Chapter 6
Do Reflectance Spectra of Different Plant Stands in Wetland Indicate Species Properties?

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Abstract This contribution discusses the relationships between reflectance spectra obtained by field spectroscopy and properties of the leaves of the species that form a stand and the relation between reflectance spectra and stand characteristics. We thus investigate the reliability of conclusions made at the species levels on the basis of the reflectance spectra of the stands. We studied monospecific and mixed stands that thrive in habitats along a hydrological gradient in the intermittent Lake Cerknica. The reflectance spectra differed significantly at the stand and leaf levels; however, although the shape of the reflectance spectra of a monospecific stand with *Phalaris arundinacea* was similar to the shape of the leaf spectra, this was not the case for mixed stands. The leaf morphological and biochemical properties that explain most of the variability of the spectra differed for graminoids and different dicotyledons. This study shows that based on the reflectance spectra, the species properties for monospecific stands can be deduced, while for mixed stands, such deductions can be misleading.

Keywords Macrophytes • Ecosystem structure • Hydrological gradient • *Phalaris arundinacea*

6.1 Introduction

Ecosystem structure and function depend on multiple environmental factors that affect habitats, species properties and their distribution (Ustin 2010). The key factor is the amount of incoming radiation and its fate in the plant community. The majority of light is absorbed by different plant organs, while some of the light can either penetrate through the stand or is reflected from the plant surface. Thus, only a small proportion of the incoming solar radiation reaches the stand floor. The interactions between the radiation and the plant communities are very complex, due

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to stand diversity, species architecture and leaf structural properties (Larcher 2003). Leaves that thrive in specific environments have specific traits that optimise their capture of solar energy and prevent damage due to excessive and/or harmful photons (Gurevitch et al. 2002). This fine-tuning is made possible through special adaptations of leaves at the morphological, anatomical, biochemical and functional levels (Robe and Griffiths 2000; Boeger and Poulson 2003; Šraj-Kržič and Gaberščik 2005; Klančnik et al. 2012).

Light that is reflected from plant leaves can provide a basis for an understanding of the photosynthetic performance and energy balance of plants (Vogelmann 1993). It also provides information on leaf biochemistry (Levizou et al. 2005; Castro and Sanchez-Azofeifa 2008) and nutrient and water status (Baltzer and Thomas 2005; Asner and Martin 2008) and can serve as a tool for stress detection (Gitelson et al. 2002); in some cases, this also allows species classification (i.e. through their spectral signatures) (Castro-Esau et al. 2006). Similarly, light that is reflected from plants can indicate the condition of a stand (Asner 1998; Ullah et al. 2012).

Different indices that are based on species and/or stand reflectance spectra have been developed to determine the properties of different plant species and plant functional groups (Levizou et al. 2005). However, without detailed knowledge of the basic parameters that define the spectral signatures at the species level, reflectance spectra might not provide reliable information (Milton et al. 2009).

In comparison to measurements of leaf optical properties, which are time-consuming, remote sensing allows for surveying and monitoring of relatively large areas, as well as comparisons of data across time and space (Ollinger 2010). Therefore, one of the main reasons for detailed research and a need to understand leaf optical properties is the establishment of libraries of species spectral signatures, along with species leaf properties (Chandrasekharan 2005).

Remote sensing includes two types of spectroscopy: ‘field spectroscopy’, which is based on measurements within or close to a stand, and ‘imaging spectroscopy’, which is the detection of the spectra from a distance (e.g. from aircrafts or satellites). In comparison to remote sensing, field spectroscopy is technically less demanding and less influenced by atmospheric conditions (Gao et al. 2009).

In the present study, we aimed to define the properties of stands and leaves in the intermittent Lake Cerknica affecting the reflectance spectra that can be obtained by field spectroscopy and to compare the reflectance spectra at the stand level to that at the leaf level. We also examined how reliable conclusions at the species level can be on the basis of the reflectance spectra of a stand.

6.2 Materials and Methods

6.2.1 Site Description

The intermittent Cerknica Lake appears at the bottom of the karst Cerknica Polje (38 km^2). Due to abundant precipitation in spring and autumn, the polje changes into a shallow lake of 20–25 km^2 in size. On average, the floods last for 260 days a year, and the dry period usually starts in late spring (Kranjc 2003). The result of this intermittence of Cerknica Lake is the zonation of the plant communities along a hydrological gradient that depends on the duration and extent of the flooding.

6.2.2 Field Spectroscopy and Stand Properties

For the purpose of the present study, we selected plant stands at 23 locations along the hydrological gradient (Table 6.1). The selected stands were homogenous, as either monospecific or mixed species. We performed two to four sets of 20 scans per stand in the vegetative period. These measurements of reflectance between 280 nm and 887 nm were carried out using a portable spectrometer (Jaz Modular Optical Sensing Suite; Ocean Optics, Inc., Dunedin, FL, USA). Prior to the leaf reflectance measurements, a white reference panel (Spectralon®, Labsphere, North Sutton, USA) was used to calibrate the spectrometer to 100 % reflectance. The reflectance spectra were then calculated as the ratios of the sample data to the white reference under the same illumination. The scans were recorded between 10:00 h and 14:00 h. The detector was positioned 90 cm above the stands, at a constant angle that was adjusted according to the position of the sun. At each sampling plot, the properties of plant stands were determined as the number of species, species abundance, total plant and specific species cover (%), height of the stand and species properties (i.e. plant phenological phases, vitality, leaf angle). The species abundance was estimated according to the Braun-Blanquet method (Braun-Blanquet 1964). The amount of photosynthetically active radiation and the air temperature and relative humidity were also measured.

6.2.3 Measurements at the Leaf Level

The reflectance spectra of the leaves were measured on the day of sampling with the above-mentioned portable spectrometer. The individual leaves were positioned under an integrating sphere (ISP-30-6-R; Ocean Optics, Inc., FL, USA) connected to the spectrometer via an optical fibre (QP600-1-SR-BX; Ocean Optics, Inc., Dunedin, FL, USA). During the illumination of the leaf with an ultraviolet-visible-near infrared (UV-VIS-NIR) light source (DH-2000, Ocean Optics, Inc., FL, USA),

Table 6.1 Plant species composition and abundance (in brackets) at selected locations during the growing season

Location	Month of measurement	RDA code[a]	Plant species composition (abundance[b])
1	May	1	*Euphorbia lucida* (3), *Phalaris arundinacea* (3), *Carex elata* (3)
	June	2	*E. lucida* (4), *P. arundinacea* (2), *C. elata* (2)
	Aug	3	*E. lucida* (5), *C. elata* (2), *P. arundinacea* (2)
	Sept	4	*P. arundinacea* (4), *E. lucida* (3), *C. elata* (2)
2	May, June, Aug, Sept	5-8	*P. arundinacea* (5)
3	Aug	9	*Myosotis scorpioides* agg. (5), *Mentha aquatica* (3), *Teucrium scordium* (2)
4	Sept	10	*T. scordium* (4), *M. aquatica* (3), *M. scorpioides* agg. (2), *Agrostis sp.* (2)
5	May	11	*Gratiola officinalis* (5), *Plantago altissima* (2)
	Aug	12	*G. officinalis* (4), *P. altissima* (3)
	Sept	13	*G. officinalis* (4), *P. altissima* (2), *C. elata* (2)
6	May	14	*Senecio paludosus* (4), *Polygonum amphibium* (3)
	Aug, 4	15-16	*S. paludosus* (5), *P. amphibium* (2)
7	June	17	*Phragmites australis* (5)
8	June	18	*Molinia caerulea* (5), *P. altissima* (2)
9	June	19	*Deschampsia cespitosa* (5), *P. altissima* (2)
10	June	20	*C. elata* (5)
11	May	21	*Apiaceae* (5), *M. scorpioides* agg. (2), *M. aquatica* (2)
	Aug	22	*M. scorpioides* agg. (3), *Apiaceae* (2), *M. aquatica* (2), *T. scordium* (2)
	Sept	23	*Apiaceae* (3), *M. aquatica* (2), *T. scordium* (2), *M. scorpioides* agg. (2)
12	May	24	*P. altissima* (4), *Carex panicea* (3), *Molinia caerulea* (2)
	Aug	25	*P. altissima* (4), *C. panicea* (3), *M. caerulea* (2)
	Sept	26	*P. altissima* (3), *M. caerulea* (2), *C. panicea* (2), *M. aquatica* (2)
13	May	27	*M. aquatica* (3), *Rorippa amphibia* (3), *P. arundinacea* (2)
	Aug, Sept	28-29	*M. aquatica* (4), *R. amphibia* (2)
14	May	30	*R. amphibia* (3), *P. amphibium* (2), *M. aquatica* (2)
	Aug, Sept	31-32	*P. amphibium* (4), *R. amphibia* (3), *M. scorpioides* agg. (2), *M. aquatica* (2)
15	May	33	*C. elata* (5), *P. altissima* (2), *G. officinalis* (2)
	Aug	34	*C. elata* (4), *G. officinalis* (3), *P. altissima* (2), *L. salicaria* (2)
	Sept	35	*C. elata* (4), *G. officinalis* (3), *P. altissima* (2)
16	May	36	*E. lucida* (5), *P. altissima* (3)
	June	37	*E. lucida* (4), *P. altissima* (3)

(continued)

Table 6.1 (continued)

Location	Month of measurement	RDA code[a]	Plant species composition (abundance[b])
	Aug, Sept	38-39	*E. lucida* (5)
17	May	40	*C. panicea* (4), *P. altissima* (3), *M. caerulea* (2), *Succisa pratensis* (2)
	June	41	*C. panicea* (3), *P. altissima* (2), *M. caerulea* (2)
	Aug	42	*P. altissima* (4), *C. panicea* (3), *M. caerulea* (3)
	Sept	43	*P. altissima* (4), *C. panicea* (2), *M. caerulea* (2)
18	May, Sept	44-45	*P. amphibium* (5)
	Aug	46	*P. amphibium* (5), *R. amphibia* (2)
19	May, Aug, Sept	47-49	*P. amphibium* (5)
20	May, Aug, Sept	50-52	*P. amphibium* (5)
21	May	53	*G. officinalis* (4), *P. altissima* (3)
	Aug	54	*P. altissima* (4), *G. officinalis* (3), *C. panicea* (2)
	Sept	55	*G. officinalis* (4), *P. altissima* (3)
22	May	56	*Schoenus nigricans* (5), *Centaurea jacea* agg. (2)
	June	57	*S. nigricans* (4), *P. altissima* (3), *C. jacea* agg. (2)
	Aug, Sept	58-59	*S. nigricans* (4), *P. altissima* (3), *C. jacea* agg. (2), *M. caerulea* (2), *C. panicea* (2)
23	May, Aug	60-54	*Salix rosmarinifolia* (5)
	Sept	55	*S. rosmarinifolia* (5), *M. caerulea* (2)

[a]RDA code in Figure 5
[b]Abundance according to Braun-Blanquet (1964)

the total adaxial reflectance spectra of the leaves were recorded between 280 nm and 887 nm, with a resolution of approximately 0.3 nm.

For the same leaves, the following morphological, anatomical and biochemical properties were determined: specific leaf area; thickness of the leaf, cuticle, epidermis and mesophyll; density and length of the leaf stomata, trichome and prickle hairs (silicified trichome in graminoids); contents of chlorophyll *a*, chlorophyll *b*, carotenoids and anthocyanins; and amount of UV-B (280–320 nm) and UV-A (320–400 nm) absorbing compounds. These analyses followed the procedures and methods as described and cited previously (Klančnik et al. 2012, 2013a).

6.2.4 Statistical Analysis

Measurements of the reflectance spectra are given as the means across 5-nm intervals. The significances of the differences between reflectance spectra were assessed by Kruskal-Wallis tests with Bonferroni correction. Detrended correspondence analysis was used for exploratory data analysis, using the CANOCO 4.5

program package. The gradient length was <3 S.D., and therefore, redundancy analysis (RDA) was used to determine the possible effects of explanatory variables (i.e. leaf traits, stand properties) on the reflectance spectra variability (ter Braak and Šmilauer 2002). Each variable was entered separately into the analysis, and the significance of its gross effects was assessed using Monte Carlo tests with 999 permutations. To avoid possible collinearity between explanatory variables, forward selection was used. Nonsignificant variables ($p > 0.05$) were excluded from the further analysis.

6.3 Results

6.3.1 Reflectance Spectra at Leaf and Stand Levels

Comparisons of the reflectance spectra differed among the stands and leaves. We compared the reflectance spectra of monospecific and mixed stands of *Phalaris arundinacea* and reflectance measurements on the leaves (Fig. 6.1). Three main differences were observed: (1) leaves reflected significantly more light than stands; (2) variability of the reflectance in different colour bands was more pronounced for leaves, with the least variability observed for mixed stands; and (3) the greatest differences were obtained in the UV, green and NIR ranges.

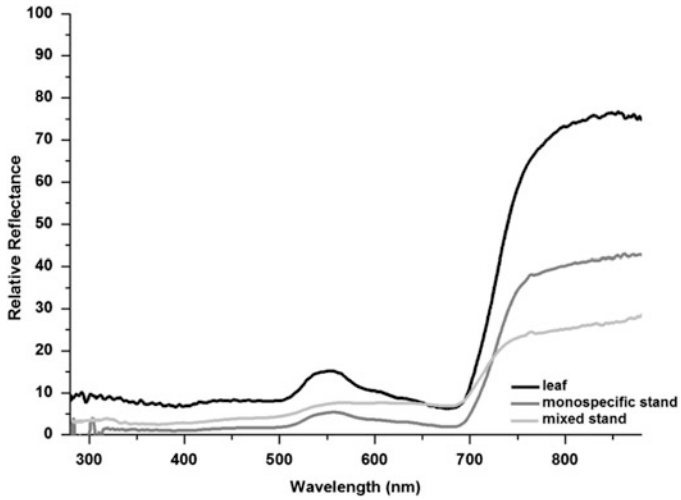

Fig. 6.1 Mean relative reflectance spectra of a *P. arundinacea* leaf, a *P. arundinacea* monospecific stand and a mixed stand where *P. arundinacea* covered 25 % of the sampling plot (Data are means over 5-nm intervals ($n = 10$))

6.3.2 Leaf Reflectance Spectra and Leaf Traits

RDA was performed to define the parameters that explained most of the variability of the reflectance spectra, taking into account the different datasets. In the first run, data on the biochemical and anatomical leaf traits and the corresponding leaf reflectance spectra were used. In this case, the thickness of the upper epidermis explained as much as 17 % of the variability of the reflectance spectra; the trichome density, 16 %; the amount of carotenoids and the length of the prickle hairs, 8 % each; and the specific leaf area, an additional 7 % (Fig. 6.2). The length of the prickle hairs was negatively related to the reflectance, while the density of the trichome showed a positive relationship. The species studied were distributed along the full gradient of visible wavelengths, which showed differences in reflectance and formed optical groups, with the exception of specimens of *Myosotis scorpioides* agg., which were scattered throughout the whole plot. The graminoids *Carex elata*, *Molinia caerulea* and *Phragmites australis* formed a single group, while the single dicotyledonous species were located distinctly apart (Fig. 6.2).

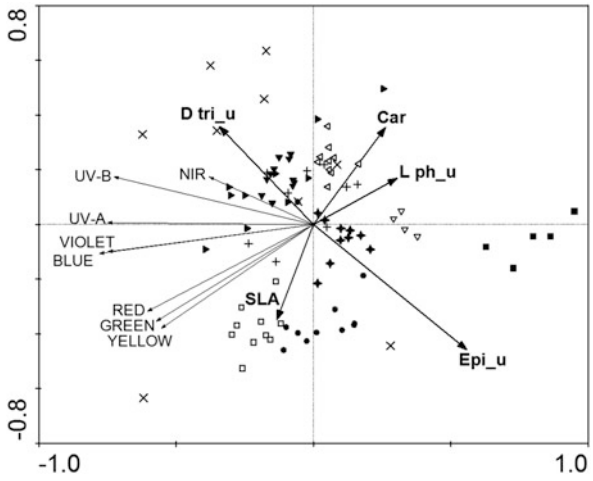

Fig. 6.2 Redundancy analysis ordination diagram showing the strength of the associations between the significant leaf traits ($p < 0.05$) and the regions of the leaf reflectance spectra. Plant species*: filled circles*, samples of *P. arundinacea*; *open squares*, *Gratiola officinalis*; *filled squares*, *Polygonum amphibium*; *filled upside-down triangles*, *C. elata*; *open upside-down triangles*, *Euphorbia lucida*; *filled right-pointing triangles*, *M. caerulea*; *open left-pointing triangles*, *P. australis*; pluses (+), *Deschampsia cespitosa*; crosses (×), *M. scorpioides* agg.; thick pluses (+), *Senecio paludosus*. **D tri_u** mean trichome density on the adaxial leaf surface, **L ph_u** mean prickle-hair length on the adaxial leaf surface, **Epi_u** epidermis thickness on the adaxial leaf surface, **SLA** specific leaf area, **Car** carotenoids content per leaf area

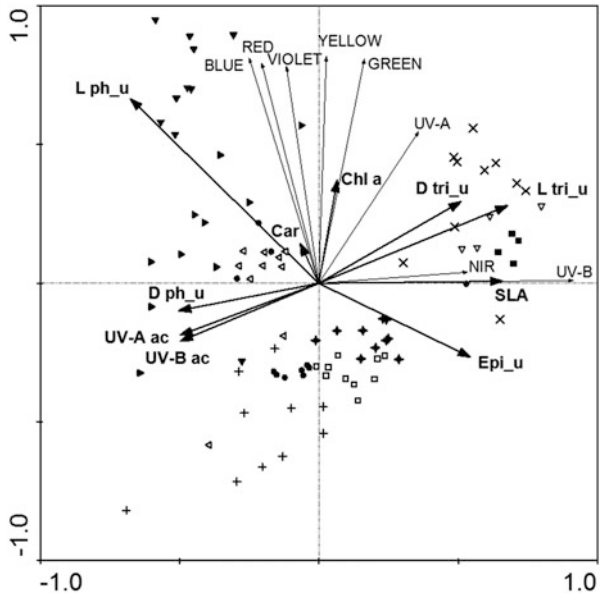

Fig. 6.3 Redundancy analysis ordination diagram showing the strength of the associations between the significant morphological and biochemical leaf traits ($p < 0.05$) and the regions of the monospecific stand reflectance spectra. Plant species: *filled circles*, samples of *P. arundinacea*; *open squares*, *Gratiola officinalis*; *filled squares*, *Polygonum amphibium*; *filled upside-down triangles*, *C. elata*; *open upside-down triangles*, *Euphorbia lucida*; *filled right-pointing triangles*, *M. caerulea*; *open left-pointing triangles*, *P. australis*; pluses (+), *Deschampsia cespitosa*; crosses (×), *M. scorpioides* agg.; thick pluses (+), *Senecio paludosus*. **D tri_u** trichome density on the adaxial leaf surface, **L tri_u** mean trichome length on the adaxial leaf surface, **D ph_u** prickle-hair density on the adaxial leaf surface, **L ph_u** prickle-hair length on the adaxial leaf surface, **Epi_u** epidermis thickness on the adaxial leaf surface, **SLA** specific leaf area, **Chl a** chlorophyll *a* content per leaf area, **Car** carotenoids content per leaf area, **UV-A ac** UV-A absorbing compounds per leaf area, **UV-B ac** UV-B absorbing compounds per leaf area

6.3.3 Monospecific Stand Reflectance and Leaf Traits

In the second RDA, we examined relationships between the reflectance spectra of monospecific stands and the biochemical and anatomical leaf traits of the species that formed these stands. The amount of total explained variance was 76 %, which was even higher than in the first RDA. The length of the prickle hairs of the upper epidermis and the density of the trichome explained 32 % and 18 % of the spectra variability, respectively; the UV-A absorbing compounds and chlorophyll *a*, 6 % each; and other significant parameters, 1–3 % each. As shown in Fig. 6.3, the graminoids reflected more in the UV range, while the reflectance in the visible range was very variable.

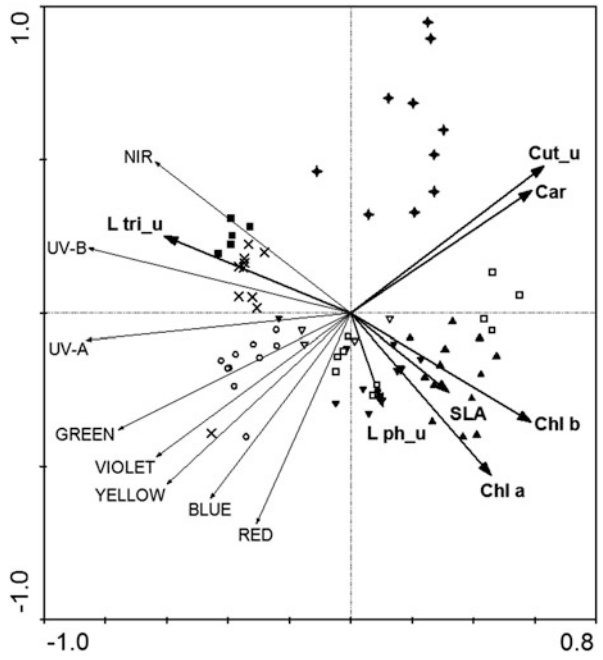

Fig. 6.4 Redundancy analysis ordination diagram showing the strength of the associations between the significant morphological and biochemical leaf traits ($p < 0.05$) and the regions of the mixed stands reflectance spectra (prevailing species covers 50 %). Prevailing plant species: *open circles*, samples of *Mentha aquatica*; *open squares*, *Gratiola officinalis*; *filled squares*, *Polygonum amphibium*; *filled upside-down triangles*, *C. elata*; *open upside-down triangles*, *Euphorbia lucida*; *filled triangles*, *Plantago altissima*; crosses (×), *M. scorpioides* agg.; thick pluses (+), *Senecio paludosus*. **L tri_u** trichome length on the adaxial leaf surface, **L ph_u** prickle-hair length on the adaxial leaf surface, **Cut_u** cuticle thickness on the adaxial leaf surface, **SLA** specific leaf area, **Chl a** chlorophyll *a* content per leaf area, **Chl b** chlorophyll *b* content per leaf area, **Car** carotenoids content per leaf area

6.3.4 Mixed Stand Reflectance and Leaf Traits

In the next step, we related the reflectance spectra of the mixed stands to the biochemical and anatomical leaf traits of the species that covered half of the sampling area of the plot. In this case, the majority of species that formed the stands were dicotyledons (except *C. elata*), and therefore, the outcomes were somewhat different. With the species traits, a total of 74 % of the variability of the reflectance spectra was explained. Chlorophyll *a* explained 31 %, the thickness of the cuticle 26 %, and other parameters exerted little influence on spectra variability (up to 5 % each). The thickness of the cuticle was negatively related to all ranges of the spectra (Fig. 6.4).

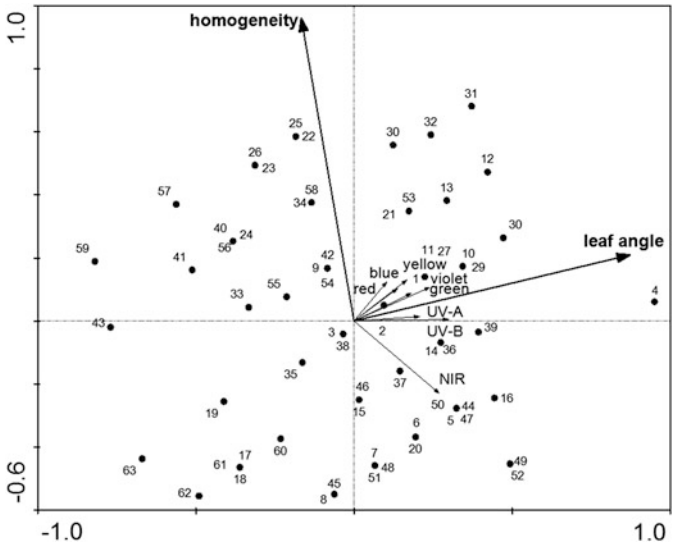

Fig. 6.5 Redundancy analysis ordination diagram showing the strength of the associations between the significant stand properties ($p < 0.05$) and the regions of the stand reflectance spectra. The detailed species compositions of the stands represented by the numbers are given in Table 6.1

6.3.5 Stand Reflectance and Stand Properties

The last RDA was performed, taking into account the stand reflectance spectra and properties of the stand. Only two variables had significant effects on the stand reflectance: leaf angle and stand homogeneity. Together, these explained 14 % of the variability (Fig. 6.5). The leaf angle was positively related to all parts of the spectra. The distribution of the stands within a plot showed that the same plots had different distributions at different times of the season.

Field spectroscopy enables determination of the properties of the analysed object. In the past decade, this method has significantly enhanced the understanding of the interactions between matter and energy at the levels of plant leaves and stands (Gamon 2006). Some studies have concentrated on the reflection in narrow wave bands, with proposals of various vegetation indices, although these have usually been tested with only a few different species (Sims and Gamon 2002). Many field spectroscopy studies have aimed to define the species composition and species properties as, for example, levels of the chlorophylls, carotenoids and anthocyanins (Gamon et al. 1990; Gitelson et al. 2009). The present study has shown that such conclusions might not be always reliable.

To establish the relationships between reflectance spectra and species traits, we studied different stand types, with different species compositions and different species properties. The measured reflectance spectra differed significantly at the leaf and stand levels, as related to the leaf and stand properties. When the

reflectance spectra of stands with different abundance of *P. arundinacea* were compared, this showed that the reflectance curves of monospecific stands of *P. arundinacea* have similar shapes to those of the *P. arundinacea* leaves, while mixed stands reflected less radiation along the whole spectra. The most pronounced differences were observed in the UV, green and NIR ranges. This was apparently related to the more complex architecture of the mixed stands, in comparison to the monospecific stands (Schulze et al. 2005).

The development of individual plant-leaf properties depends on the species genotype and site conditions, while the structure of a stand mainly depends on the species that constitute the stand, and especially on their growth forms (Larcher 2003). For Lake Cerknica, the specific water regime creates an environmental gradient (Martinčič and Leskovar 2003) that supports a variety of different communities with the different species that were included in the present study. We applied RDA to explain the variability of the spectra with the properties of the species that formed the stands. The data show that the reflectance spectra of monospecific stands can be explained by species properties, while different properties are indicative of different species or optical groups. The majority of the significant parameters to the monospecific stand reflectance were largely expected. The exceptions were for the contents of chlorophyll *a* and the carotenoids, where the relationships with reflectance were positive, although they explained minor parts of the spectra variance (i.e. 12 %). In some species and/or for some stands, the structural parameters were more important than the biochemical parameters (Klančnik et al. 2012, 2013a). It is generally accepted that the leaf surface relief greatly influences the surface reflection of light, while the structure of the mesophyll affects light penetration. The limited role of biochemical parameters in the reflectance spectra in some species/stands was therefore a consequence of structures on the leaf surface, such as the waxy cuticle, trichomes or prickle hairs, which dissipate the radiation and reduce its penetration into the mesophyll (Baldini et al. 1997; Holmes and Keiller 2002). Different trichomes are present in many plant species, as they are cost-effective due to their multiple functions, i.e. the prevention of water loss and protection against excessive radiation (Ehleringer 1980; Woodman and Fernandes 1991). The reflectance in the UV range is usually very low (<10 %) (Yoshimura et al. 2010; Qi et al. 2002; Holmes and Keiller 2002), due to the absorption of UV photons by phenolic substances, which usually accumulate in the upper leaf layers and mainly in the epidermis (Pfündel et al. 2007). However, it has also been reported that, in some cases, the increased reflectance is a consequence of silica structures (prickle hairs and cuticle) at the leaf surface (Klančnik et al. 2013a). Silica is a key structural element in graminoids, where it substitutes for carbon as a structural element, and enhances their strength, while preventing lodging and shading of leaves (Schoelynck et al. 2010; Schaller et al. 2012). Therefore, silica should be taken into account when studying reflectance of this plant group.

In the analyses of the mixed stands, mainly dicotyledonous species were included, and their biochemical properties were revealed as more important than their structural properties, together explaining 38 % of the variability of the

reflectance spectra. As expected, chlorophylls *a* and *b*, which intercept the light inside the leaf, correlated negatively with the visible parts of the spectra (Klančnik et al. 2012, 2013b). Surprisingly, the cuticle thickness correlated negatively with the entire spectra, even though many studies have shown that wax on leaf surfaces effectively reflects radiation (Holmes and Keiller 2002; Klančnik et al. 2012). This unexpected relationship potentially arose because the accompanying species in the stands contributed to the shape of the reflectance spectra and masked the role of the studied species in the light reflectance. The data obtained indicate that the reflectance of the monospecific stands can be explained by the species properties, while in mixed stands, the data might be misleading, even in the case of a very abundant species. In addition, the architecture of the stand can also contribute to the shape of the spectra. With the RDA where the stand reflectance was related to the stand properties, this revealed that the leaf angle and the stand homogeneity significantly affect the stand reflectance, as has also been shown in previous studies (Ganapol et al. 1999; Rautiainen et al. 2008).

6.4 Conclusions

We can conclude that (1) the complexity of a stand negatively affects the amount of light that is reflected; (2) in monospecific stands, the reflectance can be explained by the leaf properties of the species that constitutes the stand, although the key properties differed among the various species; (3) this is not very likely for mixed stands, including those with species that occur at high abundance; (4) plant architecture might also have an important role in explaining the reflectance spectra variability; and (5) any interpretation of the results of field spectroscopy needs detailed knowledge of the structural and biochemical properties at the stand and species levels.

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