Spectral reflectance of multispecies herbaceous and moss canopies in the boreal forest understory and open field

Lea Hallik, Olevi Kull, Tiit Nilson, and Josep Peñuelas

Abstract. The reflectance signal from the forest tree canopy is influenced by the optical properties of the background formed by understory vegetation. Our study shows that the herb–moss layer in the forest tends to be brighter in the visible wavelength when the canopy above is more closed because of the specific properties of plants grown in low light. When leaf-area-based chlorophyll content falls below approximately 150 mg·m⁻², reflectance in the red region of the spectrum increases compared with that of the background. The best descriptors of the herb–moss layer for deriving optical parameters are herb layer dry mass for the visible wavelength range and total aboveground water mass for near-infrared (NIR) reflectance. In addition, chlorophyll content per leaf area considerably improves the red reflectance estimate.

Résumé. Le signal de réflectance de la canopée des arbres forestiers est influencé par les propriétés optiques du second plan formé par la végétation des strates inférieures. Notre étude montre que la couche d’herbe/de mousse dans la forêt a tendance à être plus lumineuse dans le spectre visible lorsque la canopée au-dessus est plus fermée. Ceci est dû aux propriétés spécifiques des plantes adaptées à la faible luminosité. Lorsque la teneur en chlorophylle par unité de surface foliaire descend en dessous d’approximativement 150 mg·m⁻², la réflectance dans le spectre rouge augmente par rapport à celle du second plan. Les meilleurs descripteurs de la couche d’herbe/de mousse pour dériver des paramètres optiques sont : la masse sèche de la couche d’herbes pour estimer le spectre visible, et la masse totale d’eau de surface pour la réflectance dans le proche infrarouge (NIR). De plus, connaître la teneur en chlorophylle par surface foliaire améliore considérablement l’estimation de la réflectance dans le spectre rouge.

Introduction

A need for large-scale monitoring of vegetation cover on the Earth has led to rapid development of optical remote sensing technologies. One problem, however, in using remotely sensed reflectance information for predicting canopy parameters such as dry mass, leaf area index (LAI), or total chlorophyll is related to the heterogeneity of the canopy structure (Sellers et al., 1992; Nilson et al., 1995; Chen and Cihlar, 1996; Gastellu-Etchegorry and Trichon, 1998; Blackburn, 2002; Serrano et al., 2002). For this reason, relationships between reflectance indices and canopy parameters are not universal and need to be adjusted for different types of vegetation.

Because green plants strongly absorb visible radiation and scatter near-infrared (NIR) radiation, reflectance in the 400–1000 nm wavelength range has most often been used to derive indices characterizing plant cover. The most commonly used vegetation index, the normalized difference vegetation index (NDVI), is usually calculated based on the reflectance of two wavelength bands, namely visible (typically red) and NIR. This index is shown to be correlated with the canopy leaf area index, green biomass, chlorophyll content, or nitrogen (Yoder and Waring, 1994; Gamon et al., 1995; Chen and Cihlar, 1996; Serrano et al., 2000; Broge and Mortensen, 2002; Boegh et al., 2002; Kodani et al., 2002). The functionality of the NDVI and analogous vegetation indices is based on the soil line concept (Gilabert et al., 2002). Soil reflectances in the red and NIR wavelengths are usually linearly related. Due to the presence of green vegetation, the measured values of NIR reflectance increase while those of red reflectance decrease compared with those of the soil background, causing the NDVI, which is essentially related to the slope of the NIR–red relationship, to change. Because the soil line may vary depending on the soil type, several other vegetation indices have been developed that consider the properties of bare soil (Baret and Guyot, 1991;
Broge and Mortensen, 2002; Gilabert et al., 2002; Meza Diaz and Blackburn, 2003).

A specific feature of natural and seminatural plant communities, especially forests, is that these communities are vertically and horizontally strongly heterogeneous. Several investigators have shown that the reflectance signal from the forest tree stand is influenced by differences in optical properties of background formed by ground-layer herbaceous and bryophyte vegetation (Nilson and Peterson, 1994; Waring, 1998; Hanan, 2001). This has created interest in studying the optical properties of the understory and its temporal and functional relationships with overstory vegetation. Miller et al. (1997) studied understory reflectance in boreal forest stands and showed that the inclusion of this information significantly enhanced correlation of the vegetation indices with the overstory LAI. Several models of reflectance from layered plant communities have been developed, and all these model calculations have shown that community reflectance may be very sensitive to background conditions (Asner and Wessman, 1997; Hanan, 2001; Kuusk, 2001; Gemmell et al., 2002; Liangrocapart and Petrou, 2002).

The herbaceous and moss canopies beneath the tree canopy are not independent of the tree canopy. However, the relationship is not unique. Growth of herbaceous layer vegetation is a compromise between light availability and soil resources (Kull et al., 1995). With decreasing tree cover, more light reaches the understory, promoting the growth of ground-layer vegetation. Apparently, such a compensatory mechanism is one reason for the decreasing sensitivity of the reflectance signal to changes in forest stand LAI. Remote sensing studies usually focus on agricultural monocultures or forest trees, whereas multispecies herbaceous canopies have rarely been investigated (Darvishzadeh et al., 2008). Here we attempt to make our contribution to filling the gap in estimating vegetation parameters from reflectance data for heterogeneous multispecies herbaceous–moss canopies.

We measured the reflectance of herb, moss, and soil layers in the understory of two pine forests with different productivity and, for comparison, also in an old field meadow (without any tree cover) along the productivity gradient. The main aim of this study was to investigate the reflective properties of the forest ground layer as a background for the tree canopy. We also aimed to search for the causes of variability in the optical properties of the understory vegetation and the parameters of ground-layer vegetation that are best related to its reflective properties and a possible interrelationship between the tree canopy and the understory light environment.

Methods

Study sites

The study was conducted near Tartu in the southern part of Estonia (58°22′N, 27°20′E; elevation 35–45 m). The average annual rainfall is 650 mm. The average temperature is 17.0 °C in July and −6.7 °C in January. The vegetation period of activity usually lasts 175–180 days, from mid-April to October. The maximum LAI and biomass in these conditions occur at the end of July and beginning of August. All measurements in this study were therefore made in the second half of July. Ten sample plots (1 m × 1 m) were chosen under pine (Pinus sylvestris) forest. To have a gradient for leaf area, half the plots were located under a denser tree canopy, referred to here as dense forest (height = 14.3 m, density = 0.142 stems·m−2, diameter at breast height (DBH) = 15.0 cm), and half under a more open canopy, referred to here as sparse forest (height = 18.0 m, density = 0.092 stems·m−2, DBH = 17.0 cm). The measurement plots were selected as representative of the field layer for both forests. Another set of 10 plots was established in old field meadow without any tree cover (referred to here as open field). At this site, plots were located along the slope of a small hillock to cover a range of soil moisture and fertility gradients, which effectively produces a gradient in LAI. Aan et al. (2006) provide a detailed description of soil and vegetation properties in “open field.”

The general characteristics of the plots are given in Table 1. In open field, the most important forb species by total dry mass were Achillea millefolium, Cirsium arvense, and Taraxacum officinale, and the most important grasses were Dactylis glomerata, Festuca pratensis, and Phleum pratense. In the “dense forest,” the most important species in the field layer were the broad-leaved species Impatiens parviflora, Mycelis muralis, Epilobium angustifolium, Moehringia trinervia, and Knautia arvensis and the grass species Agrostis capillaries and Festuca gigantea. The moss layer was dominated by Pleurozium schreberi, Hylocomium splendens, and Dicranum polysetum. In the “sparse forest,” the most important broad-leaved species in the field layer were Vaccinium myrtillus, Ledum palustre, Vaccinium vitis-idea, and Melampyrum pratense, and the main grass species were Molinia caerulea and Carex sp. The moss layer composition in this forest was otherwise similar to that of the dense forest, with some patches of Sphagnum capillifolium.

Reflectance measurements

Reflectance was measured above the herbaceous canopy. Then, immediately after the removal of the herb layer, we measured “background reflectance” above the moss layer and reflectance above bare soil after removal of the moss layer. The reflectance of the upper soil layer, rich in organic material at varying stages of decomposition (O horizon), was measured immediately after the removal of the moss layer to ensure that soil moisture content would not change during the set of reflectance measurements at the given plot (herb, moss, and soil layer). A four-channel field radiometer KFM-4M (Tartu Observatory, Tõravere, Estonia) was used for reflectance measurements. This radiometer has spectral bands of blue (λmax = 487 nm, Δλ0.5 = 10 nm), green (λmax = 556 nm, Δλ0.5 = 14 nm), red (λmax = 650 nm, Δλ0.5 = 9 nm), and NIR (λmax = 791 nm, Δλ0.5 = 11 nm). In each of the spectral bands the radiometer has a nadir-looking channel with a 13° aperture and an upward-looking
<table>
<thead>
<tr>
<th>Plot No.</th>
<th>Relative incident light</th>
<th>Relative share of graminoid LAI</th>
<th>Dry mass per ground area (g·m$^{-2}$)</th>
<th>Water per ground area (g·m$^{-2}$)</th>
<th>No. of species</th>
<th>Chlorophyll per ground area (mg·m$^{-2}$)</th>
<th>Chlorophyll per leaf area (mg·m$^{-2}$)</th>
<th>Total LAI (dead + alive; m$^2$·m$^{-2}$)</th>
<th>Dry mass per ground area (g·m$^{-2}$)</th>
<th>Water per ground area (g·m$^{-2}$)</th>
<th>Chlorophyll per ground area (mg·m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Herb layer</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dense forest</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.082</td>
<td>0</td>
<td>3.2</td>
<td>28.2</td>
<td>2</td>
<td>5.5</td>
<td>48.6</td>
<td>0.114</td>
<td>902.7</td>
<td>4000</td>
<td>3778</td>
</tr>
<tr>
<td>2</td>
<td>0.065</td>
<td>0</td>
<td>10.9</td>
<td>52.1</td>
<td>5</td>
<td>8.6</td>
<td>31.9</td>
<td>0.271</td>
<td>495.4</td>
<td>2707</td>
<td>863</td>
</tr>
<tr>
<td>3</td>
<td>0.063</td>
<td>0.290</td>
<td>20.2</td>
<td>123.0</td>
<td>10</td>
<td>48.6</td>
<td>94.4</td>
<td>0.514</td>
<td>621.7</td>
<td>2120</td>
<td>1161</td>
</tr>
<tr>
<td>4</td>
<td>0.079</td>
<td>0.010</td>
<td>15.7</td>
<td>82.2</td>
<td>11</td>
<td>54.0</td>
<td>130.6</td>
<td>0.413</td>
<td>658.4</td>
<td>2218</td>
<td>1870</td>
</tr>
<tr>
<td>5</td>
<td>0.067</td>
<td>0</td>
<td>12.8</td>
<td>122.8</td>
<td>5</td>
<td>15.2</td>
<td>29.0</td>
<td>0.526</td>
<td>397.6</td>
<td>1737</td>
<td>1278</td>
</tr>
<tr>
<td>Sparse forest</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>0.310</td>
<td>0</td>
<td>117.6</td>
<td>114.8</td>
<td>3</td>
<td>123.9</td>
<td>262.7</td>
<td>0.472</td>
<td>932.9</td>
<td>2120</td>
<td>615</td>
</tr>
<tr>
<td>7</td>
<td>0.300</td>
<td>0.020</td>
<td>119.9</td>
<td>135.3</td>
<td>5</td>
<td>165.8</td>
<td>266.5</td>
<td>0.622</td>
<td>1420.9</td>
<td>4224</td>
<td>2061</td>
</tr>
<tr>
<td>8</td>
<td>0.310</td>
<td>0</td>
<td>102.3</td>
<td>85.0</td>
<td>3</td>
<td>100.1</td>
<td>249.2</td>
<td>0.402</td>
<td>917.2</td>
<td>7506</td>
<td>1163</td>
</tr>
<tr>
<td>9</td>
<td>0.290</td>
<td>0.001</td>
<td>192.7</td>
<td>148.6</td>
<td>5</td>
<td>241.0</td>
<td>293.9</td>
<td>0.820</td>
<td>811.1</td>
<td>2493</td>
<td>2139</td>
</tr>
<tr>
<td>10</td>
<td>0.290</td>
<td>0.800</td>
<td>111.8</td>
<td>99.6</td>
<td>7</td>
<td>102.0</td>
<td>113.2</td>
<td>0.900</td>
<td>617.2</td>
<td>1421</td>
<td>873</td>
</tr>
<tr>
<td>Open field</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>1</td>
<td>0.700</td>
<td>372.8</td>
<td>881.6</td>
<td>13</td>
<td>829.8</td>
<td>228.8</td>
<td>6.034</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>1</td>
<td>0.480</td>
<td>331.8</td>
<td>385.9</td>
<td>16</td>
<td>510.5</td>
<td>200.3</td>
<td>4.320</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>1</td>
<td>0.480</td>
<td>506.6</td>
<td>388.9</td>
<td>13</td>
<td>640.4</td>
<td>221.7</td>
<td>4.900</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>1</td>
<td>0.390</td>
<td>296.9</td>
<td>486.1</td>
<td>11</td>
<td>752.3</td>
<td>258.2</td>
<td>5.140</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>1</td>
<td>0.780</td>
<td>236.2</td>
<td>357.8</td>
<td>7</td>
<td>392.4</td>
<td>180.4</td>
<td>4.140</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>1</td>
<td>0.380</td>
<td>327.2</td>
<td>489.9</td>
<td>11</td>
<td>791.8</td>
<td>360.3</td>
<td>5.410</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>1</td>
<td>0.450</td>
<td>194.0</td>
<td>308.7</td>
<td>13</td>
<td>213.2</td>
<td>128.0</td>
<td>3.100</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18</td>
<td>1</td>
<td>0.440</td>
<td>150.6</td>
<td>199.8</td>
<td>12</td>
<td>289.0</td>
<td>203.9</td>
<td>2.410</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>1</td>
<td>0.540</td>
<td>163.9</td>
<td>288.7</td>
<td>18</td>
<td>346.9</td>
<td>194.9</td>
<td>2.870</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>1</td>
<td>0.460</td>
<td>170.0</td>
<td>192.5</td>
<td>20</td>
<td>238.5</td>
<td>187.1</td>
<td>2.310</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 1. Measured herb and moss layer parameters in studied plots.
hemispheric channel. Relative incident irradiances at 1.5 m above each plot were calculated as ratios of the hemispheric irradiance in the plot to that measured simultaneously in the clearing located near the study stands. Reflectance measurements were made from 1.5 m height, with the instantaneous field-of-view of the radiometer on the ground being 0.12 m². To achieve reliable results in conditions of high temporal and spatial irradiance variability, like those under the tree canopy, one measuring sequence (i.e., reading) lasted 50 s. Results from all channels were registered twice a second by a Campbell CR-10 datalogger (Campbell Scientific Ltd.). Sunny periods of time were chosen for the measurements. The measurement area was partly in shadow. The timing of measurements was chosen to correspond to a 45° solar angle (approximately). Ten readings were taken on each plot to obtain better spatial sampling within the 1 m² plot. To calibrate the measured reflectances in the reflectance factor units, a grey field reference panel was placed over the plot at a height of 30 cm above the ground and the panel reflectance was measured immediately after the measurements on the plot. The reflectance factors of the grey field panel were determined by a comparison of its reflectance with that of a white Spectralon panel in laboratory conditions using a NIRSystems 6500 spectrometer (FOSS NIRSystems Inc.). It was not possible to use exactly the same illumination geometry in the laboratory as that used during the field measurements. However, the panels were also measured in the normal direction, and the illumination angle was approximately the same (45°).

The four bands of the radiometer used represent characteristic wavelengths to describe the visible–NIR portion of reflectance of a typical green leaf. Certainly, four bands are unable to describe all details of the reflectance spectra. Some details remain undescribed, like the exact shape of the red edge and specific behaviour of reflectance in the green part of the spectrum (e.g., photochemical reflectance index (PRI) wavelengths) (Gamon et al., 1992). In addition to the reflectance factors in all four spectral bands, the following reflectance indices were calculated:

\[ SR = \frac{R_{\text{NIR}}}{R_R} \] (1)

\[ \text{NDVI} = \frac{(R_{\text{NIR}} - R_R)}{(R_{\text{NIR}} + R_R)} \] (2)

\[ \text{TSAVI} = B(R_{\text{NIR}} - BR_R - A)[R_R + B(R_{\text{NIR}} - A) + X(1 + B^2)] \] (3)

where \( SR \) is the simple ratio vegetation index; \( R_{\text{NIR}} \) and \( R_R \) are reflectance factors in the NIR and red bands, respectively; \( \text{TSAVI} \) is the transformed soil-adjusted vegetation index; \( B \) is the slope of the soil line; \( A \) is the intercept; and \( X = 0.08 \) (Baret and Gourlay, 1991).

The reflectance difference from the background (\( R_{\text{dif}} \)) was also calculated:

\[ R_{\text{dif}} = R_{\text{layer}} - R_{\text{background}} \] (4)

where \( R_{\text{layer}} \) denotes the reflectance factor measured above the layer of interest, and \( R_{\text{background}} \) is the reflectance factor of the layer immediately below the layer of interest.

### Determination of LAI and biomass

In the forest plots, field layer vegetation was removed from the whole 1 m² plot. In the open field where the herbaceous layer was deeper and the canopy more uniform, the vegetation was harvested within a 0.5 m × 0.5 m area in the centre of the sample plot in three to five vertical layers depending on the vegetation height. Harvested material was sorted by species into leaves and stems. Fresh mass was measured immediately after sorting. Dry mass was determined after drying at 80 °C for 3 days. Some leaves from every species in all harvested canopy layers were taken for leaf area determination. Images of fresh leaves were digitized, and area was calculated with a self-developed computer program. After this, the leaves were dried separately to calculate leaf mass to area ratio (LMA). Dry mass data of leaves from every sampled canopy layer were then divided by LMA to find total leaf area of every species in every layer.

### Chlorophyll and nitrogen determination

Samples were taken from all species that had enough foliage within a sampled layer. Chlorophyll concentration was determined in 80% aqueous acetone with a PS2000 spectrometer (Ocean Optics) using equations of Porra et al. (1989). Nitrogen content was measured by the Kjeldahl method with a Kjeltec Auto 1030 analyser (Tecator AB).

### Statistical analysis

Correlation analysis and stepwise multiple regression were performed using Statistica software version 5.5 (StatSoft Inc.). A forward stepwise regression method was used to predict the best moss–herb layer parameters describing changes in reflectances in different spectral bands. \( F > 1 \) criteria were used to include a parameter in the equation.

### Results

#### Herb–moss layer characteristics

The measured characteristics of the herb–moss layers of the studied plots are given in Table 1. Green LAI of herbaceous vegetation ranged from 0.11 to 0.90 in forest sites and from 1.27 to 3.63 in open field plots. However, because of the massive moss layer, the total aboveground dry weight of the ground vegetation at forest sites (410–1540 g·m⁻²) was considerably more than that in open field (150–507 g·m⁻²). Although chlorophyll concentration in mosses was not high, because of mass, total chlorophyll in the moss layer was considerable, leading to higher total chlorophyll values in the herb–moss layer at forest sites compared with those at open field site (Table 1). Water content in the moss layer was particularly high compared with that in herbaceous species.
Species diversity was higher in open field (7–20 vascular species per plot) than in forest herb layers (3–11 species). Species lists were quite different at different sites. The forest sites were dominated by typically shade-tolerant species, whereas light-demanding species were abundant in open field. Therefore, to investigate the influence of species composition on the reflective properties of the canopy, we used the total species number as an indicator of uniformity and relative share of grasses and sedges with erect growth form as an indicator of differences in leaf angular distribution (Table 1).

Soil lines

Soil reflectance in the studied plots followed a linear relationship between reflectances in the NIR and red spectral channels (Figure 1C). Soil was generally brighter in open field, and on-site soil reflectance variability was greater at forest sites. The soil line was similar in open field and sparse forest (Figure 1C, soil line 2), whereas dense forest appeared to have lower reflectance in the NIR region (Figure 1C, soil line 1). Hence, the parameters of soil line 2 were used for open field and sparse forest and those of soil line 1 for dense forest in the calculation of TSAVI.

Reflectance difference from background

Based on the soil line concept, the presence of green vegetation should increase the reflectance in the NIR spectral region and decrease the reflectance in the red (visible) region compared with that of the soil background. This is the expected mechanism behind the relationship between green vegetation and vegetation indices like NDVI. In open field, reflectance from the herb layer was clearly less than that from the soil in the red wavelength, whereas reflectance increased slightly in the NIR region (Figure 1A), which is in accordance with expectations. By contrast, the moss layer in forests tended to be brighter than soil in both the red and NIR regions in both forests (Figure 1B). Surface reflectance measured above the herb layer increased even more in dense forest, which had a thin herb layer (Figure 1A, circles). Hence, in contrast with expectations that the presence of green vegetation should decrease reflectance in the red spectral region compared with that of the background, we observed exactly the opposite in the understory vegetation of dense forest. Red reflectance was highest above the herb layer, intermediate above the moss layer (measured immediately after harvesting the herb layer), and lowest above bare soil (measured after removing the herb and moss layers) in dense forest (Figure 1, circles).

We looked at differences in reflectance between the layer and its background ($R_{\text{dif}}$). Red reflectance from the layer tended to be greater than that from the background at low layer biomass values, whereas NIR region reflectance increased at any value of layer dry mass (Figure 2). The difference in red reflectance from the layer and background was related to layer dry mass along separate lines for the herb and moss layers. At the same value of red reflectance difference as that from the background, the moss layer dry mass was notably larger compared with herb layer dry mass (Figure 2B).

It appeared that reflectance in the red region was strongly dependent on leaf-area-based chlorophyll content. Data on the herbaceous layer showed that plots where red reflectance increased compared with that of the background were those with low average leaf-area-based chlorophyll content (Figure 3). The regression line crossed the zero value at approximately 150 mg·m$^{-2}$ of chlorophyll content.
Unfortunately, we do not have data on the moss leaf area to dry weight ratio and therefore do not have estimates for the moss leaf area and for the leaf-area-based chlorophyll content. However, the reason for the high brightness of the moss layer in the red region (Figures 1B, 2B) may stem from a large leaf area and consequent low value for leaf-area-based chlorophyll content.

**Herb layer reflectance relationships with its mass and chemical traits**

Optical properties of the herb–moss layer in the forests were best correlated with tree canopy cover (relative incident light), vegetation dry mass, and herb-layer chlorophyll content (Table 2). When analyzing forest and open field data together, the number of significant correlations between reflectance parameters and descriptors of vegetation increased (Table 2). Increased ranges of values for parameters and systematic differences between forest and open field data can largely cause this increase. The correlation analysis revealed that the reflectance in the red wavelength region was generally the best correlated parameter with vegetation. In our data, reflectance in the red spectral region appeared to respond to chlorophyll content only in the herb layer and was not related to the total chlorophyll content summarizing both the herb and moss layers. On the contrary, reflectance in the NIR region (measured above the herbaceous canopy) was better related to the total biomass and water content of both the herb and moss layers than to those of the herb layer alone (Table 2). Vegetation indices usually combine the reflectance in the red and NIR regions, but, as we demonstrated here, in our data these two spectral regions “saw” into different depths of vegetation. Despite this, the empirical correlation of vegetation parameters with SR and NDVI were good, and TSAVI, the index that takes into account differences in soil background, was the least correlated derived index (Table 2).

Species composition (number of herb species) had a strong effect on the optical parameters of the herbaceous layer (Table 2). At least partially, however, this may be a pseudo-correlation. Significant positive correlation between species number and blue or red reflectances in forest sites (Table 2) turned to weak positive correlation in blue reflectance and weak negative correlation in red reflectance when all the data were analyzed together (Table 2). Similar changes happened with correlations between green and NIR reflectances with species number (Table 2). One reason for such a change in correlations is related to the fact that, in forest sites, species number increased with an increase in herbaceous cover, whereas in open field the opposite relationship tended to dominate (Table 1). A better grounded influence of species composition on optical properties was related to relative share of grass–sedge growth form in foliage. A significant negative correlation appeared between relative share of graminoid LAI and green, red, or NIR reflectance when all data were taken together (Table 2). Although this correlation weakened when
Table 2. Correlation coefficients of reflectances and vegetation indices measured above herbaceous layer with herb and moss layer parameters.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Relative incident light</th>
<th>Relative share of graminoid LAI</th>
<th>Herb dry mass</th>
<th>Herb water</th>
<th>No. of herb species</th>
<th>Herb chlorophyll per ground area</th>
<th>Herb chlorophyll per leaf area</th>
<th>Herb total LAI (dead + alive)</th>
<th>Moss + herb dry mass</th>
<th>Moss + herb water</th>
<th>Moss + herb chlorophyll</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Forest only</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blue</td>
<td>-0.44</td>
<td>0.33</td>
<td>-0.46</td>
<td>0.13</td>
<td>0.79*</td>
<td>-0.36</td>
<td>-0.32</td>
<td>0.03</td>
<td>-0.39</td>
<td>-0.15</td>
<td>-0.27</td>
</tr>
<tr>
<td>Green</td>
<td>-0.37</td>
<td>-0.33</td>
<td>-0.43</td>
<td>-0.28</td>
<td>0.37</td>
<td>-0.35</td>
<td>-0.23</td>
<td>-0.30</td>
<td>-0.28</td>
<td>0.10</td>
<td>0.00</td>
</tr>
<tr>
<td>Red</td>
<td>-0.88*</td>
<td>-0.10</td>
<td>-0.85*</td>
<td>-0.33</td>
<td>0.68*</td>
<td>-0.73*</td>
<td>-0.68*</td>
<td>-0.47</td>
<td>-0.66*</td>
<td>-0.22</td>
<td>-0.06</td>
</tr>
<tr>
<td>NIR</td>
<td>0.29</td>
<td>-0.24</td>
<td>0.21</td>
<td>0.20</td>
<td>0.10</td>
<td>0.26</td>
<td>0.40</td>
<td>0.15</td>
<td>0.27</td>
<td>0.50</td>
<td>0.00</td>
</tr>
<tr>
<td>SR</td>
<td>0.91*</td>
<td>-0.02</td>
<td>0.92*</td>
<td>0.51</td>
<td>-0.44</td>
<td>0.87*</td>
<td>0.85*</td>
<td>0.58</td>
<td>0.73*</td>
<td>0.39</td>
<td>0.05</td>
</tr>
<tr>
<td>NDVI</td>
<td>0.89*</td>
<td>-0.02</td>
<td>0.85*</td>
<td>0.41</td>
<td>-0.49</td>
<td>0.78*</td>
<td>0.78*</td>
<td>0.52</td>
<td>0.67*</td>
<td>0.35</td>
<td>0.04</td>
</tr>
<tr>
<td>TSAVI</td>
<td>0.71*</td>
<td>-0.17</td>
<td>0.67*</td>
<td>0.34</td>
<td>-0.39</td>
<td>0.65*</td>
<td>0.67*</td>
<td>0.40</td>
<td>0.59</td>
<td>0.45</td>
<td>0.14</td>
</tr>
<tr>
<td><strong>All plots together</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blue</td>
<td>-0.19</td>
<td>0.13</td>
<td>-0.33</td>
<td>-0.07</td>
<td>0.24</td>
<td>-0.22</td>
<td>-0.32</td>
<td>-0.15</td>
<td>-0.17</td>
<td>-0.01</td>
<td>-0.14</td>
</tr>
<tr>
<td>Green</td>
<td>-0.77*</td>
<td>-0.64*</td>
<td>-0.68*</td>
<td>-0.53*</td>
<td>-0.48*</td>
<td>-0.61*</td>
<td>-0.39</td>
<td>-0.67*</td>
<td>0.46*</td>
<td>0.60*</td>
<td>0.47*</td>
</tr>
<tr>
<td>Red</td>
<td>-0.82*</td>
<td>-0.56*</td>
<td>-0.81*</td>
<td>-0.60*</td>
<td>-0.38</td>
<td>-0.71*</td>
<td>-0.65*</td>
<td>-0.71*</td>
<td>0.27</td>
<td>0.44</td>
<td>0.41</td>
</tr>
<tr>
<td>NIR</td>
<td>-0.55*</td>
<td>-0.48*</td>
<td>-0.30</td>
<td>-0.19</td>
<td>-0.46*</td>
<td>-0.26</td>
<td>0.06</td>
<td>-0.40</td>
<td>0.61*</td>
<td>0.70*</td>
<td>0.43</td>
</tr>
<tr>
<td>SR</td>
<td>0.62*</td>
<td>0.40</td>
<td>0.87*</td>
<td>0.69*</td>
<td>0.24</td>
<td>0.78*</td>
<td>0.72*</td>
<td>0.70*</td>
<td>-0.01</td>
<td>-0.19</td>
<td>-0.22</td>
</tr>
<tr>
<td>NDVI</td>
<td>0.64*</td>
<td>0.39</td>
<td>0.78*</td>
<td>0.59*</td>
<td>0.23</td>
<td>0.69*</td>
<td>0.74*</td>
<td>0.63*</td>
<td>-0.03</td>
<td>-0.19</td>
<td>-0.25</td>
</tr>
<tr>
<td>TSAVI</td>
<td>0.23</td>
<td>0.05</td>
<td>0.52*</td>
<td>0.43</td>
<td>-0.08</td>
<td>0.48*</td>
<td>0.58*</td>
<td>0.35</td>
<td>0.29</td>
<td>0.18</td>
<td>0.10</td>
</tr>
</tbody>
</table>

**Note:** *, significant at $p < 0.05$. 

TSA VI
only forest data were analyzed, the sign of the correlation coefficient remained negative (Table 2).

Regression analysis

A multiple regression analysis with stepwise inclusion of variables in the model was conducted to find the herb–moss layer parameters that are the most influential in predicting reflectance properties. The best correlated parameter that was chosen first in the model did not always remain significant in the final model (Table 3). Nevertheless, comparison of stepwise multiple regression analyses made with forest data only with analysis of all data demonstrated that the first chosen parameter remained the same in equations for NIR, red, and green reflectances regardless of the size of the dataset. Blue reflectance had very high variability in forest and was relatively stable in open field, causing substantial differences in the regression equation structure, depending on the choice of dataset.

We conclude from this part of the analysis that reflectance in the visible wavelength range from the herb–moss layer is primarily predicted by the herb layer dry mass, whereas in the NIR region the total amount of aboveground water was the most powerful predictor of reflectance. Leaf-area-based chlorophyll content was included in the final regression model for red reflectance, with a statistically significant coefficient when all the data were analyzed together (Table 3). Although species composition had a significant influence on regression equations for forest floor reflectance, species-composition-related parameters did not remain significant in the final equations for the entire dataset.

We also conducted similar multiple regression analyses of all sites with soil reflectance as an additional vegetation parameter on a list of possible variables (data not shown). The only difference that appeared in comparison with the data in Table 3 was in the equation for NIR reflectance, where soil reflectance was chosen in the equation at the third step instead of LAI and remained with a statistically significant coefficient in the final equation. This also increased the adjusted $R^2$ from 0.518 to 0.602. In the visible wavelength, background reflectance was not included in the regression equations at any step.

Discussion

Remote sensing of forests is often used to obtain information about forest stands, and reflectance properties of forests are often related only to tree layer parameters (Chen and Cihlar, 1996; Blackburn, 2002; de Wasseige and Defourny, 2002; Huete et al., 2002; Kodani et al., 2002). However, it has been shown on the basis of experimental studies and layered reflectance models that reflectance from the community is highly sensitive to background properties, especially at low values of upper layer canopy cover (Smith et al., 1991; Goetz and Prince, 1996; Gemmell et al., 2002; Huete et al., 2002; Meza Diaz and Blackburn, 2003; Eriksson et al., 2006). The significant results of our study reveal that there is considerable

Table 3. Results of stepwise multiple regression analysis.

<table>
<thead>
<tr>
<th>Forest only</th>
<th>Blue</th>
<th>Green</th>
<th>Red</th>
<th>NIR</th>
<th>All plots together</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herb LAI</td>
<td>1</td>
<td>1*</td>
<td>1</td>
<td>1*</td>
<td>1*</td>
</tr>
<tr>
<td>Herb chlorophyll per leaf area</td>
<td>3*</td>
<td>2*</td>
<td>1*</td>
<td>1*</td>
<td>1*</td>
</tr>
<tr>
<td>Herb dry mass</td>
<td>6</td>
<td>7</td>
<td>2*</td>
<td>1*</td>
<td>1*</td>
</tr>
<tr>
<td>Herb water mass</td>
<td>7</td>
<td>2*</td>
<td>1*</td>
<td>1*</td>
<td>1*</td>
</tr>
<tr>
<td>Moss LAI (dead + alive)</td>
<td>6</td>
<td>5</td>
<td>1</td>
<td>4</td>
<td>4*</td>
</tr>
<tr>
<td>Moss dry mass</td>
<td>3*</td>
<td>2</td>
<td>2*</td>
<td>1*</td>
<td>1*</td>
</tr>
<tr>
<td>Moss + herb dry mass</td>
<td>6</td>
<td>5</td>
<td>1</td>
<td>4</td>
<td>4*</td>
</tr>
<tr>
<td>Moss + herb water mass</td>
<td>7</td>
<td>2*</td>
<td>1*</td>
<td>1*</td>
<td>1*</td>
</tr>
<tr>
<td>Moss + herb chlorophyll</td>
<td>1*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Herb total chlorophyll per ground area</td>
<td>3*</td>
<td>2*</td>
<td>1*</td>
<td>1*</td>
<td>1*</td>
</tr>
<tr>
<td>No. of herb species</td>
<td>5*</td>
<td>4*</td>
<td>1*</td>
<td>1*</td>
<td>1*</td>
</tr>
<tr>
<td>Relative share of graminoid</td>
<td>1</td>
<td>1*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
</tbody>
</table>

Note: Values in the table indicate the step when the particular herb–moss layer parameter was included in the regression equation for reflectance. *, parameters that appeared to be statistically significant ($P < 0.05$) in the final equation; ns, not significant.
variability in ground-layer optics that is correlated with tree canopy cover. Relative incident light, which depends on tree canopy cover, was one of the strongest predictors of the reflectance indices measured above the herbaceous layer. Modelling studies have shown that background optical properties become important in predicting total community reflectance at low values of upper canopy cover (Nilsson and Peterson, 1994; Asner and Wessman, 1997; Hanan, 2001). These calculations are based on the assumption that the background properties are independent of the main canopy cover. As shown here, however, this assumption does not hold for a boreal coniferous forest. The optical properties of the understory are related to tree canopy cover because growth of ground vegetation depends on light availability predicted by the tree canopy above (Kull et al., 1995; Smith et al., 1991; Scanlon et al., 2002).

Based on the soil line concept, it is to be expected that the herb layer under a dense tree canopy should grow less extensively than that on a more open site and therefore be more reflective in the red wavelength. Our data basically confirm this; however, as shown by our study, the reasoning is more complex because in low incident light conditions the ground reflectance is greater, not only because relatively reflective background can be seen through the herb canopy but also because the herb canopy itself is considerably brighter than the soil background while grown at low light levels. With an increasing layer of biomass, a component of reflectance that is independent of wavelength increases, but another component related to chlorophyll absorption in the red region decreases. Hence, leaves with no chlorophyll should increase reflectance in the red region proportional to the increase in the NIR region, and it has been shown in several studies that reflectance in visible wavelengths increases considerably with a decrease in leaf chlorophyll content because of scattering from cell–air–water interfaces inside the leaf (Terashima and Saeki, 1983; Brakke et al., 1989; Brakke, 1994; Schultz, 1996; Feldhake and Glenn, 1997). Our data show that leaf canopy is becoming brighter than the background in the red spectral region when leaf-area-based chlorophyll content is less than 150 mg·m⁻². This also agrees with studies of leaf photosynthesis showing that the apparent quantum yield of photosynthesis is declining rapidly because of decreased absorbance and increased transmittance and reflectance if leaf chlorophyll content falls below approximately 200 mg·m⁻² (Gabrielsen, 1948; Terashima and Saeki, 1983; Leverenz, 1987; Poorter et al., 2000).

Little is known about the leaf area and chlorophyll content of mosses. We know of only a few estimates of moss leaf area (Proctor, 2000) and no data about leaf-area-based chlorophyll measurements. Given that most mosses have very thin leaves, often only one cell layer thick and evidently transparent, it is quite likely that mosses are brighter than the soil background, even at the wavelength of strong chlorophyll absorption because reflectance from cell–air–water interfaces dominates over absorption by chlorophyll. This has indirectly been confirmed in the study by Hamerlynck et al. (2000), who showed that reflectance from the moss *Tortula ruralis* carpet was strongly dependent on moss water content in the diurnal cycle. Additionally, Solheim et al. (2000) have shown that mosses have exceptionally high backscatter properties in the visible wavelength. In their study of Antarctic mosses, Lovelock and Robinson (2002) found that differences in reflectance characteristics across sites and species were not clearly linked to changes in pigment concentrations but were more strongly linked to differences in water content and morphology. In our data, the reflectance in the red spectral region was not related to total chlorophyll content of the moss and herbaceous layer, but corresponded only to the chlorophyll content of the herbaceous layer (Table 2). The effect of layer dry mass on red reflectance was also different between the herbaceous and moss canopies (Figure 2B). However, reflectance in the NIR region was better related to the total biomass of both moss and herb layers than to that of the herbaceous layer alone. If reflectance in the red and NIR spectral regions corresponds to the different vertical depths of vegetation, this can offer an additional explanation of why the empirical relationships between vegetation parameters and reflectance indices like NDVI are not universal but rather need separate ground verification for each site.

Stepwise regression has been used in several studies to find the combination of wavelength ranges that best describes some properties of vegetation (O’Neill et al., 2002; Serrano et al., 2002). Our task here was the opposite: we tried to define the best descriptors of ground-layer vegetation that need to be measured to predict the optical properties of that layer. Although chlorophyll is the main constituent in foliage that selectively changes absorption in the visible wavelength range, reflectance from the herb–moss canopy was considerably better related to the dry mass of herbs. Because of scattering from leaves, the NIR wavelength appears to “see” deeper into the canopy than visible light. This also explains our finding that the regression equation for NIR reflectance was improved (adjusted $R^2$ increased from 0.518 to 0.602) when the NIR of the soil background was allowed to be used in the equation, whereas in the visible wavelengths soil reflectance was not included in the equations at any step in the stepwise regression (data not shown in the tables).

The best descriptor of NIR reflectance in the whole dataset was total aboveground water content in the herb and moss canopies. Our instrument measures NIR outside the known wavelength of water absorption, and the relationship between NIR reflectance and canopy water content was positive, so it is clear that this relationship is not related to water absorption features. The most likely explanation is that water content scales with the number of cell–air–water interfaces in mosses and herbs better than dry mass, and this is why we see that the mass of total aboveground water is the best descriptor for NIR reflectance. O’Neill et al. (2002) also found that the correlation coefficient between the water content of Sitka spruce needles and reflectance became positive in the wavelength region between 700 and 1400 nm, although they explained the lack of good correlation between reflectance...
and known water absorption features with saturation. Meanwhile, manipulations with sample water content of *Sphagnum* mosses by Vogelmann and Moss (1993) showed that increased water content caused a decrease in reflectance in the whole NIR range.

Model calculations have shown that the influence of leaf angles on canopy reflectance may even be in the same magnitude as the influence of LAI (Bacour et al., 2002; Liangrocapart and Petrou, 2002). The fact that species composition, and particularly the relative share of graminoid growth, in the ground vegetation had some, albeit marginal, influence on our regression models is most likely related to different leaf angle distributions in these canopies. However, we cannot rule out the possibility that it is also caused by species-specific anatomical peculiarities. However, we could not find a universal model for old field and forest herb layers that had a high level of predictive power for herb–moss layer optical properties.

**Conclusions**

1. The herb–moss layer in the forest tends to be brighter in the visible wavelength when the canopy above is more closed and the herb–moss layer is less developed. This is not caused by the increased contribution of soil to total reflectance but because of specific properties of herb–moss layer plants grown at low light levels.

2. A wavelength-independent increase in reflectance from air–cell interfaces seems to predominate over absorption in chlorophyll with decreasing herb–moss biomass at low incident light levels.

3. The best descriptors from the herb–moss layer for the derivation of optical parameters for forest canopy background are herb layer dry mass for the visible wavelength range and total aboveground water mass for near-infrared (NIR) reflectance. In addition, knowing the average chlorophyll content per leaf area considerably improves the estimate for red reflectance.

4. Optical properties of the soil background in the studied coniferous forest only have an influence in the NIR range and do not affect herb–moss layer reflectance in the visible range because of intensive moss cover.

**Acknowledgements**

This study was supported by the Estonian Science Foundation (grants 8290 and 8110) and the Estonian Ministry of Education and Science (grant SF0182732s06). JP also acknowledges partial funding from the Spanish Government grants CGL2006-04025/BOS and Consolider-Ingenio Montes CSD2008-00040 and the Catalan Government grant SGR 2009-1458. This paper is dedicated to the memory of Professor Olevi Kull (22 June 1955 – 31 January 2007).

**References**


