459 conservation and competitive strategies and are influenced by local meteorological,
460 topographic and soil variations (Dahlgren et al., 2007). It is beyond the capabilities of RS to
461 measure leaf lifespan of evergreen species. But for plant communities that periodically change
462 their foliar apparatus, time series of RS data provide an effective means of extracting land
463 surface phenology (LSP) indicators including start, end, duration and maximum peak of the
464 vegetation season (Liang and Schwartz, 2009; Reed et al., 1994). Considering strictly the
465 definition of leaf phenology by Cornelissen et al. (2003) then the length of the vegetation
466 season is the equivalent RS proxy of leaf phenology. It is important to realize that LSP

467 indicators are related, but not identical, to field observed plant phenology indicators such as
468 budburst, leaf unfolding, flowering (Liang and Schwartz, 2009).

469 Typical temporal and spatial resolutions of RS data used for LSP analysis are biweekly
470 composites of VIs of global spatial extent and a pixel size ranging from 0.25 to 8 km (e.g.,
471 MODIS land products (Huete et al., 2002), AVHRR NDVI time series (Tucker et al., 2005)).
472 The estimation of the LSP indicators from the satellite RS is influenced by four factors: i)
473 temporal resolution (Kross et al., 2011), ii) missing or noisy data due to clouds or snow cover
474 (Delbart et al., 2006), iii) magnitude of the seasonal amplitude in vegetation greenness to
475 override other sources of variation (e.g. earlier greening of understory), and iv) a method
476 extracting the phenology indicators (de Beurs and Henebry, 2010; White et al., 2009). White
477 et al. (2009) demonstrated that different extraction methods (e.g. global and local threshold
478 values, inflection points in time series curves) applied on NDVI time series can yield
479 differences up to 60 ± 20 days in the estimation of the start of the vegetation season. This
480 suggests that there is no agreement on a single, globally appropriate extraction method of LSP
481 (Schwartz and Hanes, 2010; White et al., 2009).

482 Consistent and long time series of RS data enable analyzing inter-annual variability in
483 vegetation trends (de Jong et al., 2012) and land surface phenology (White et al., 2009) (see
484 Remote Sensing special issue on monitoring global vegetation with AVHRR NDVI3g Data
485 (1981-2011); http://www.mdpi.com/journal/remotesensing/special_issues/monitoring_global).
486 Particular attention has been drawn on high latitude regions (Delbart et al., 2006), where
487 climatic changes have been pronounced. Prolongation of the vegetation season has been
488 revealed in Europe (Stöckli and Vidale, 2004) and globally (Julien and Sobrino, 2009) in
489 1980's and 90's, but the extent and quantification of these changes are still under discussion.
490

491 **3.6. Specific leaf area and leaf dry matter content**

492 Plant scientists consider leaf dry matter content (LDMC in mg g^{-1}) and specific leaf area (SLA
493 in $\text{m}^2 \text{g}^{-1}$) as two separate traits. LDMC negatively correlates with SLA (Garnier et al., 2001;
494 Shipley and Vu, 2002; Vile et al., 2005) and both traits are related to plant growth rate and
495 leaf resistance to physical damage. We want to clarify first that some RS studies use terms
496 “leaf dry matter content” or “dry matter content” when actually referring to leaf mass per area
497 (LMA) – the inverse ratio of SLA (Riaño et al., 2005; Schaepman et al., 2004; Vohland et al.,
498 2010).

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

516 and cellulose variability in a pine forest, Serrano et al. (2002) could explain up to 80% of
517 lignin variability in chaparral communities.

518 SWIR wavelengths are most important for LMA estimation (Asner et al., 2011; Kokaly et
519 al., 2009), but they are also strongly influenced by water absorption (Riaño et al., 2005). The
520 masking effect of water and canopy structure decreases the accuracy of LMA estimates from
521 optical RS. Therefore a water removal algorithm is required or one could estimate leaf water
522 content instead, because it is a complementary measure of LMA and can be retrieved with
523 higher accuracy than LMA using RTM inversion (Clevers et al., 2008; Colombo et al., 2008).

524

525 **3.7. Leaf and canopy nitrogen**

526 Nitrogen (N) is an important component in proteins, nucleic acids and chlorophylls and
527 therefore strongly linked to plant photosynthesis (Reich et al., 1995) and gross primary
528 productivity (LeBauer and Treseder, 2008; Smith et al., 2002). Currently the best way to
529 estimate N from optical RS is by means of empirical methods, because physically-based
530 retrievals are not well established. The only leaf RTM having N as an input is the LIBERTY
531 model (Dawson et al., 1999). This model is not often used among the RS research community,
532 which prefers using a simpler model – PROSPECT (Jacquemoud et al., 1996). Though there
533 were attempts to incorporate N into PROSPECT, they were abandoned due to its strong
534 covariance with other N containing compounds leading to inconsistent results (Jacquemoud et
535 al., 1996; Kokaly et al., 2009). Among many empirical approaches, several VIs were
536 proposed specifically to estimate leaf N and they were mainly established for crops (Chen et
537 al., 2010; Tian et al., 2011). Also band selection techniques, such as stepwise or partial least
538 square regressions, were successfully applied on transformed reflectance spectra (Smith et al.,
539 2003; Yoder and Pettigrew-Crosby, 1995). Based on our literature review (Appendix S1) and
540 Fig. 2, we can conclude that empirical RS methods can retrieve N with high accuracy. The

541 average R^2 between RS-estimated and measured N was equal to 0.72 ± 0.16 and the average
542 relative RMSE was equal to $15 \pm 7\%$.

543 Wavelengths that were frequently reported as important for N estimation are summarized
544 in Fig. 3. These wavelengths can be integrated into three broad spectral regions: i) red-edge
545 region (680-780 nm) that is characterized by low reflectance in red due to strong C_{ab}
546 absorption and high reflectance in NIR due to leaf internal scattering , ii) NIR region around
547 1200 nm that is associated also with water absorption, and iii) SWIR region where three main
548 protein absorption features are located around 1680 nm, 2050 nm and 2170 nm (Kumar et al.,
549 2001). Recent work of Knyazikhin et al. (2012) showed that a positive correlation between N
550 and NIR reflectance, which was previously found in some temperate and boreal forests
551 (Ollinger et al., 2008), is actually a result of canopy structure effects. They emphasized that
552 quantification of biochemical traits from NIR in general is strongly influenced by radiation
553 scattering processes, which have to be accounted for in order to achieve correct results.

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

567 (Hallik et al., 2009); Appendix S2) and therefore more suitable for communities with lower
568 species diversity.

569

570 [Fig. 3. and Table 3 about here]

571

572 **3.8. Leaf and canopy phosphorus**

573 Leaf phosphorus (P) is an indicator of plant growth rate and nutrient quality. We found only
574 limited number of studies that estimated P from RS data (Appendix S1). Only Porder et al.
575 (2005) used airborne RS to estimate canopy P concentration of broadleaf tropical forest. The
576 rest of the reviewed studies used airborne-based or proximal sensing to estimate P
577 concentration in structurally homogeneous canopies, such as crops and grasslands. Based on
578 results of our literature review (Appendix SA1) and Fig. 2, we can conclude that P can be
579 retrieved from optical RS with lower accuracies than N. The average R^2 between RS-
580 estimated and measured P was equal to 0.57 ± 0.16 and the average relative RMSE was equal
581 to $23 \pm 7\%$. In all cases empirical retrieval methods were used. The selection of spectral bands
582 used in regression models was inconsistent among the reviewed studies, which can be mainly
583 attributed to the low P concentration in leaves (less than 1% of dry leaf mass) and the absence
584 of pronounced P absorption features. NIR and SWIR spectral bands were often included in the
585 regression models, but these bands are strongly influenced by water absorption and canopy
586 structure. When the effect of leaf water content was suppressed by applying a water removal
587 technique (Schlerf et al., 2010), the accuracy of the P prediction in savana grasslands from
588 proximal sensing increased (Ramoelo et al., 2011). We have not found any VI that is
589 specifically designed for P estimation and previously designed indices for C_{ab} or N estimation
590 did not perform satisfactorily (Pimstein et al., 2011). Similar to nitrogen, the biomass
591 weighted canopy P concentration can be retrieved with higher accuracy than leaf-level
592 concentration (Pimstein et al., 2011).

593

594 **4. Concluding remarks**

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

- 599 • Classification of plant growth and plant life forms cannot be entirely reproduced by RS.
600 Global RS-based land cover classification schemes classify vegetation to broad classes,
601 which are by definition closer to plant growth forms. Their classification accuracy is
602 around 70%. High resolution RS facilitate local classifications of some plant growth forms
603 or even individual species, but the classification accuracy vary between 50 and 95%.
604 Combination of optical RS with multi-directional RS or laser scanning can improve
605 existing plant classifications by increasing the separability among vegetation types.
- 606 • Plant flammability as a combined trait cannot be quantified using optical RS observations.
607 However, when combining optical passive and active RS then the combustibility of entire
608 plant communities can be well assessed. RS data are currently being used to quantify fire
609 properties such as moisture content, plant height and the proportion between live and dead
610 biomass. These are valuable input data for fire models and fuel classification schemes.
- 611 • Use of optical RS for mapping C3 and C4 photosynthetic pathways remains rare. Instead,
612 RS data has been widely exploited for spatio-temporal mapping of plant photosynthetic
613 activity using proxies of fraction of absorbed photosynthetic radiation and light use
614 efficiency. Direct estimation of light use efficiency by means of chlorophyll fluorescence
615 has emerged as a very promising approach. Though major challenges in RS of chlorophyll
616 fluorescence are currently being investigated, recent results already demonstrated that
617 large scale mapping of chlorophyll fluorescence from RS is possible.

- 618 • Plant height can be directly and most accurately estimated from active laser scanning data.
619 The relative error of height estimation from discrete return laser systems is usually below
620 10% in tall forest canopies and increases up to 20% in lower canopies. Full waveform
621 lasers do not necessarily provide improvement in absolute height estimation, but they
622 certainly offer better insight into the 3D vegetation structure. Understanding the effects of
623 canopy structure on reflectance is a major challenge in RS of vegetation.
- 624 • Multi-temporal satellite RS can deliver relevant land surface phenological indicators, such
625 as start, end, maximum peak and duration of the vegetation season for plant communities
626 periodically changing their foliage. Recent comparative studies suggested that there is no
627 agreement on a single, globally appropriate method to extract land surface phenology.
628 There is critical need to effectively validate RS-based phenology indicators and therefore
629 field data are required across global biomes. Future studies should attempt to employ data
630 from active RS systems to separate asynchronous phenology of understory and the main
631 canopy. Moreover, the future chlorophyll fluorescence observations from space can
632 provide an accurate identification of the photosynthesis onset and offset.
- 633 • Specific leaf area or its inverse ratio leaf mass per area can be estimated from the optical
634 RS data using empirical, as well as physical methods. Despite this possibility, the retrieval
635 accuracy substantially varied and it was the lowest among the reviewed plant biochemical
636 traits. Inconsistencies are mainly due to confounding effects of water present in the plant
637 tissue and the atmosphere. An algorithm that significantly suppresses the absorption effect
638 of water or improvements in atmospheric corrections is prerequisite for an accurate
639 retrieval of leaf mass per area from optical RS.
- 640 • Nitrogen can be estimated from optical RS using empirical methods achieving the highest
641 accuracies among the reviewed plant biochemical traits. The highest uncertainty was
642 observed in coniferous canopies, which is due to their complex canopy structure.
643 Therefore there is an urgent need for improved RS methods accounting and correcting for

644 canopy structure effects. We supported the hypothesis that RS of chlorophyll content can
645 be used as an operational proxy for N estimation, since moderately strong relationship
646 between nitrogen and chlorophyll exists. Moreover, the future multi-temporal
647 observations of chlorophyll fluorescence might also improve N retrieval methods.

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

653

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

658 We see an urgent need to address in a more comprehensive fashion the effects of
659 vegetation structure in interpretation of RS data. Therefore advanced measurements of traits
660 such as the volume of intracellular air spaces, leaf thickness, leaf angle distribution,
661 proportion of non-photosynthetic biomass within canopy light acclimation are required.
662 Generally, more coherent collection of field trait data together with proximal and remote
663 sensing observations will be required to develop robust scaling schemes and support airborne
664 and satellite based RS methods of trait estimation. Such an interdisciplinary cooperation
665 resulted recently in a novel concept of “optical traits”, i.e. assessing combined effects of
666 vegetation physiological, structural and phenological properties on reflectance measurements
667 (Ustin and Gamon, 2010).

668 The most important advantage of using RS is its ability to provide spatially explicit and
669 continuous maps of relevant traits repeatedly during the vegetation season. If combined with

670 eco-physiological models that are designed having the current and future capabilities of RS
671 data in mind, substantial progress will be achieved in spatio-temporal mapping of ecosystem
672 functioning.

673

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680

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682

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1379

1380 **Supporting Information**

1381 Additional Supporting Information may be found in the online version of this article:

1382 **Appendix S1** Literature review of remote sensing of leaf biochemical traits

1383 **Appendix S2** Relationship between leaf chlorophyll and nitrogen content in alpine grass

1384 species

1385

1386 **List of figures:**

1387

1388

1389 **Fig. 1.**

1390 Link between ecological and remote sensing spatial scales with examples of typical remote
1391 sensing spectroradiometers operational at variety of spatial scales.

1392

1393

1394 **Fig. 2.**

1395 Performance of remote sensing methods evaluated by (a) the coefficient of determination R^2
1396 and (b) the relative root mean square error RMSE for the estimation of nitrogen, phosphorus
1397 concentration and content and leaf mass per area from various type of remote sensing data.

1398 (Legend: Central line in a box is median, box height is the interquartile range (i.e. 50% of the
1399 data) and whiskers represent minimum and maximum unless the observed values exceed 1.5
1400 of the interquartile range in that case they are marked as outliers (crosses). Number (in format
1401 of x/y) above each box indicates number of reported accuracy indicators (x) and
1402 corresponding number of scientific articles (y) they were extracted from.).

1403

1404

1405 **Fig. 3.**

1406 Overview of spectral wavelengths used in scientific literature for estimation of nitrogen
1407 concentration and content in green and dry plant leaves. Each dot represents a reported
1408 spectral wavelength. A typical reflectance response of green vegetation (grey line) is plotted
1409 for clarity.

1410

1411 **List of tables:**

1412

1413

1414 **Table 1**

1415 Example of scaling of leaf nitrogen concentration and content from the leaf to the canopy

1416 level.

1417

1418

1419 **Table 2**

1420 Link between plant traits as described by Cornelissen et al. (2003) and possible remote

1421 sensing counterparts.

1422

1423

1424 **Table 3**

1425 Pearson's correlation coefficient (R) between measured leaf chlorophyll and leaf nitrogen

1426 concentration and content as reported for some plant species in literature and from our own

1427 field measurements. The number of stars in the superscript indicates the statistical

1428 significance of the reported correlations (**** $p \leq 0.001$, *** $p \leq 0.01$, ** $p \leq 0.05$, * $p \leq 0.1$, in

1429 case the statistical significance was not reported the R value is without a superscript).

1430

Figure 1

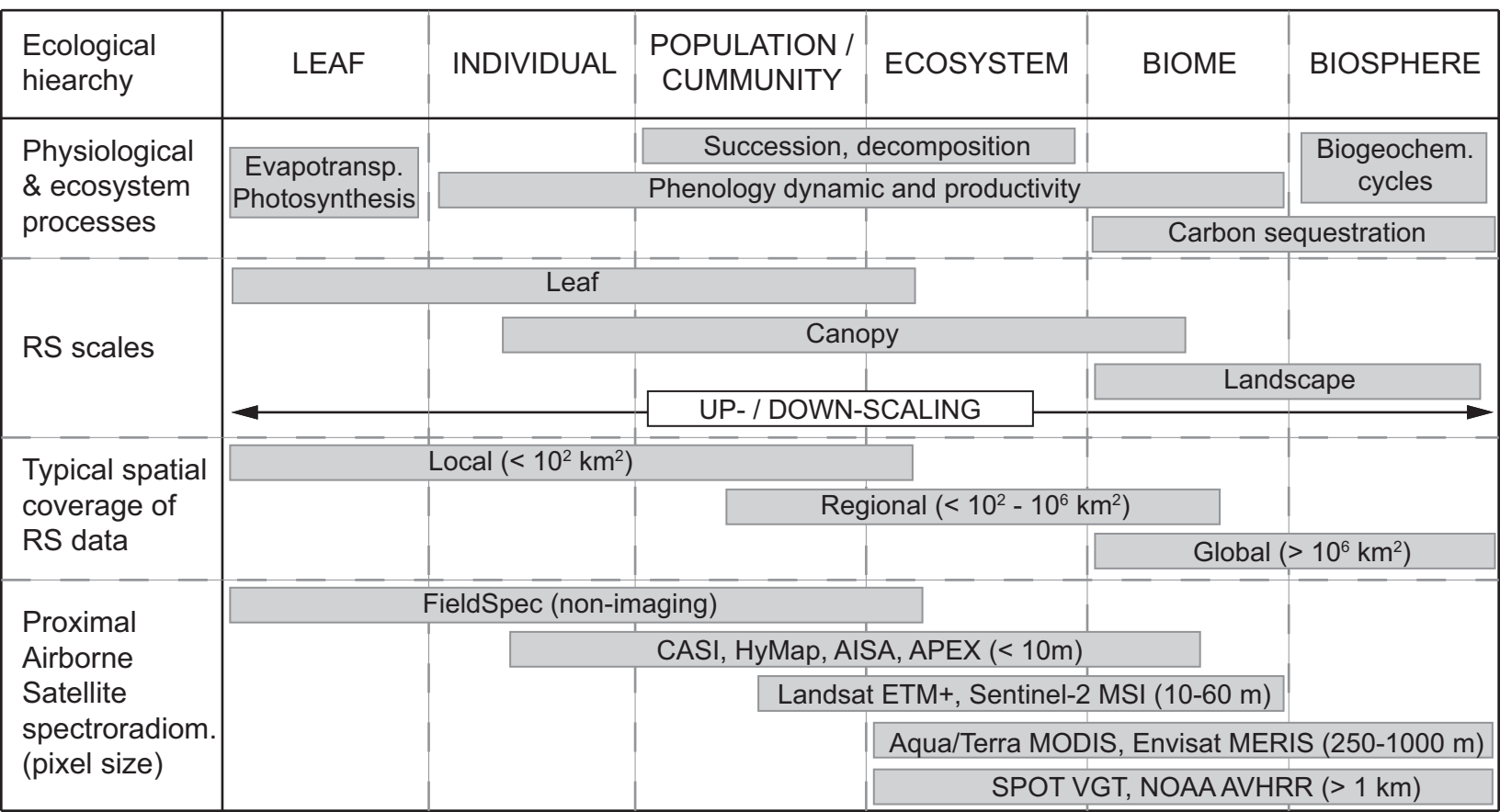


Figure 2

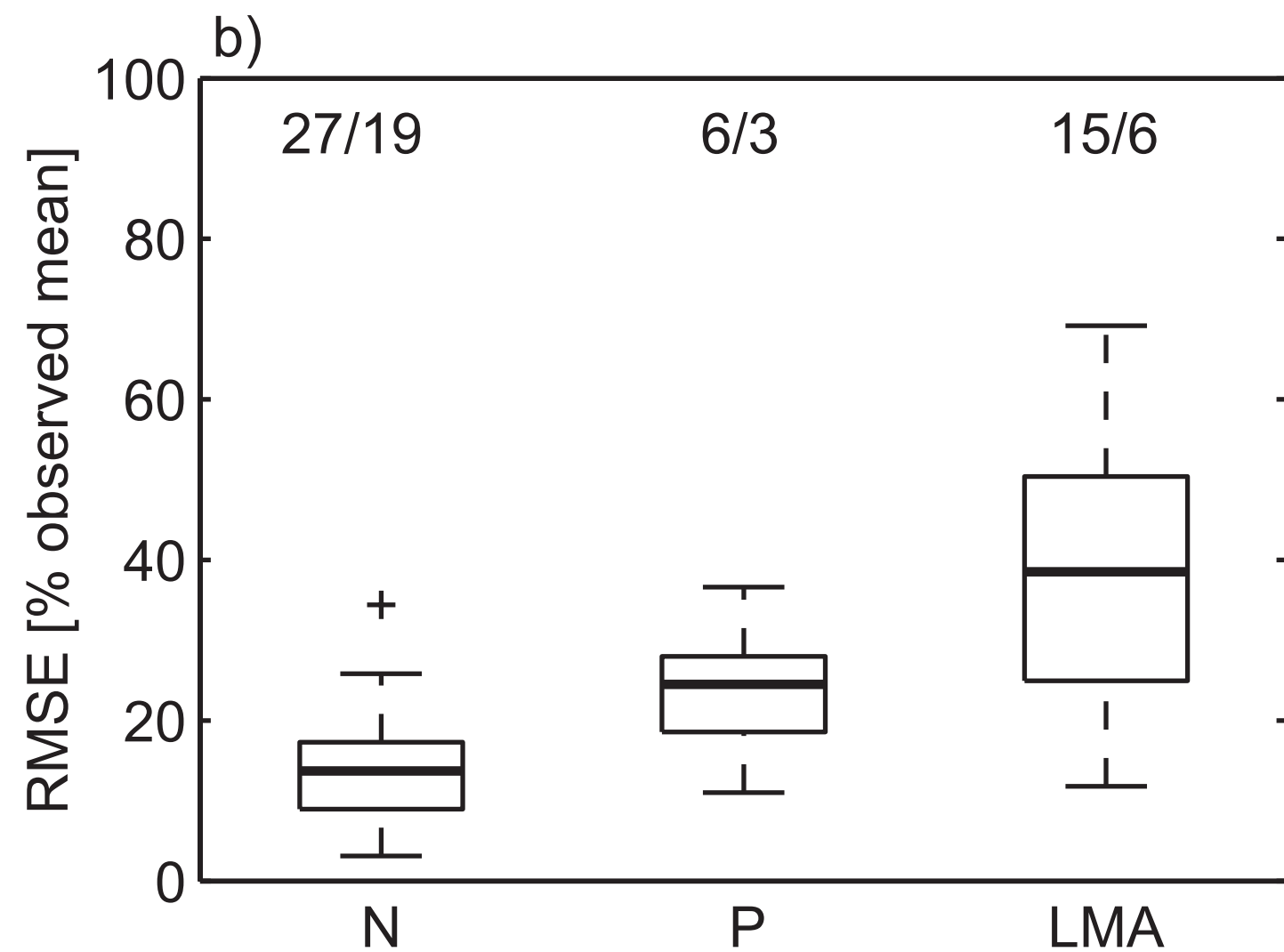
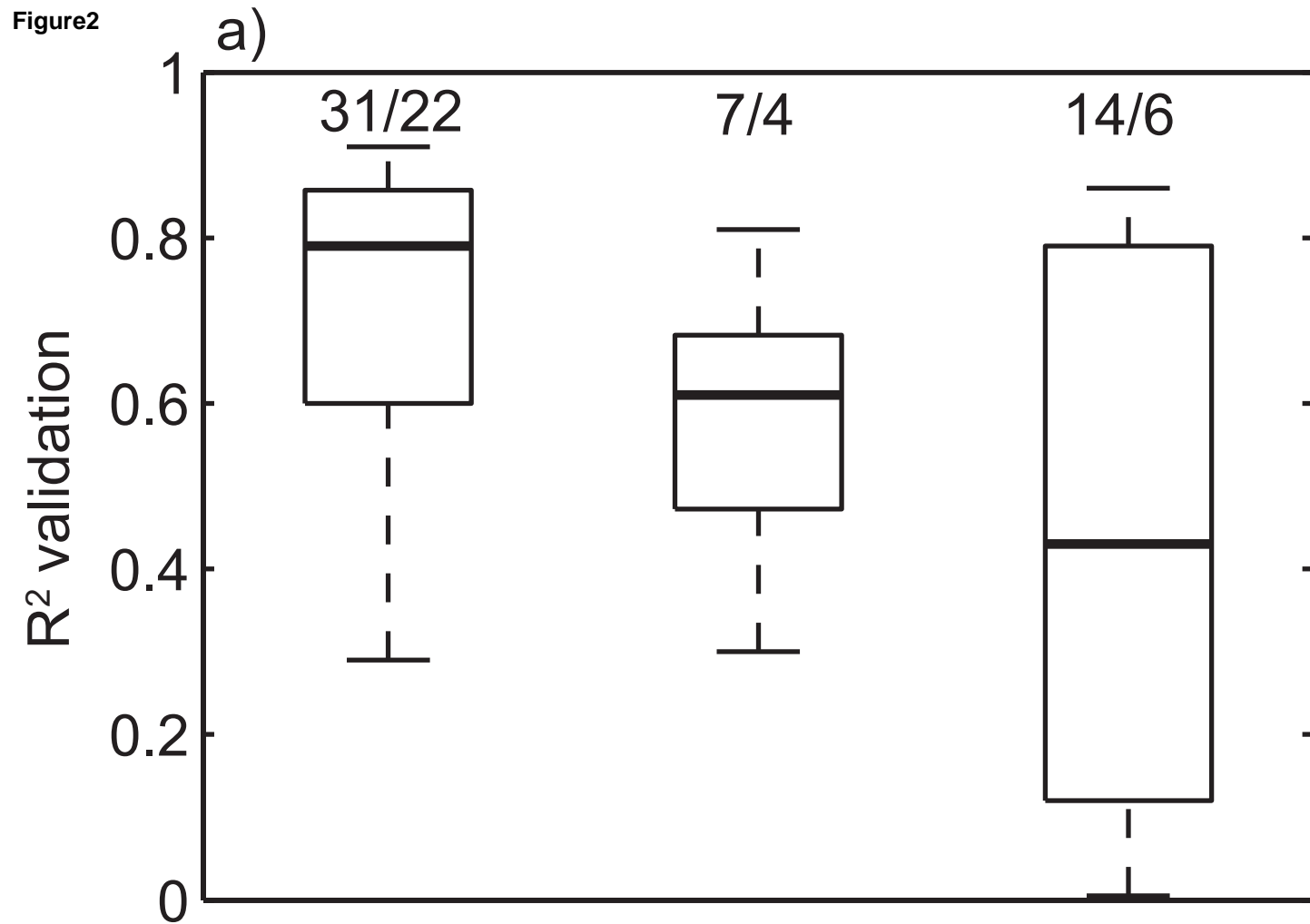


Figure3

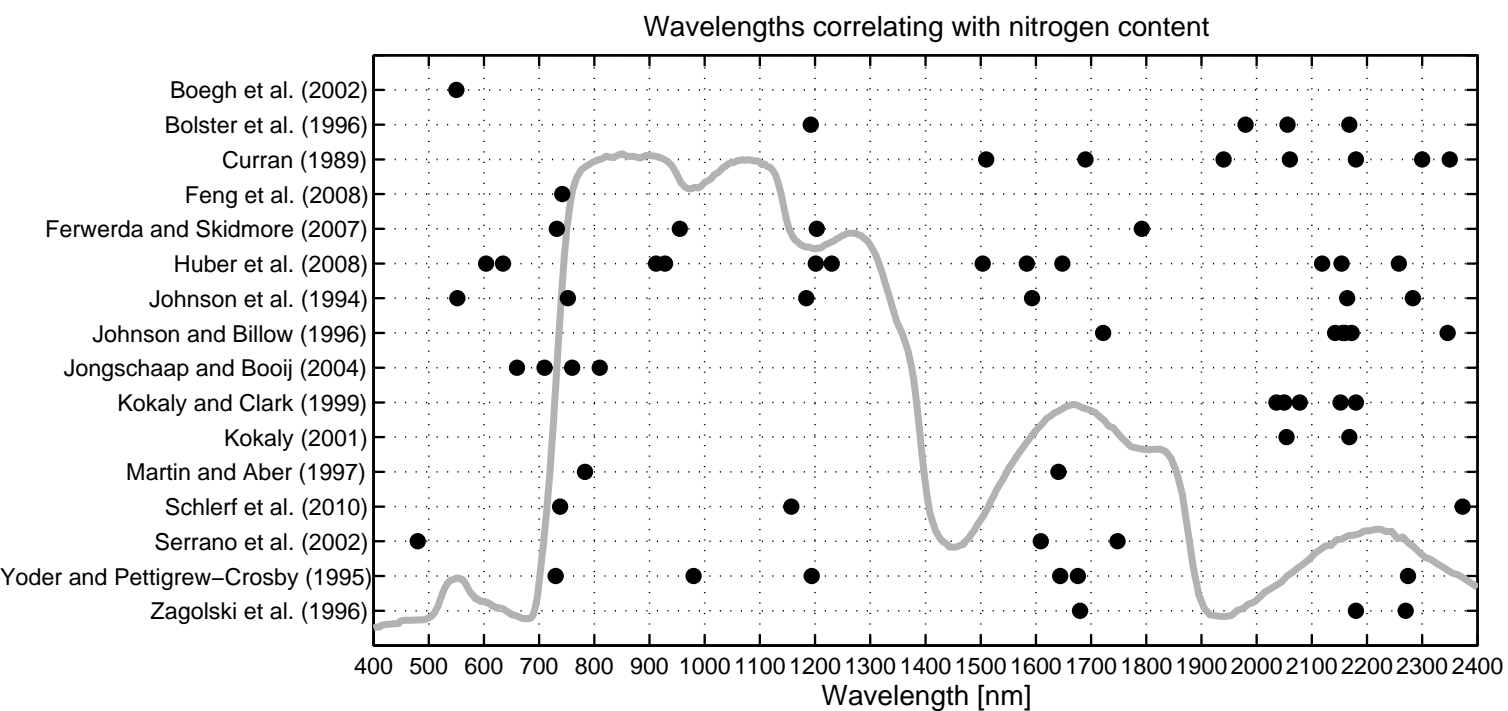


Table 1

Trait	Leaf trait of a species <i>i</i>	Leaf trait of a community	Canopy trait property)
N concentration [units]	N_i [mg g ⁻¹ of leaf mass]	$N_{CWM} = \text{SUM}(N_i * F_i)$ [mg g ⁻¹ of leaf mass]	$N_{CWM}[\text{mg g}^{-1}] * \text{BIO} [\text{g m}^{-2}]$ [mg m ⁻² of surface area]
N content [units]	N_i [mg cm ⁻² of leaf area]	$N_{CWM} = \text{SUM}(N_i * F_i)$ [mg m ⁻² of leaf area]	$N_{CWM}[\text{mg m}^{-2}] * \text{LAI} [\text{m}^2 \text{m}^{-2}]$ [mg m ⁻² of surface area]
		← RS up/downscaling (Malenovsky et al., 2007) →	
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

Table 2

Plant traits from Cornelissen et al. (2003) [typical units]	Trait definition	RS methods	RS references	Operational scale					
				Leaf	Individual	Pop./Com.	Ecosystem	Biome	LOSU ¹
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	Not available						
		But RS can asses vegetation fire properties: Canopy moisture content	(Chuvienco 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

(Continued on next page)

Table 2 (continued)

Plant traits from Cornelissen et al. (2003) [typical units]	Trait definition	RS methods	RS references	Operational scale					
				Leaf	Individual	Pop./Com.	Ecosystem	Biome	LOSU ¹
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 size [m ²]	One-sided surface area	Not available	Not available						
		But for entire plant communities it can be linked to leaf area index	(Chen et al., 2002; Fernandes et al., 2004; Garrigues et al., 2008)			*	*	*	4
Specific leaf area [m ² 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	(Fourty and Baret, 1998; Riaño et al., 2005; Vohland et al., 2010)			*	*		2-3
		Related to leaf water content that can be estimated from RTM inversion or empirical methods	(Clevers et al., 2008; Colombo et al., 2008)	*	*	*	*		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

(Continued on next page)

Table 2 (continued)

Plant traits from Cornelissen et al. (2003) [typical units]	Trait definition	RS methods	RS references	Operational scale					LOSU ¹
				Leaf	Individual	Pop./Com.	Ecosystem	Biome	
Leaf nitrogen concentration/content [mg g ⁻¹ / mg m ⁻²]		Directly estimated using empirical RS methods	(Martin et al., 2008; Oppelt and Mauser, 2004; Serrano et al., 2002)	*	*	*			3
		Indirectly related to chlorophyll content that can be estimated using RTM inversion	(Dash and Curran, 2004; Zarco-Tejada et al., 2004)	*	*	*	*		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						

⁽¹⁾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).

Table 3

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

Appendix S1: Literature review of remote sensing of leaf biochemical traits

Relevant peer-reviewed scientific articles presenting the estimation of important leaf functional biochemical traits (i.e. nitrogen and phosphorus concentration, leaf mass per area) using optical remote sensing (RS) methods were collected from Scopus using an appropriate set of keywords (e.g. “nitrogen content” and “remote sensing”). The reviewed papers are summarized in Table S1.1. We limit our search only to recent articles published since 2000, including some important studies published in the 1990's. We included a paper only if it was cited more than five times before 2009 (not applied to articles published since 2009). From each article we extracted the following main features of the study: i) leaf functional trait, ii) vegetation type (broadleaf, conifers, crops, grasslands, mixed type), iii) trait units, iv) leaf or canopy scale of trait and RS measurements (leaf trait measurements of individual species are upscaled to the canopy level by calculating community weighted trait mean using species relative abundance; leaf RS measurements are acquired from individual leaves using laboratory or in-situ spectrometers, whereas canopy RS measurements are acquired by airborne or satellite spectrometers), v) RS spectrometer type (laboratory, field, airborne, spaceborne), vi) applied RS retrieval method, vii) coefficient of determination (R^2) reported for validation, viii) R^2 reported for calibration (i.e. building predictive relation between a trait and RS data), ix) relative root mean square error (RMSE) and x) the source (table or figure) from where the R^2 or RMSE was extracted. For those studies presenting results without the statistical accuracy indicators (R^2 and RMSE), we extracted the input data from figures and calculated the statistical results of the published relationship ourselves whenever possible. The absolute RMSE was converted to relative units by normalizing it to the mean observed trait value. Accuracy indicators (i.e. R^2 and RMSE) of remote sensing methods for the estimation of nitrogen, phosphorus concentration and content and leaf mass per area in different vegetation types are presented at Fig. S1.1.

Table S1.1

Summary of important features extracted from articles presenting RS methods to estimate nitrogen (N), phosphorus (P) content or concentration and leaf mass per area (LMA) or specific leaf area (SLA). (Legend: Trait/Spect. Scales (L – leaf, C – canopy defines at which organization level trait/spectral data were measured); Sensor type (cf. original papers for exact sensors' acronyms, L – laboratory, F – field, A – airborne, and S – satellite); RS methods (R – reflectance, CR – continuum removal, FD – first derivative, LR – linear regression, MLR – multiple linear regression, SLR – stepwise linear regression, PLS – partial least square regression, VI – vegetation index); R^2 val. and cal. (coefficient of determination for validation and calibration, n.a. – data not available), RMSE % (relative root mean square error), figure # / table # is the number in the original publication)

Trait	Vegetation type	Trait units	Trait / Spect. scales	Sensor type	Remote sensing methods	R^2 val.	R^2 cal.	RMSE %	Figure # / Table #	Reference
N	broadleaf	%	L / C	AVIRIS (A)	Radiative transfer + empirical	0.91	n.a.	13.8	2a / -	(Asner and Vitousek, 2005)
N	crops	mg g ⁻¹	L / C	CASI (A)	LR with R@550nm	n.a.	0.78	n.a.	eq. 10	(Boegh et al., 2002)
N	mixed	%	L / L	NIRSystem 6500 (L)	PLSR of log(1/R)	0.87	0.97	25.8	2a,3a / -	(Bolster et al., 1996)
N	crops	mg g ⁻¹	L / C	CASI (A)	LR - VI (DCNI)	0.51	n.a.	15.7	sec.3.5.2	(Chen et al., 2010)
N	crops	mg g ⁻¹	L / C	FieldSpec (F)	LR - VI (DCNI)	0.62	0.64	13.7	fig.7a / sec.3.5.1	(Chen et al., 2010)
N	crops	%	L / L	GER 3700 (L)	LR with red edge	n.a.	0.86	n.a.	6e / -	(Cho and Skidmore, 2006)
N	grassland	%	L / L	GER 3700 (L)	LR with red edge	n.a.	0.47	n.a.	6e / -	(Cho and Skidmore 2006)
N	grassland	%	L / C	GER 3700 (F)	LR with red edge	n.a.	0.82	n.a.	6e / -	(Cho and Skidmore 2006)
N	grassland	g m ⁻²	C/C	FieldSpec (F)	LR – VI	0.77	n.a.	23.8	5,6 / v	(Clevers and Kooistra, 2012)
N	crops	g m ⁻²	C/C	CropScan (F)	LR – VI	0.85	n.a.	42.3	8,9 / vi	(Clevers and Kooistra, 2012)
N	broadleaf	%	C / C	Hyperion (S)	PLSR of log(1/R)	0.64	n.a.	13.1	3 / 4	(Coops et al., 2003)
N	crops	%	L / C	FieldSpec (F)	LR – VI (MCARI/MTVI2)	n.a.	0.48	n.a.	- / 3	(Eitel et al., 2007)
N	crops	%	L / C	FieldSpec (F)	LR with red edge	0.75	n.a.	17.8	5a / -	(Feng et al., 2008)
N	crops	g m ⁻²	L / C	FieldSpec (F)	LR with FD@742nm	0.87	n.a.	17.4	6a / -	(Feng et al., 2008)
N	mixed	%	L / C	GER 3700 (F)	LR – VI (NDVI-based)	0.72	n.a.	n.a.	- / 2	(Ferwerda et al., 2005)
N	mixed	%	L / L	GER 3700 (L)	SLR of FD	0.86	n.a.	n.a.	- / 4	(Ferwerda and Skidmore, 2007)
N	crops	%	L / C	SD2000 (F)	LR – VI (NDVI-based)	n.a.	0.56	n.a.	4e / 3	(Hansen and Schjoerring, 2003)
N	crops	g m ⁻²	C / C	SD2000 (F)	LR – VI (NDVI-based)	n.a.	0.69	n.a.	4f / 3	(Hansen and Schjoerring, 2003)
N	coniferous	%	L / C	HyMap (A)	CR	0.45	n.a.	8.5	7b / 3	(Huber et al., 2008)
N	broadleaf	%	L / C	HyMap (A)	CR	0.29	n.a.	9.7	- / 3	(Huber et al., 2008)
N	coniferous	kg ha ⁻¹	C / C	AVIRIS (A)	SLR of FD	0.9	n.a.	24.8	5c / -	(Johnson et al., 1994)
N	coniferous	mg cm ⁻²	L / C	AVIRIS (A)	SLR of FD	0.85	n.a.	20.0	6a / -	(Johnson et al., 1994)
N	crops	g m ⁻²	C / C	CropScan TM (F)	LR	n.a.	0.82	n.a.	5 / -	(Jongschaap and Booij, 2004)
N	grassland	%	L / C	CAO (A)	Neural networks	0.41	0.53	13.2	5 / 2	(Knox et al., 2011)
N	mixed	%	C / C	AVIRIS (A)	MLR of FD	0.87	n.a.	8.7	4a / 7	(Martin and Aber, 1997)

Table S1.1 (continued)

Trait	Vegetation type	Trait units	Trait / Spect. scales	Sensor type	Remote sensing methods	R ² val.	R ² cal.	RMSE %	Figure # / Table #	Reference
N	mixed	%	C / C	AVIRIS (A)	PLSR	0.83	n.a.	13.1	- / 2 sec3.2	(Martin et al., 2008)
N	mixed	%	C / C	Hyperion (S)	PLSR	0.82	n.a.	17.0	- / 2 sec3.2	(Martin et al., 2008)
N	grassland	mg g ⁻¹	L / C	GER 3700 (F)	LR with red edge	0.89	n.a.	n.a.	- / 3	(Mutanga and Skidmore, 2007)
N	grassland	%	L / C	GER 3700 (F)	SLR of CR	0.52	n.a.	24.4	4 / -	(Mutanga et al., 2004)
N	mixed	%	C / C	AVIRIS (A)	PLSR of FD of log(1/R)	n.a.	0.79	n.a.	2a / -	(Ollinger et al., 2008)
N	mixed	%	C / C	MODIS (S)	PLSR of FD of log(1/R)	n.a.	0.88	n.a.	2b / -	(Ollinger et al., 2008)
N	mixed	%	C / C	AVIRIS (A)	PLSR of FD of log(1/R)	0.79	0.83	11.9	6b / 2	(Ollinger and Smith, 2005)
N	mixed	%	C / C	Hyperion (S)	PLSR of FD of log(1/R)	0.60	0.82	15.6	6a / 2	(Ollinger and Smith, 2005)
N	crops	g m ⁻²	C / C	AVIS (A)	LR - VI (CAI)	n.a.	0.77	n.a.	6b / -	(Oppelt and Mauser, 2004)
N	crops	kg ha ⁻¹	C / C	IKONOS (S)	LR - VI (NDVI)	n.a.	0.70	n.a.	- / 6	(Reyniers and Vrindts, 2006)
N	crops	kg ha ⁻¹	C / C	CropScan TM (F)	LR - VI (NDVI)	n.a.	0.75	n.a.	- / 7	(Reyniers and Vrindts, 2006)
N	mixed	%	L / C	AVIRIS (A)	LR - VI (NDNI)	n.a.	0.34	n.a.	2a / -	(Serrano et al., 2002)
N	mixed	%	C / C	AVIRIS (A)	SLR of FD	0.75	n.a.	34.4	1a / 3	(Serrano et al., 2002)
N	coniferous	%	C / C	HyMap (A)	SLR of CR	0.56	n.a.	4.9	2d / 4	(Schlerf et al., 2010)
N	coniferous	%	L / L	FieldSpec (L)	SLR of CR	0.47	n.a.	7.0	2b / 3	(Schlerf et al., 2010)
N	mixed	%	C / C	AVIRIS (A)	PLSR of FD of log(1/R)	0.79	0.83	10.4	- / 2	(Smith et al., 2003)
N	mixed	%	C / C	Hyperion (S)	PLSR of FD of log(1/R)	0.6	0.82	15.7	- / 2	(Smith et al., 2003)
N	mixed	%	C / C	AVIRIS (A)	PLSR of FD of log(1/R)	0.82	n.a.	13.4	- / 3	(Smith et al., 2002)
N	broadleaf	%	C / C	AVIRIS (A)	PLSR of FD	0.86	n.a.	3.1	2b / -	(Townsend et al., 2003)
N	broadleaf	%	C / C	Hyperion (S)	PLSR of FD	0.83	n.a.	3.6	2a / -	(Townsend et al., 2003)
N	broadleaf	mg g ⁻¹	L / L	NIRSystem 6500 (L)	SLR of log(1/R)	0.85	n.a.	4.6	- / 2	(Yoder and Pettigrew-Crosby, 1995)
N	broadleaf	g m ⁻²	C / C	GER (F)	SLR of log (1/R)	0.63	n.a.	n.a.	- / 3	(Yoder and Pettigrew-Crosby, 1995)
N	coniferous	%	L / C	AVIRIS (A)	SLR	0.55	n.a.	13.9	7a / -	(Zagolski et al., 1996)
P	mixed	%	L / L	GER 3700 (L)	SLR of FD	0.51	n.a.	n.a.	- / 4	(Ferwerda and Skidmore, 2007)
P	grassland	%	L / C	CAO (A)	Neural networks	0.79	0.57	17.6	5 / 2	(Knox et al., 2011)
P	grassland	%	L / C	HyMap (A)	Neural networks	0.63	n.a.	28.0	3 / 4	(Mutanga and Kumar, 2007)
P	grassland	%	L / C	GER 3700 (F)	SLR of CR	0.70	n.a.	11.0	4 / -	(Mutanga et al., 2004)
P	crops	%	L / C	FieldSpec (F)	LR - VI (NDVI-based)	0.30	n.a.	23.4	- / 4	(Pimstein et al., 2011)
P	crops	g m ⁻²	C / C	FieldSpec (F)	LR - VI (NDVI-based)	0.61	n.a.	36.6	4bd / 5	(Pimstein et al., 2011)
P	crops	g m ⁻²	C / C	FieldSpec (F)	PLSR of FD	0.81	n.a.	25.6	5d / 6	(Pimstein et al., 2011)
P	crops	%	L / C	FieldSpec (F)	PLSR of FD	0.46	n.a.	18.6	5b / 6	(Pimstein et al., 2011)
P	broadleaf	%	L / C	AVIRIS (A)	Radiative transfer + empirical	n.a.	n.a.	n.a.	3b / -	(Porder et al., 2005)
P	grass	%	C / C	FieldSpec (F)	SLR of water-removed R	0.64	n.a.	17.6	- / 1	(Ramoelo et al., 2011)

Table S1.1 (continued)

Trait	Vegetation type	Trait units	Trait / Spectr scales	Sensor type	Remote sensing methods	R ² val.	R ² cal.	RMSE %	Figure # / Table #	Reference
LMA	mixed	g cm ⁻²	L / L	Perkin-Elmer (L)	PROSPECT inver.	n.a.	n.a.	28.0	- / 2	(Baret and Fourty, 1997)
LMA	mixed	g cm ⁻²	L / L	Varian Cary 17 DI (L)	PROSPECT inver.	0.48	n.a.	42.1	6 / 2	(Baret and Fourty, 1997)
LMA	broadleaf	g cm ⁻²	L / L	FieldSpec (L)	PROSPECT inver.	0.01	n.a.	n.a.	4b / -	(Colombo et al., 2008)
LMA	broadleaf	g cm ⁻²	L / C	MIVIS (A)	PROSAIL inver.	0.00	n.a.	23.9	8c / -	(Colombo et al., 2008)
LMA	mixed	g cm ⁻²	L / L	Perkin-Elmer (L)	MLR	0.84	n.a.	17.0	6 / -	(Fourty and Baret, 1998)
LMA	broadleaf	g m ⁻²	L / L	FieldSpec (L)	LR – VI (NDVI-based)	n.a.	n.a.	47.1	5a / 4	(le Maire et al., 2008)
LMA	broadleaf	g m ⁻²	L / L	FieldSpec (L)	LR – VI (NDVI-based)	n.a.	n.a.	28.0	5b,c / 4	(le Maire et al., 2008)
LMA	broadleaf	g m ⁻²	C / C	FieldSpec (F), Hyperion (S)	LR – VI (NDVI-based))	n.a.	n.a.	11.8	7 / 5	(le Maire et al., 2008)
SLA	broadleaf	m ² kg ⁻¹	C / C	LandsatTM (S)	LR - VI (red/nir)	n.a.	0.91	n.a.	5a / 9	(Lymburner et al., 2000)
SLA	broadleaf	m ² kg ⁻¹	C / C	LandsatTM (S)	LR - VI (SLAVI)	n.a.	0.84	n.a.	5c / 9	(Lymburner et al., 2000)
LMA	mixed	g cm ⁻²	L / L	Perkin-Elmer (L)	PROSPECT inver.	0.38	n.a.	n.a.	2a / -	(Riaño et al., 2005)
LMA	mixed	g cm ⁻²	C / C	GER 2600 (F)	PROSPECT-Lillesaeter inver.	0.12	n.a.	n.a.	5a / -	(Riaño et al., 2005)
LMA	coniferous	g cm ⁻²	L / C	DAIS 7915 (A)	PROSPECT-GeoSAIL inver.	0.15	n.a.	22.2	3d / -	(Schaeppman et al., 2004)
LMA	coniferous	g m ⁻² *LAI	C / C	DAIS 7915 (A)	PROSPECT-GeoSAIL inver.	0.79	n.a.	30.6	3f / -	(Schaeppman et al., 2004)
LMA	crops	g cm ⁻² *LAI	C / C	HyMap (A)	PROSAIL inver.	0.86	n.a.	144.8	4d / 4	(Vohland et al., 2010)
LMA	crops	g cm ⁻² *LAI	C / C	HyMap (A)	PROSAIL inver.	0.72	n.a.	134.5	4d / 4	(Vohland et al., 2010)
LMA	crops	g cm ⁻² *LAI	C / C	HyMap (A)	PROSAIL inver.	0.85	n.a.	69.0	4d / 4	(Vohland et al., 2010)
LMA	crops	g cm ⁻²	L / C	HyMap (A)	PROSAIL inver.	0.10	n.a.	38.5	- / 7	(Vohland et al., 2010)
LMA	crops	g cm ⁻²	L / C	HyMap (A)	PROSAIL inver.	0.25	n.a.	69.2	- / 7	(Vohland et al., 2010)
LMA	crops	g cm ⁻²	L / C	HyMap (A)	PROSAIL inver.	0.72	n.a.	51.3	- / 7	(Vohland et al., 2010)
LMA	Mixed	g cm ⁻²	L / L	FieldSpec (L)	LR – VI (NDVI-based)	0.68	0.64	n.a.	5 / 2	(Wang et al., 2011)

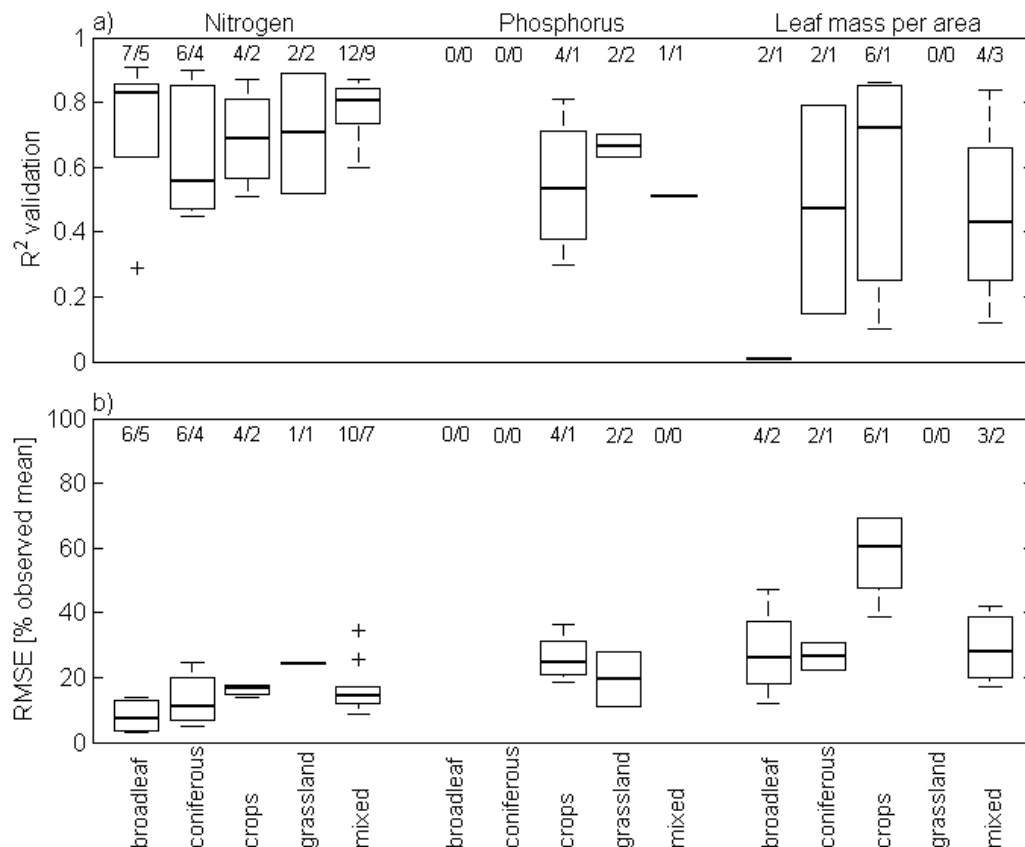


Fig. S1.1. Performance of remote sensing methods for the estimation of nitrogen, phosphorus concentration and content and leaf mass per area in different vegetation types evaluated by using the coefficient of determination R^2 (a) and relative root mean square error RMSE (b). (Legend: Central line in 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.)

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Appendix S2. Relationship between leaf chlorophyll and nitrogen content in alpine grass species.

Leaf samples of 27 plant species growing at two study sites located in the area of Col de Lautaret, in the central French Alps (within 5 km from the Joseph Fourier alpine station, 45°02'09"N, 06°24'04"E) were collected during the vegetation season of 2008. The first test site is located on the south facing slopes above the village Villar-d'Arène (1800 – 2100 m a.s.l.). A detailed description of this site, which is affected by a long history of agricultural and pastoral land use, is given in Quétier et al. (2007). The second test site is located in a valley between Lautaret and Galibier Pass (2000 – 2800 m a.s.l.). The prevailing vegetation cover is mosaic of bare rocks and alpine meadow species.

Leaf trait data of 27 dominant subalpine and alpine species, i.e. specific leaf area, leaf chlorophyll and nitrogen content, were measured in July 2008. Well developed individuals that were growing under sun exposed conditions, were collected from three locations along the altitude gradient at each study site. Depending on species occurrence, we collected 5 to 20 samples per species. Specific leaf area (SLA) was calculated as one-sided fresh leaf area per unit dry mass ($\text{cm}^2 \text{g}^{-1}$). Leaf chlorophyll a and b were determined spectrophotometrically from an extract of grinded leaves in ethanol according to Wellburn (1994) following methods proposed by Porra, et al. (1989). Leaf nitrogen was obtained from dried and grinded leaves samples of 3 – 5 mg, which were analysed with a FlashEA 1112 elemental analyser (Thermo Fisher Scientific Inc., Milan, Italy). Both, leaf total chlorophyll and nitrogen per unit dry mass were multiplied by SLA to obtain final leaf chlorophyll ($\mu\text{g cm}^{-2}$) and nitrogen (mg cm^{-2}) content. Correlation coefficients and linear relationships established between leaf chlorophyll and nitrogen content of 27 subalpine and alpine species is presented at Fig. S2.1.

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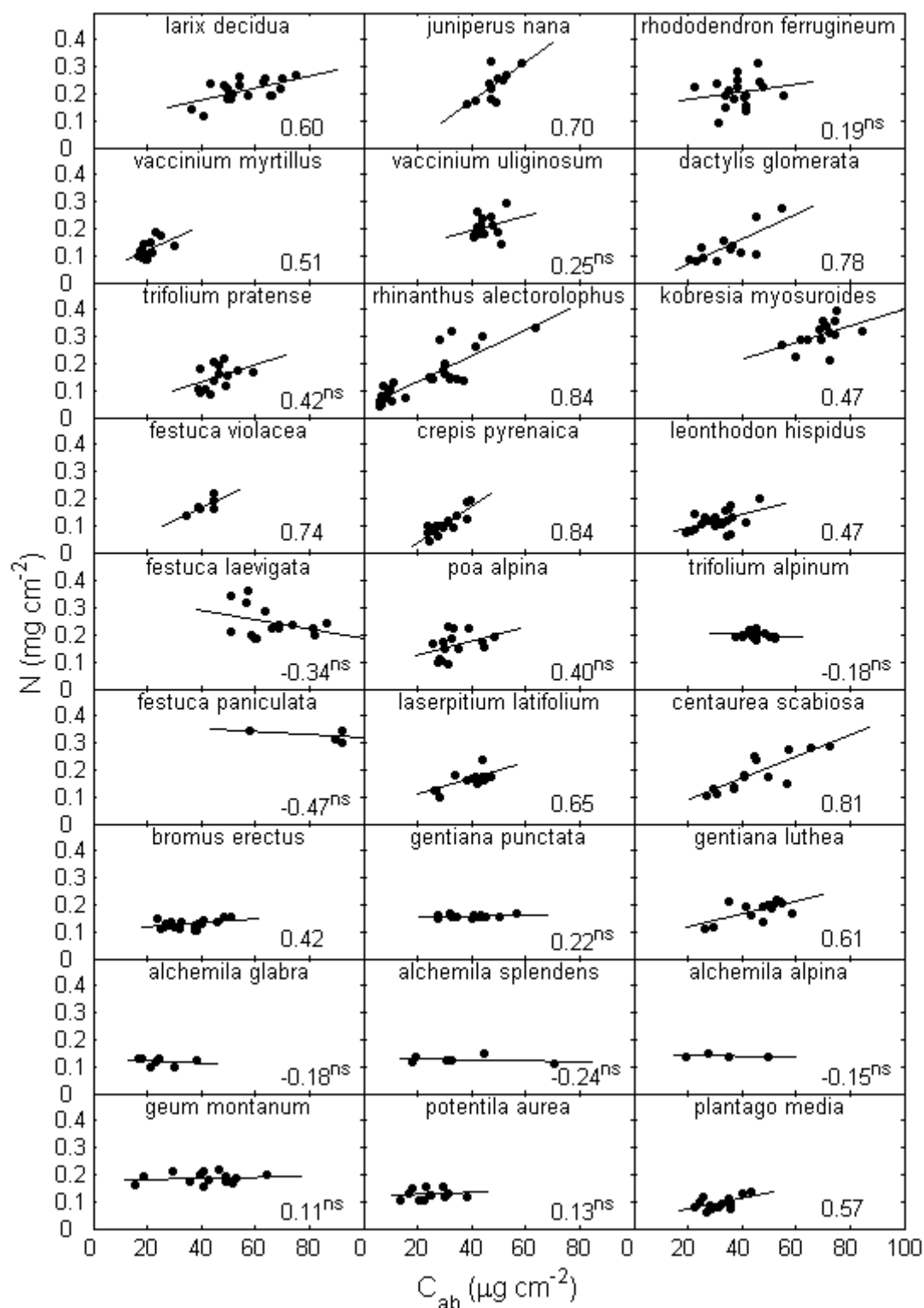


Fig. S2.1. Relationship between leaf chlorophyll (C_{ab} ($\mu\text{g cm}^{-2}$)) and nitrogen (N (mg cm^{-2})) content for 27 dominant subalpine and alpine species. For each relationship we report Pearson's correlation coefficient, the superscript "ns" indicates that the correlation is not significant ($p \leq 0.1$).