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Assessment of Hyperspectral Remote Sensing for Analyzing the Impact of Human Trampling on Alpine Swards

Marlena Kycko^{1*}, Bogdan Zagajewski¹, Magdalena Zwijacz-Kozica², Jerzy Cierniewski³, Elżbieta Romanowska⁴, Karolina Orłowska^{1,5}, Adrian Ochtyra^{1,5}, and Anna Jarocińska¹

* Corresponding author: marlenakycko@uw.edu.pl

¹ Department of Geoinformatics, Cartography and Remote Sensing, University of Warsaw, Krakowskie Przedmieście 30, 00-325, Warsaw, Poland

² Tatra National Park, Kuźnice 1, 34-500, Zakopane, Poland

³ Department of Soil Science and Remote Sensing of Soils, Adam Mickiewicz University, Długa 27, 61-680, Poznań, Poland

⁴ University of Warsaw, Faculty of Biology, Department of Molecular Plant Physiology, Miecznikowa 1, 02-096, Warsaw, Poland

⁵ University of Warsaw, College of Inter-Faculty Individual Studies in Mathematics and Natural Sciences, Al. Żwirki i Wigury 93, 02-096, Warsaw, Poland

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Tourist traffic has been observed to cause changes in vegetation cover, particularly in alpine areas. These changes can be monitored using remote-sensing methods.

This paper presents an analysis of the condition of the dominant sward species surrounding the most frequented alpine tourist trails in the Tatra National Park, one of the most visited natural mountain parks in Poland and a UNESCO Man and the Biosphere Reserve. Hyperspectral measurements of interactions between the electromagnetic spectrum and the morphology and physiology of plants were presented. The spectral properties of plants and remote-sensing vegetation indices could be used at

a later date for monitoring, for example from the air. The results identified the species' sensitivity and resistance to trampling and allowed an assessment of their physiological condition. Differences were observed in the conditions of trampled and control plants. The alpine swards in the Tatra National Park were assessed as being in good condition, with only small areas located close to the most popular trails showing damage. The proposed method for analyzing the condition of alpine swards could be a useful tool for the future management of protected areas.

Keywords: Tatra National Park; vegetation; vegetation indices; trampling; spectrometer; chlorophyll content; photosynthetically active radiation.

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Introduction

In the natural world, plants are exposed to different environmental factors, which may induce stress reactions and inhibit many physiological functions (Kreslavski et al 2007). Trampling, an example of a mechanical stress factor (Grabherr 1982; Sørensen et al 2009), causes physical damage either by applying excess flexural load or by crushing the plant organs (Sun and Liddle 1993). Several mechanical traits, including leaf toughness, root strength, and stem flexibility, play a key role in a plant's tolerance to trampling (Kobayashi et al 1999; Striker et al 2011). Although the responses of plants to other forms of mechanical stress have been documented, little is known about the reaction in the form of changes within plant cells to trampling itself.

Defoliation occurs simultaneously during trampling, and plants typically respond to this process by increasing

the allocation of water and nutrients to leaves at the expense of the roots and stems (Xu et al 2013). Trampling-induced defoliation causes direct loss of nutrients and reductions in photosynthetic surface. This makes plants more vulnerable to mechanical damage and may cause soil erosion along with a decrease in biomass. The differences in resistance are mainly a result of plant morphology (Whinam and Chilcott 1999, 2003).

Popular tourist destinations such as natural mountain parks are especially vulnerable to trampling. Trampling has a destructive influence on natural alpine vegetation (Grabherr 1982). Tourist trampling has been found to have a significant effect on the condition of alpine grasslands, particularly at the beginning of the vegetation season (Piscová et al 2011). The regeneration of plants near tourist trails is difficult, even for species that are highly resistant to trampling (Klug et al 2002). Appropriate management of tourist activities, including

hiking, plays an important role in alpine ecosystem management.

In the Tatra Mountains on the border between Poland and Slovakia, which are the focus of this study, various studies of human influence (including trampling) have been conducted and have shown that these impacts are not constant in time and intensity (Czochański and Szydarowski 2000; Pociask-Karteczka et al 2007)—for example, the impact of skiing is less intense than that of sheep grazing (Guzik 2001). In the Tatra National Park (Poland), the most significant influence of tourists occurs in the central part of the High Tatras (Gąsienicowa Valley and Kasprowy Peak) during the peak growing season.

The increasing number of tourists leads to trampling of vegetation, which causes changes in species composition of plant communities and progressive erosion of trails (Rączkowska and Kozłowska 2010). To preserve the natural environment, it is necessary to track these changes and to take protective measures. There is currently no universal and comprehensive method of plant monitoring in mountain parks. Remote-sensing methods, which are much faster and more reliable than the traditional laboratory-based spectrometry, have not yet been used for this purpose. Remote sensing methods based on spectrometry offer more reliable and precise tools to analyze the state of vegetation. Since each object absorbs and reflects different quantities of radiation, it is possible to describe its characteristics by analyzing the reflectance of the electromagnetic spectrum (Jensen 1983; Bannari et al 1995; Zagajewski et al 2005, 2006; Jarocińska and Zagajewski 2008; Kycko 2012). Research on vegetation cover was conducted by Zha et al (2003), but the spatial resolution of Landsat data does not show the heterogeneity of swards cover well. Changes may occur over a few meters, especially in high mountain areas (Asner and Lobell 2000). Researchers have also noted that grassland surfaces are highly heterogeneous, which is a challenge for remote-sensing techniques, because their reflectance can be complex (Roder et al 2007).

To detect small-scale changes in the vegetation, it is necessary to increase spatial resolution; to this end, WorldView-2 images (Wiesmair et al 2016) and hyperspectral measurements (Kycko et al 2014) have been tested. Much of the current research on vegetation condition is based on both field and airborne hyperspectral data—for example, alpine grassland research in Switzerland (Rapp et al 2013) and nonforest vegetation analysis in the Karkonosze Mountains in Poland (Jarocińska et al 2016) using APEX hyperspectral data or vegetation monitoring (Aspinall 2002; Schmidlein and Sassini 2004; Zarco-Tejada et al 2012).

Hyperspectral data allow very precise assessment of the biochemical and biophysical state of vegetation (Darvishzadeh et al 2008). Therefore, hyperspectral field measurements may serve as a source of data to calculate

remote-sensing vegetation condition indices. The indices used in this study provide information about a plant's biophysical parameters and could have multiple applications in the quantitative and qualitative analysis of mountain vegetation (Zwijacz-Kozica 2010; Zwijacz-Kozica et al 2010; Kycko et al 2012, 2014; Jarocińska 2014; Ochtyra et al 2016).

Previous information on the merits of using such methods and showing differences in the state of trampled vegetation has not determined specific, precise parameters or indicators for a large number of species. The objectives of this study were to use remote-sensing methods to determine the effect of trampling on alpine swards in mountain areas, identify species that are sensitive to trampling, and determine the most suitable vegetation indices to investigate these influences using hyperspectral measurements, which could be verified by airborne detectors in the near future. The study offers a possible method to assess the impact of trampling and thus inform decisions on sustainable management and development of protected areas.

Study area

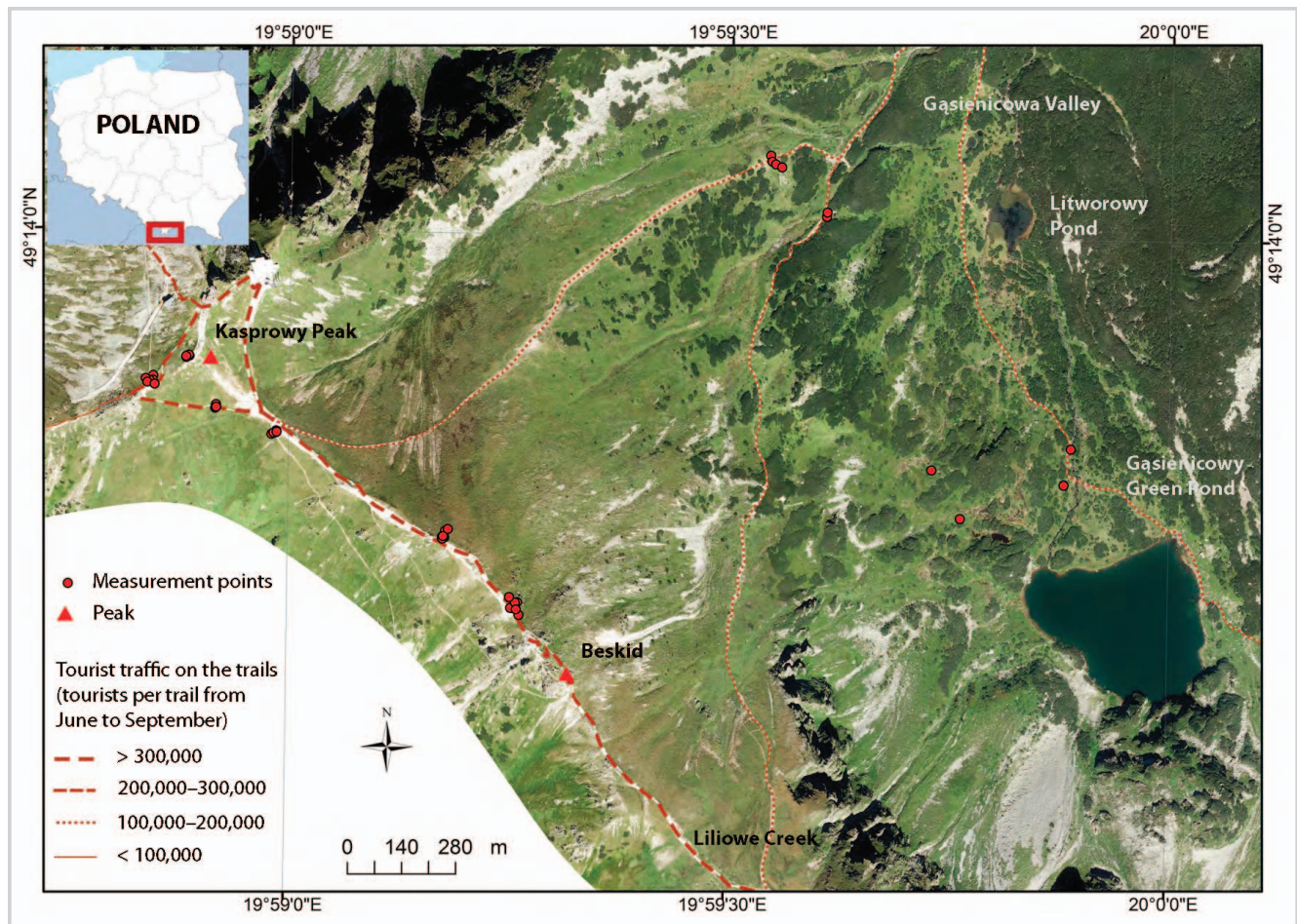
The Tatra Mountains are the only alpine environment in Poland and Slovakia (Paryska and Paryski 1995). The Polish part of the Tatras covers an area of 150 km²; its highest peak is Rysy at 2499 m (Klimaszewski 1988). The surveyed plant communities belong to the alpine and subalpine zones. The alpine zone in the Tatra Mountains extends from approximately 1800 to 2300 m above sea level and consists mostly of high-mountain grasslands (Paryska and Paryski 1995). The subalpine zone extends from 1500 to 1800 m above sea level and consists of mountain pine scrub as well as grazed and nongrazed grassland.

Specific study sites were selected along the Gąsienicowa Valley (Figure 1) in the central part of the Tatras, where the most intensive hiking in the Tatra National Park occurs (Skrzydłowski 2010). Thanks to its attractive location, easy accessibility, and natural values, the Gąsienicowa Valley was visited by about 1 million tourists in 2011 (almost 30% of all visitors to the Tatra National Park). In 1935–1936, a cable car line was built on top of nearby Kasprowy Peak, which intensified tourist development in this part of the Tatras (Paryska and Paryski 1995).

Methods

Although most vegetation communities are heterogeneous, the acquired spectral response undergoes various interferences and is the averaged spectral response for many species. To obtain a spectral signal from a single species at a time, measurements were taken on highly homogeneous alpine sward areas along hiking

FIGURE 1 The research area (using an orthophotomap from 2012, made available by the Tatra National Park). (Map by Marlena Kycko)



trails. The initial analysis of alpine sward plant communities located along the trails was conducted with a vegetation map at a scale of 1:10,000 (Kozłowska and Plit 2002; Kozłowska 2006). The following species were selected for detailed analysis: *Juncus trifidus*, *Oreochloa disticha*, *Agrostis rupestris*, *Deschampsia flexuosa*, *Festuca airoides*, *Festuca picta*, *Luzula alpinopilosa*, and *Nardus stricta*. The main criterion for selection was the dominant presence of the species.

The measurement locations were homogeneous patches of the selected species located in trampled zones (<5 m from a trail) and control areas (5–10 m from a trail). A distance of 5 m is considered the maximum that tourists are likely to walk away from the trail, because of the steepness of the slope. The highest number of test polygons were along the trail from the Kasprowy Peak to the Beskid Peaks. Others were located along the Kasprowy Peak and Gąsienicowa Valley trails and near the Gąsienicowy Green Pond (Figure 1).

Measurements

Approximately 30 measurements for each species were acquired from each test polygon. The field measurements were conducted from 17 to 21 August 2011 when weather conditions were stable (Figure 2), with the following data collected:

- Spectrometric measurements were carried out using a field spectrometer (ASD FieldSpec 3) operating in the range from 350 to 2500 nm. The measurements were preceded by spectrometer optimization and calibration. Each measurement was performed only on plant leaves using the ASD PlantProbe. Each type of plant was analyzed with 30 averaged measurements (1 spectral measurement was averaged from 30 independent reflectance samples; Kycko et al 2013).
- The total content of chlorophyll—the principal pigment responsible for the light energy absorption required for photosynthesis and plant growth—was measured with a CCM-200 chlorophyll meter.

FIGURE 2 The first 2 authors of the present article conducting field measurements in the Gąsienicowa Valley. (Photo by Magdalena Oprządek)



- Photosynthetically active radiation (PAR)—the expression of a plant's energy storage capacity—was sampled on dense vegetation cover using the AccuPAR ceptometer. The fraction of absorbed PAR (fAPAR) operates between 400–700 nm and describes energy, mass, and momentum exchanges between the canopy and the atmosphere, and productivity of plant cells. The fAPAR was calculated as follows:

$$fAPAR = (PAR_o + PAR_s - PAR_t - PAR_c) / PAR_o$$

where PAR_o = total incoming radiation, PAR_s = soil-reflected PAR, PAR_t = PAR transmitted through the canopy, and PAR_c = canopy-reflected PAR (Weiss and Baret 2011).

Analysis

Calculation of vegetation indices was based on the spectral characteristics of the selected species. The differences between the reflectance of plants located near the trails (0–5 m) and in the control sites (5–10 m from trails) were analyzed by calculating the vegetation indices from 7 different groups. The 7 groups of indices (calculated based on spectrometer measurements) describe different plant parameters such as chlorophyll or nitrogen and water content. One additional bioradiometric group is based on the Chlorophyll Content Index (CCI) and fAPAR, which were used to verify the information acquired with the spectrometer (Table 1).

All statistical analyses were performed with the STATISTICA 12 software based on 23 testing areas near the trails and 25 control areas. In each measured area and for each species, spectral characteristics and chlorophyll content were measured 30 times for species. fAPAR was measured only 3 times in each research area, because the dense vegetation cover and the weather conditions did

not change much. For each species, the average spectral reflectance of trampled and control vegetation patches was compared. Statistically significant differences between polygons were evaluated with a 1-way analysis of variance (ANOVA) at 3 levels of significance (0.05, 0.01, and 0.001). The ANOVA of reflectance and remote-sensing vegetation indices compared the spectra of trampled and control plants. The 3 levels of statistical significance allowed us to determine the maximum acceptable probability of type I error, which determines the maximum acceptable risk of error. In sum, we tried to determine, to an accuracy of 95%, 99%, and 99.9%, which species and what part of the spectrum ranges and remote sensing vegetation indices showed the differences between the control and trampled areas.

For additional analysis, the remote-sensing vegetation indices were correlated with the values of biophysical variables (CCI and fAPAR) using the Pearson product-moment correlation coefficient (R), a measure of the strength and direction of the linear relationship between 2 variables. The verification of the actual use of light in photosynthesis was conducted using fAPAR.

Results

The remote-sensing indices derived from the hyperspectral measurements confirmed different levels of plant resistance to trampling, water stress, and limitations of PAR absorption. (The indices and their abbreviations are listed in Table 1.) Most statistically significant changes could be observed in chlorophyll content (CCI), cell structure (Normalized Difference Vegetation Index [NDVI], Atmospherically Resistant Vegetation Index [ARVI], Modified Red Edge Simple Ratio Index [mSR₇₀₅], and Modified Red Edge Normalized Difference Vegetation Index [mNDVI₇₀₅]), and water content in leaves (Water Band Index [WBI] and Normalized Difference Water Index [NDWI]). These differences were observed in over 87.5% of the analyzed patches ($P < 0.001$). Changes were visible in the absorption of PAR (50–62.5% of all measured cases of Structure-Insensitive Pigment Index (SIPI) and Photochemical Reflectance Index (PRI), $P < 0.001$). The total amount of carbon (dry mass of the cellulose and lignin; eg Cellulose Absorption Index [CAI] and Plant Senescence Reflectance Index [PSRI]) showed statistically significant changes in 62.5% of all measured cases (*Supplemental material*, Table S1: <http://dx.doi.org/10.1659/MRDJOURNAL-D-15-00050.S1>).

A. rupestris and *O. disticha* were the most susceptible to trampling: 30 independent measurements showed significant differences (95.8–100% of the analyzed polygons at $P < 0.05$; 79.2–91.7% of the analyzed polygons at $P < 0.001$). *N. stricta* was impacted by trampling in only 41.7% of the polygons near the trails. *J. trifidus* was impacted by trampling to a lesser degree, with only 37.5% of observations for a statistical significance level $P <$

TABLE 1 Remote-sensing vegetation indices.

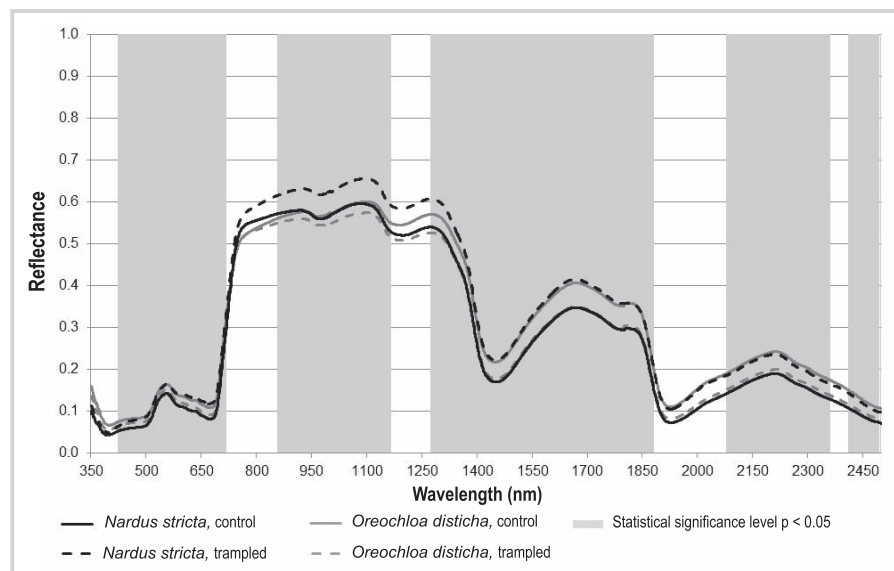
Groups of indices	Abbreviation	Index name	Citation
Broadband greenness	NDVI ^{a)}	Normalized Difference Vegetation Index	Rouse et al 1973
	SR ^{a)}	Simple Ratio Index	Rouse et al 1973
	EVI ^{a)}	Enhanced Vegetation Index	Huete et al 1997
	ARVI ^{a)}	Atmospherically Resistant Vegetation Index	Kaufman and Tanre 1992
Narrowband greenness	NDVI ₇₀₅	Red Edge Normalized Difference Vegetation Index	Gitelson and Merzlyak 1994
	mSR ₇₀₅	Modified Red Edge Simple Ratio Index	Datt 1999
	mNDVI ₇₀₅	Modified Red Edge Normalized Difference Vegetation Index	Datt 1999
	VOG1	Vogelmann Red Edge Index 1	Vogelmann et al 1993
	VOG2	Vogelmann Red Edge Index 2	Vogelmann et al 1993
	VOG3	Vogelmann Red Edge Index 3	Vogelmann et al 1993
Light use efficiency	PRI	Photochemical Reflectance Index	Gamon et al 1992
	SIPI	Structure Insensitive Pigment Index	Peñuelas et al 1995
Canopy nitrogen	NDNI	Normalized Difference Nitrogen Index	Fourty et al 1996
Dry or senescent carbon	NDLI	Normalized Difference Lignin Index	Fourty et al 1996
	CAI	Cellulose Absorption Index	Nagler et al 2003
	PSRI	Plant Senescence Reflectance Index	Merzlyak et al 1999
Leaf pigments	CRI1	Carotenoid Reflectance Index 1	Gitelson et al 2002
	CRI2	Carotenoid Reflectance Index 2	Gitelson et al 2002
	ARI1	Anthocyanin Reflectance Index 1	Gitelson et al 2001
	ARI2	Anthocyanin Reflectance Index 2	Gitelson et al 2001
Canopy water content	WBI	Water Band Index	Peñuelas et al 1995
	NDWI	Normalized Difference Water Index	Gao 1996
	MSI	Moisture Stress Index	Rock et al 1985
	NDII	Normalized Difference Infrared Index	Hardisky et al 1983
Bioradiometric index	CCI	Chlorophyll Content Index	Campbell et al 1990
	fAPAR	Fraction of absorbed photosynthetically active radiation	Moneith 1977

^{a)}To implement these data in multispectral hyperspectral indices, we used the following ranges of wavelength bands: for red, 600–700 nm; for green, 500–600 nm; for blue, 400–500 nm; for NIR, 760–960 nm.

0.001. *N. stricta* and *J. trifidus* were most resistant to trampling. All other species were sensitive to trampling, but the trampling-related changes could be observed in different spectral characteristics (*Supplemental material*, Table S2: <http://dx.doi.org/10.1659/MRDJOURNAL-D-15-00050.S1>). A hierarchical classification of species vulnerability was established based on the vegetation index values in both the trampled and control areas. The highest fragility occurred in *O. disticha*.

ANOVA was performed on all individual measurements, that is, on all spectral reflectance curves. We compared ranges of the spectrum that showed a statistically significant difference for the species between the trampled and control sites. Figure 3 compares *O. disticha*, the most sensitive species, and *N. stricta*, which did not present significant differences between trampled and control areas. The spectral properties of *O. disticha* confirmed that most shortwave infrared ranges are sensitive to water content, lignin, and cellulose content in

FIGURE 3 Spectral characteristics of *Nardus stricta* and *Oreochloa disticha* acquired at the statistical significance level of 0.05 in the trampled and control areas. Ranges marked in gray denote statistically significant differences between the control and trampled groups.



leaves (depicted by gray areas in Figure 3). Changes were also observed in wavelengths of 650 nm and 650–750 nm (red edge), the ranges responsible for the absorption of photons by chlorophyll (indicating general stress of vegetation), and in the ranges 850–1160 nm, 1270–1880 nm, 2078–2360 nm, and 2410–2496 nm.

All index values were correlated with the CCI and fAPAR indices, measuring chlorophyll content and energy accumulated by plants. A review of the condition of the alpine swards species in general, for trampled and control areas, was performed using the correlation coefficients (*R*; Table 2). The CCI and NDVI of the trampled areas oscillated around $R = 0.57$ ($n = 30$, $P < 0.05$). The CCI correlated in the same way for trampled plants with the

CAI ($R = -0.65$), which means that when there is less chlorophyll in a plant, there is a greater quantity of dry biomass as defined by cellulose. Control plants also showed a high correlation between the CCI and CAI ($R = -0.67$). The energy accumulated by plants (fAPAR) showed a strong correlation with the general condition (Red Edge Normalized Difference Vegetation Index [NDVI₇₀₅], $R = 0.71$), and the same index was highly correlated with the SIPI (-0.55) in the trampled areas, which indicates a reduced use of light in the process of photosynthesis. The use of light through photosynthesis also depends on the water content of the plant, which is confirmed by the value of correlation ($R = 0.42$) for control plants.

Discussion and conclusions

This study shows that field spectrometer data can be used to analyze anthropogenic changes in plants, specifically those caused by tourist trampling. It also identifies vegetation indices calculated from spectral reflectance curves acquired in situ that are the most useful in monitoring damage to alpine vegetation.

The field measurements indicated that alpine swards near popular trails in the Gąsienicowa Valley and near the Kasprowy Peak were generally in good condition, which was confirmed by comparison with more distant control patches. Most of the vegetation indices for the species studied were within the optimal values. In the analysis of species' spectral reflectance curves, values in wavelengths sensitive to pigment content, cell structure, and water absorption were analogous to those presented in the literature and within the ranges typical for plants in good condition.

TABLE 2 Verification of chlorophyll content and energy accumulation (fAPAR) by plant index, based on correlation with indices calculated from the data derived from the spectrometer ($n = 30$, $P \leq 0.05$).^{a)}

Type of area	Indices	Correlation coefficient (<i>R</i>)
Trampled plants (<5 m from trail)	CCI with NDVI	0.57
	CCI with CAI	-0.65
	fAPAR with SIPI	-0.55
	fAPAR with NDVI ₇₀₅	0.71
Control plants (5–10 m from trail)	CCI with SIPI	-0.36
	CCI with CAI	-0.67
	fAPAR with NDNI	0.40
	fAPAR with NDII	0.42

^{a)} The full names of the indexes are given in Table 1.

An increase in trampling intensity has been associated with an 11% decrease in plant biomass (Grabherr 1982). Research has shown that after 30 passes (people walking through the area) the amount of biomass decreased by 2% of the original volume, and after 200 passes per annum by 27% of the original amount (Whinam and Chilcott 1999, 2003). Our analyses made it possible to identify species that showed a deterioration in physiological condition after being subjected to trampling. The species that showed the least difference between trampled and nontrampled areas in remote-sensing vegetation index values were *N. stricta*, *J. trifidus*, *F. picta* (all indices), and *A. rupestris*. The greatest differences in vegetation index values between trampled and control sites were observed in *L. alpinopilosa*, *F. airoides*, *O. disticha*, and (for some indices) *D. flexuosa*. These results may be due to differences in the morphology of the species, such as the fact that *L. alpinopilosa* has broad (about 2–3 mm) green leaves, whereas the leaves of *J. trifidus* are thin and filamentous.

In laboratory studies of alpine swards, an increase of reflectance by 10% in the visible range of the electromagnetic spectrum was found to correspond to an increase in carotenoid content (Jakomulska 1999). Pigment content in *N. stricta* reached reflectance values of 0.5–0.1 in an earlier study (Sobczak 2009), whereas in our study the values were 0.5–0.15. Decreases in midinfrared wavelength reflectance suggest a more compact cell structure. For example, *L. alpinopilosa*, with peak reflectance in the near-infrared spectral range, has a spongier structure than *J. trifidus*. An increase of reflectance by 5–10% in the midinfrared wavelength is sufficient for such conclusions to be drawn. Sobczak (2009), in a visual comparison of spectral reflectance curves of *Luzula spadicea* (synonym *L. alpinopilosa*), found that reflectance in the spectral range sensitive to cell structures had values of 0.25–0.35, whereas in our research, the values were 0.6–0.7. The reflectance of *D. flexuosa* in the spectrum describing cellular structures was 0.5–0.64 in our study and 0.35–0.44 in Sobczak's.

In the comparison of water absorption wavelengths, our findings were similar to those of previous studies and showed a dependency between water content and cell structure. Jakomulska (1999) found that tissue hydration was higher in the loose, spongy tissue of *L. spadicea* (synonym *L. alpinopilosa*; 78.9% water content in the plant tissues) than in the tight cell structure of *J. trifidus* (71.3% water content in tissues). Regarding reflectance values, the range dependent on water content for *J. trifidus* was 0.1–0.2 in Sobczak's (2009) study and 0.1–0.3 in our study.

In addition to the spectral reflectance curve analysis, remote-sensing vegetation indices were calculated. Eight groups of vegetation indices were measured, but only 3 of these were statistically significant in more than 70% of cases at a significance level of $P < 0.001$: the broadband greenness, narrowband greenness, and canopy water

content groups. Of these, 3 broadband greenness indices proved to be applicable in the trampling-vulnerability analysis: NDVI, ARVI, and enhanced vegetation index (EVI). The most suitable narrowband greenness indices were mSR₇₀₅ and mNDVI₇₀₅, whereas the best indices for canopy water content were WBI, NDWI, and Normalized Difference Infrared Index [NDII]. This means that (potentially trampled) plants near the trail had significantly lower chlorophyll, water content, and overall health than the control plants.

Based on the wavelengths, the remote-sensing vegetation indices such as NDVI, soil adjusted vegetation index 2, and red edge position index (Dawson and Curan 1998) were calculated. The value of these indices depends on the amount of chlorophyll, which is a very sensitive indicator of vegetation stress. With the development of remote sensing, existing indicators are being modernized, and researchers are developing new indicators that accurately utilize particular wavelengths corresponding to the characteristics and parameters of plants, such as water, pigments, and chemical elements that build plants (Rodríguez-Pérez et al 2007). Indicators like NDVI and MSAVI 2 (the modified soil-adjusted vegetation index 2, which is a soil-adjusted vegetation index that seeks to address some of the limitations of NDVI when applied to areas with a high degree of exposed soil surface) have also been used to evaluate and monitor the impact of sheep grazing on vegetation in the Aragvi Valley in Georgia (Wiesmair et al 2016). The most-used bands for the analysis of water content and water stress are 950–970, 1150–1260, and 1520–1540 nm (Sims and Gamon 2002; Rodríguez-Pérez et al 2007), whereas in our study the statistically significant ranges were 422–716, 850–1160, 1270–1880, 2078–2360, and 2410–2496 nm.

The methods presented in this paper can be used for other monitoring studies of mountain plant species. Trampling damage, observed through remote-sensing methods, varied between species. The processes of reconstruction and regeneration of the vegetation cover are particularly difficult in mountainous terrain (because of the gradient; Wiesmair et al 2016). Although novel methods to retain fractional vegetation cover from satellite images have been developed (Li et al 2014; Wiesmair et al 2016), monitoring should always be supported by field surveys (Gintzburger and Saidi 2010). Therefore, hyperspectral data constitute a promising—and what is more, noninvasive—tool for monitoring hiking trails and mountainous areas. Remote-sensing methods are increasingly being proposed for the study, restoration, and sustainable management of the region (Akiyama and Kawamura 2007). In future studies, a focus on trampling-related morphological and physiological changes would improve the understanding of plant resistance to mechanical stress.

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Supplemental material

Table S1 Statistical significance of vegetation indices for the analyzed species (sample size for each species: $n = 30$).

Table S2 Trampling tolerance of the analyzed species determined on the basis of statistical significance of vegetation indices (sample size for each species: $n = 30$).

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