ABS ACTA BIOLOGICA SLOVENICA
LJUBLJANA 2022 Vol. 65, Št. 2: 26–41

Optical properties of different structures of some herbaceous understorey plant species from temperate deciduous forests

Optične lastnosti različnih struktur pri nekaterih zelnatih rastlinskih vrstah v podrasti zmernega listopadnega gozda

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Abstract: This contribution discusses the optical properties of different structures of some herbaceous understorey plant species from temperate deciduous and mixed forests. These forests are marked by annual dynamics of radiation level that is related to the vegetation cycle of forest trees. During winter and early spring, the understorey is exposed to full solar radiation, while later in the growing season radiation is limited due to the closing of the tree storey. The plasticity of optical properties of photosynthetic structures of understorey plants is directly related to their structural and biochemical phenotypic plasticity that optimises harvesting and use of energy. The optimisation of energy harvesting is also achieved by specific adaptations of green leaves, such as variegation (*Pulmonaria officinalis*, *Cyclamen* sp.), anthocyanic lower epidermis (*Cyclamen* sp.), and by using structures other than green leaves for photosynthesis, such as bracts (*Hacquetia epipactis*) and sepals (*Helleborus* sp.). The optical properties of these structures are similar to those of green leaves. The understanding of optical responses of different structures contributes to the understanding of the forest understorey functioning.

Keywords: bracts, leaves, light conditions, optical properties, sepals, temperate deciduous forest, understorey plants

Izvleček: Prispevek povzema optične lastnosti različnih struktur nekaterih zelnatih rastlinskih vrst v podrasti listnatega in mešanega gozda zmernega pasu. Te gozdove zaznamuje letna dinamika ravni sevanja, ki je povezana z vegetacijskim ciklom gozdnega drevja. Pozimi in zgodaj spomladi je podrast izpostavljena polnemu sončnemu sevanju, kasneje pa je sevanje omejeno zaradi olistanja krošenj. Plastičnost optičnih lastnosti fotosinteznih struktur rastlin v podrasti je neposredno povezana z njihovo strukturno in biokemijsko plastičnostjo, ki optimizira privzem in rabo energije. Optimizacijo pridobivanja energije rastline dosežejo tudi s posebnimi prilagoditvami zelenih listov, kot sta pisanost (*Pulmonaria officinalis*, *Cyclamen* sp.) in antocianska spodnja povrhnjica (*Cyclamen* sp.) ter z uporabo drugih struktur poleg zelenih listov za fotosintezo, kot so podporni (*Hacquetia epipactis*) in čašni listi (*Helleborus* sp.). Optične lastnosti teh struktur so podobne optičnim lastnostim zelenih listov. Razumevanje optičnih odzivov različnih struktur prispeva k razumevanju delovanja rastlin v podrasti.

Ključne besede: čašni listi, listi, optične lastnosti, podporni listi, podrast, svetlobne razmere, zmerni listopadni gozd

Introduction

Temperate deciduous and mixed forests are marked by annual dynamics of radiation regime that is related to the vegetation cycle of forest trees (Klančnik et al. 2015). The amount of radiation at the forest floor in a certain time of the year is a consequence of canopy structure, especially leaf area index (Larcher 2003). During winter and early spring, the understorey is exposed to full solar radiation, while later in the growing season radiation is limited due to the closing of the tree storey (Rothstein et al. 2001, Klančnik et al. 2015). In a fully foliated forest, light enters the system *via* gaps in the canopy forming sun flecks that provide up to 80% of solar energy for understorey species (Larcher 2003). However, these sun flecks are very variable regarding their quality, intensity, and duration (Chazdon et al. 1991, Lambers et al. 1998, Leakey 2004). The radiation conditions in the understorey layer during the vegetation period define the functional traits of photosynthetic organs, including their optical properties (Esteban et al. 2008, Grašič et al. 2020), which enable efficient light use (Reich et al. 2003, Yoshimura et al. 2010). Such traits are leaf tissue thickness and density, spotted and variegated leaves (Klančnik et al. 2016), and the production of additional pigments, such as anthocyanins (Smillie et al. 1999). Optical properties depend on plant tissue structure and may thus be species-specific (Marín et al. 2016). However, they can vary significantly during tissue ontogenetic development (Grašič et al. 2021 a,b) and due to species phenotypic plasticity, which is related to environmental changes in the habitat (Liew et al. 2008, Klančnik et al. 2016, Klančnik et al. 2014 a).

Herbaceous understorey species exhibit different life histories that are related to variable radiation environments during specific phenological phases. The first group of plants develops all organs before the full foliation of trees. These organs are based on storage accumulated in underground organs (Larcher 2003) and possess a variety of traits that support quick development in the period with abundant light (Kim et al. 2015). The second group develops leaves prior to tree foliation and reproductive organs after the closure of the canopy (Gilliam 2014). The third group consists of, for example, the genus *Vinca* (Darcy et al. 2002) and some *Helleborus* species (Bavcon et al. 2012). These species have evergreen leaves that enable photosynthesis throughout the whole year, especially during high-light conditions in late winter and early spring. Some species within these groups increase their carbon and energy budget through additional photosynthetic organs, such as sepals and bracts (Grašič et al. 2020, Aschan et al. 2003), and in some species, the colour of sepals turns green after pollination, as shown for *H. orientalis* cv. *Olympicus* (Shahri et al. 2011).

Photosynthetic organs optimise light harvesting by various adaptations of their biophysical structure (Ustin et al. 2001). Optical properties that comprise light reflectance, absorbance, and transmittance (Woolley 1971) vary among different ecological groups of plants (Klančnik et al. 2012, Klančnik et al. 2014 b, Klančnik and Gaberščik 2016). In addition, they can be tissue- or species-specific, or they can vary due to tissue ontogenetic development and species phenotypic plasticity in relation to environmental changes in the habitat (Liew et al. 2008, Klančnik et al. 2012). Therefore, they also vary among different understorey species and their organs in time and space. The reflectance spectra of photosynthetic organs are a very useful parameter since they reflect specific organ traits, such as biochemical structure (Carter et al. 2002, Gitelson et al. 2002, Castro et al. 2008, Kováč et al. 2013, Roelofsen et al. 2014, Klančnik and Gaberščik 2016), and content of nutrients and hydration (Baltzer et al. 2005, Lukeš et al. 2013, Roelofsen et al. 2014). They also provide information about energy balance (Noda et al. 2013, Ullah et al. 2012), the potential presence of stress, and contribute to the understanding of photosynthetic performance (Coops et al. 2005). In some studies, it was shown that reflectance spectra act as a "plant signature", enabling the identification of different plant groups (Klančnik and Gaberščik 2016), or even species classification (Castro-Esau et al. 2006).

The present article presents the optical properties of different structures of some understorey plant species in temperate deciduous forests. The insight into these optical properties and the traits supporting them contributes to the understanding of the forest ecosystem and enables the maintenance of some of these plants in man-made environments, which usually differ significantly from those of the floor of deciduous forests.

Leaf traits and their optical properties

Phenotypic plasticity

Plant traits are a result of the evolutionary process, which favours a variety of adaptations that enable an optimal response to specific environmental conditions (Šraj Kržič et al. 2005, Rascio et al. 1999, Boeger et al. 2003). The persistence of these traits in plant species is related to the stability of conditions in the habitat. However, species phenotypic plasticity enables the acclimation of specific traits to current conditions (Larcher 2003). Therefore, phenotypic plasticity presents the potential of an organism to produce various phenotypes when exposed to different environmental conditions (Sommer 2020). The highest level of phenotypic plasticity is found in environments with pronounced environmental changes. Environmental conditions in the forest understorey may be very heterogeneous in time and space, as is the case in temperate deciduous and mixed forests (Valladares 2003). This highly heterogeneous environment differs in multiple factors. Besides variable light conditions, understorey plants are subjected to changes in temperature, soil moisture, and fertility. However, these factors usually co-vary in nonlinear ways (Valladares et al. 2007). The adaptation to light depends on a trade-off with plant responses to other factors (Larcher 2003). Different species in the forest understorey exhibit different levels of phenotypic plasticity, as shown for *Asarum arifolium* and *Hepatica nobilis*, the latter showing a higher level of plasticity (Warren et al. 2013). Plasticity may be expressed in different organs and at different levels of plant structure and function, and it also differs among different environments, as is the case in *Hacquetia epipactis* (Grašič et al. 2021 a). The plasticity of understorey plants in response to light is relatively low in shade-tolerant woody species in the tropics, where the environment is rather stable (Valladares et al. 2000). Warren et al. (2013) reported an ecological convergence in trait values along environmental gradients between ecologically similar, but phylogenetically different evergreen understorey herbs. The plastic response of plant structural traits due to different environmental conditions results in undisturbed functioning, including the processing of available energy. Thus, the plasticity of leaf optical properties is directly related to their structural and biochemical phenotypic plasticity (Klančnik et al. 2014 a, Grašič et al. 2021 a,b). Differences in species responses to variable light environments affect the success of understorey species in forest dynamics (Santos et al. 2021). In the case of fern *Phyllitis scolopendrium*, light along with other environmental factors significantly affected the frond biochemical structure, and consequently also their optical properties (Fig. 1). However, the photochemical efficiency of PS II remained the same (Grašič et al. 2020). Thus, photosynthetic acclimation to specific light conditions, which also includes pigment levels, is one of the most important plant abilities (Popović et al. 2006). Changes in biochemical leaf traits and their optical properties during the growing season were observed in *Cyclamen purpurascens*, where the contents of carotenoids and anthocyanins decreased between February and April, and affected optical properties (Klančnik et al. 2016). This is also a consequence of lower levels of radiation that reached their habitat due to canopy closing (Rothstein et al. 2001). Besides anthocyanins, changes in carotenoid contents are also important since they can present accessory pigments under light limitation (Demmig-Adams et al. 1996).

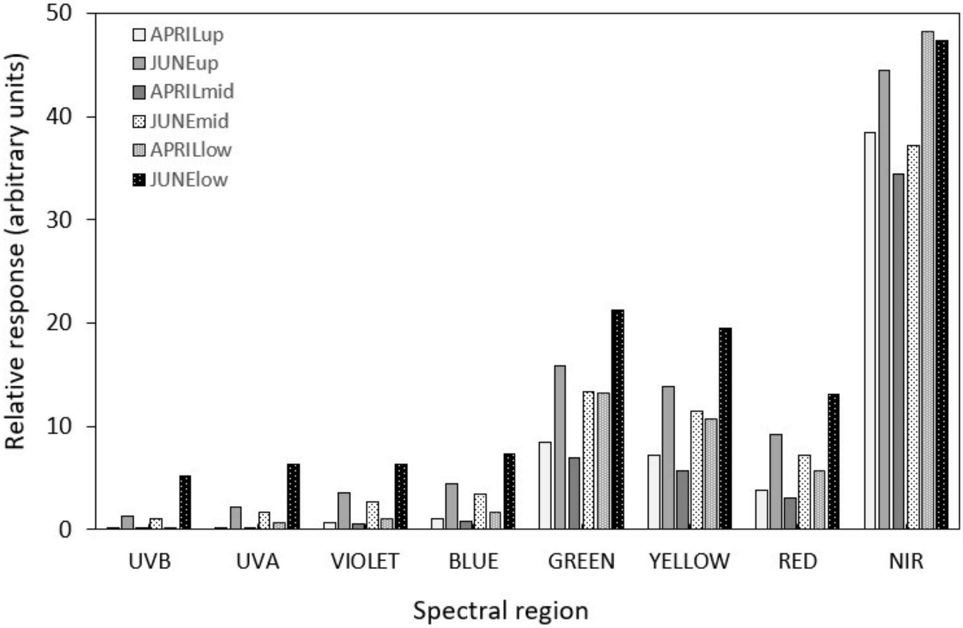

Figure 1: Mean reflectance of radiation in *Phyllitis scolopendrium* fronds in different spectral regions from locations with various light regimes at different times of the year. Locations along the light gradient: up - upper (high light level), mid – in the middle (middle light level), low - lower (low light level).

Slika 1: Povprečna odbojnost sevanja pri listih vrste *Phyllitis scolopendrium* v različnih območjih sevanja z lokacij z različnimi svetlobnimi režimi v različnih delih sezone. Lokacije vzdolž svetlobnega gradienta: up - zgoraj (visoka raven svetlobe), mid - sredina (srednja raven svetlobe), low - spodaj (nizka raven svetlobe).

The optical properties of understorey species are shaped by leaf structure and thickness, which are represented by specific leaf area (SLA). SLA of understorey species may vary from 0.66 to 0.01 cm^2/mg (Prado et al. 2015), which results in different light capture efficiency (Reich et al. 2003). Lower SLA increases light backscattering, which positively affects light absorbance, reduces sieving effects, and prolongs the path of photons within the tissue (Lee et al. 2000). It determines photosynthetic efficiency per leaf mass, which increases with increasing SLA (Evans et al. 2001). Correlations between SLA and light reflectance spectra were observed by Asner et al. (2008), who studied the optical properties of tropical forest canopy species.

Leaf colouration

Plant biochemical and morphological structure is determined by organ-specific interactions with the environment (Bongers et al. 2019), which also includes light conditions. Many studies have revealed an important role of pigments in shaping leaf optical properties (Slaton et al. 2001, Gitelson et al. 2002, Baltzer et al. 2005, Levizou et al. 2005, Castro et al. 2008, Klančnik, et al. 2014 a, Klančnik et al. 2016). The contents of chlorophylls, which are the main light-harvesting pigments, usually negatively affect the reflectance spectra (Klančnik et al. 2014 a). This effect may be altered in plants with different structures at the leaf surface, e.g., in many understorey species. For example, the presence of trichomes as the first target of light may significantly affect leaf optical properties (Baldini et al. 1997, Klančnik et al. 2012).

Anthocyanins play an important role in the adaptive strategy of plants to their radiation environment, including in forest understorey species. Anthocyanins mitigate or prevent plant stress, as they function as sunscreens, antioxidants, and chelating substances (Landi et al. 2015). Anthocyanins in leaves of understorey plants filter high-intensity radiation during sun flecks (Gould et al. 1995, Gould 2004). *In vivo* anthocyanins exhibit an absorption peak around 550 nm, and this peak magnitude is related to anthocyanin content (Gitelson et al. 2022). In general, anthocyanins accumulate in upper leaf layers (Chalker-Scott 1999, Lev-Yadun 2002, la Rocca et al. 2014). However, some understorey plant species accumulate them in their abaxial epidermis as well (Hughes et al. 2008, Lee et al. 1979, Lee et al. 2001), as is the case in the genus *Cyclamen* (Klančnik et al. 2016) (Fig. 2).

Figure 2: The red abaxial epidermis in *Cyclamen purpurascens* may vary in colour intensity and homogeneity.
Slika 2: Rdeča spodnja povrhnjica vrste *Cyclamen purpurascens* se lahko razlikuje po intenzivnosti in homogenosti barve.

Some researchers suggest that the reduction of light transmission through the leaf due to anthocyanins might negatively affect competitors, especially in spring before the development of the canopy. A study of leaves of tropical trees at the beginning of the last century showed that red abaxial epidermis contributes to enhanced leaf temperatures, however, this was not confirmed in later studies (Gould et al. 1995, Lee et al. 1979). Klančnik et al. (2016) showed significant differences in transmittance in the visible and NIR regions between the leaves with and without the red abaxial epidermis. The visible region is used for photosynthesis but also has a thermal effect, while the effect of NIR is mainly thermal (Ross 1981). In addition, lower transmittance in the green and yellow regions was measured for the red-coloured lower epidermis in comparison to the epidermis with fewer anthocyanins. The study of *Begonia heracleifolia* revealed that the red anthocyanic lower epidermis did not affect the reflectance of red light in the mesophyll (Hughes et al. 2008). The study of *Colocasia esculenta* leaves with different anthocyanin contents showed no differences in CO_2 uptake under shade conditions between the studied leaf types (Hughes et al. 2014). *Erytronium dens-canis* red patches are due to a single layer of cells in the upper parenchyma that accumulate anthocyanins and have lower photochemical efficiency in comparison to the green sections (Esteban et al. 2008).

Variegated leaves

Plant leaves are usually uniformly coloured. However, some understorey plants develop leaves in such a way that they have different colour patterns at their surface, optimising the use of both high and low light levels in the forest understorey (Tsukaya et al. 2004). These coloured patterns are very popular, therefore, such species can be used as ornamental plants (e.g., *Aglaonema*, *Begonia*, *Cyclamen*). *Pulmonaria officinalis*, a perennial forest herb that grows in biodiverse, mixed, and open forests, has variable light green spots at the green leaf surface (Fig. 3). Variegation patterns are mainly not related to pigments, but rather to the differences in the palisade mesophyll (Konoplyova et al. 2008). Light green spots in *P. officinalis* are caused by the presence of loosely arranged cells instead of a well-established layer of packed cells in the palisade parenchyma (Esteban et al. 2008). SLA in light green parts was higher in comparison to dark green parts (3.16 and 2.75 dm^2/g DM, respectively). Consequently, dark green parts had somewhat higher contents of all pigments, however, the differences were not significant. All these aspects affected plant optical properties, as shown in Figure 4. Light green parts reflected and transmitted more light in the green, yellow, and red regions, while shorter wavelengths and NIR showed a similar pattern in both light green and dark parts of the leaf. In addition, chlorophyll fluorescence imaging revealed a decrease in photochemical efficiency for light green spots in comparison to the green sections (Esteban et al. 2008). Under higher levels of UV radiation that are found in more open habitats, the light green spots become less transparent to visible light (Gaberščik et al. 2001).

Figure 3: *Pulmonaria officinalis* leaves with light green spots.
Slika 3: Listi vrste *Pulmonaria officinalis* s svetlozelenimi pikami.

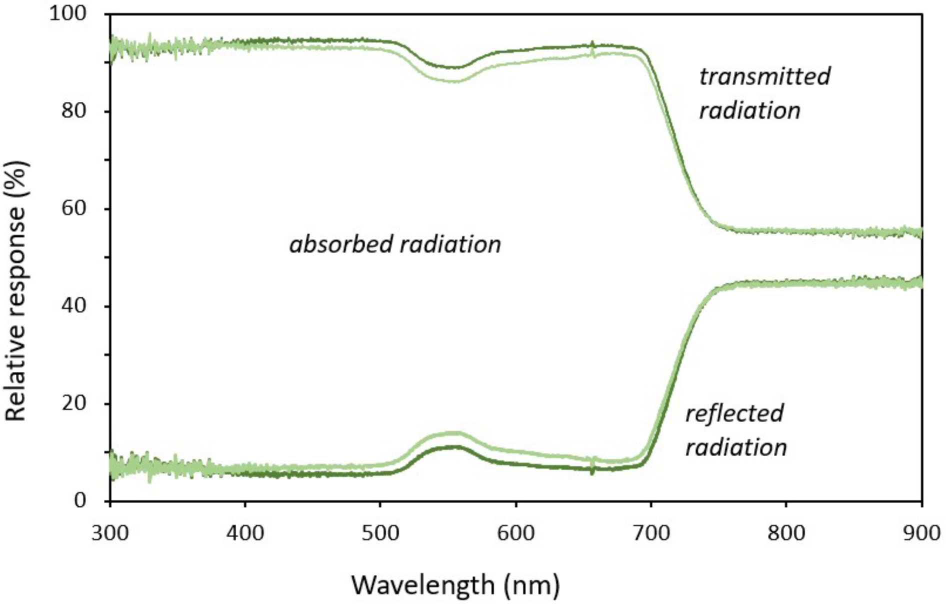

Figure 4: Mean radiation reflectance (area below the lower curves), light transmittance (area above the upper curves), and absorbance (area between the upper and lower curves) measured on the dark (dark green curves) and light green (light green curves) parts of the *Pulmonaria officinalis* leaves.

Slika 4: Povprečna odbojnost sevanja (površina pod spodnjimi krivuljami), prepustnost sevanja (površina nad zgornjimi krivuljami) in absorbanca (površina med zgornjo in spodnjo krivuljo), izmerjene na temnih (temnozelene krivulje) in svetlozelenih (svetlozelene krivulje) delih listov vrste *Pulmonaria officinalis*.

In *Cyclamen purpurascens* leaves, more evident differences in light reflectance of dark and light green parts were obtained in comparison to *P. officinalis* (Figs. 5 and 6). These differences were negligible in the UV region, but very pronounced in VIS, and then again less pronounced in NIR. The light green leaf parts also transmitted more radiation than the dark green leaf parts, wherein the most differences in transmission were seen for the green region (Klančnik et al. 2016). In spite of the differences in light management, the light green parts of the variegated leaves perform photosynthetic activities similar to those of the dark green leaf parts or of fully green leaves (Konoplyova et al. 2008, la Rocca et al. 2011, Sheue et al. 2012, la Rocca et al. 2014).

Figure 5: The light green pattern at the upper leaf surface of *Cyclamen purpurascens* may vary in intensity and shape.
Slika 5: Svetlozelen vzorec na zgornji površini listov vrste *Cyclamen purpurascens* se lahko razlikuje po jakosti in obliki.

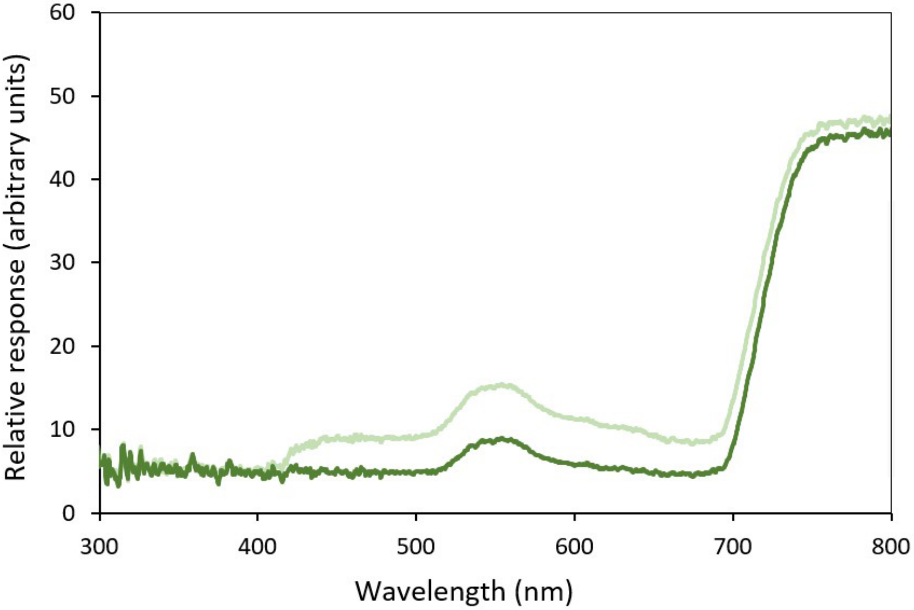

Figure 6: Reflectance of radiation measured on the dark green (dark green curve) and light green (light green curve) parts of the *Cyclamen purpurascens* leaves.

Slika 6: Odbojnost sevanja, izmerjena na temnozelenih (temnozelena krivulja) in svetlozelenih (svetlozelena krivulja) delih listov vrste *Cyclamen purpurascens*.

The higher reflectance in the light green leaf parts is mainly a consequence of the morphological differences. The mesophyll below the light green leaf parts shows a polygonal light reflection pattern, composed of white polygons formed around the epidermal cell edges (Zhang et al. 2009, Sheue et al. 2012, Klančnik et al. 2016). This pattern is associated with air spaces between the epidermal and mesophyll cells (Zhang et al. 2009), and thus the light green colouration is also a consequence of leaf mesophyll structure (Sheue et al. 2012). The palisade mesophyll cells of these leaf parts are larger and loosely arranged, therefore having a greater volume of intercellular air spaces (Konoplyova et al. 2008, Sheue et al. 2012, la Rocca et al. 2011), which increase light reflection and the scattering of light (Esteban et al. 2008). In *C. purpurascens* the differences in tissue density between the light and dark green leaf parts were most pronounced in April under high light conditions, when tissue density was significantly higher in the dark green leaf sections (Klančnik et al. 2016). This additionally supports the importance of variegation for light management. This increased light reflectance of the light green leaf parts may serve as photoprotection and may prevent damage caused by high light during sun flecks (Holmes et al. 2002, Esteban et al. 2008). However, the dark green leaf parts are protected against excessive radiation by carotenoids (Filella et al. 1999, Schulze et al. 2005), as their carotenoid contents were higher when the canopies were not yet closed (Klančnik et al. 2016). In the case of *Actinidia kolomikta* leaf colour was also related to leaf structure and leaf pigment contents (Wang et al. 2015), and the reflectance of white leaves was significantly higher than that of green leaves (Wang et al. 2020).

Structures other than leaves

Some species in the understorey of mixed and deciduous forests may use structures other than leaves, such as bracts and sepals, for harvesting energy in the early period with abundant light.

Sepals may function as petals, as they attract pollinators, protect flowers, and regulate flower temperature, however, they can also serve as photosynthetic organs (Grašič et al. 2021 b, Herrera 2005). This is also the case in the genus *Helleborus*, which comprises 22 species of herbaceous or evergreen perennials originating in Europe and Asia (Bavcon et al. 2012, Fassou et al. 2020, Grašič et al. 2021 b). In some species, the colour of flowers changes during flower development. In *H. orientalis* cv. *Olympicus*, creamy white sepals turned green at later developmental stages (Shahri et al. 2011) and sepals of pollinated flowers contained more chlorophyll in comparison to non-pollinated and senescent flowers (Schmitzer et al. 2013). In some *Helleborus* species with coloured sepals, the evolutionary selection in sepals was not directed to floral function, but rather to the development of sepals into photosynthetic organs (Salopek-Sondi 2002, Salopek-Sondi et al. 2000). This was confirmed by the presence of stomata in the sepals (Grašič et al. 2021 b), even though their density is relatively low in comparison to leaves (Aschan et al. 2005). In *H. odorus* with green-coloured sepals, photochemical efficiency is permanently high, whereas this is not the case in *H. niger* with initially white sepals (Grašič et al. 2021 b). However, the photochemical efficiency of *H. niger* sepals increases during flower development, as they turn green since their chlorophyll content increases (Grašič et al. 2021 b). Along with chlorophylls, sepal carotenoid, anthocyanin, and UV-B–absorbing substances contents were also gradually increasing (Grašič et al. 2021 b). A study of *H. niger* showed an increase in the contents of total anthocyanins, but not flavonols, which absorb in the UV region (Schmitzer et al. 2013). The reflectance and transmittance spectra of the green sepals in *H. odorus* and *H. niger* (Grašič et al. 2021 b) had similar shapes as those of green leaves (Klančnik et al. 2012). Sepal reflectance in VIS and NIR regions was in a negative relationship with chlorophylls and anthocyanins in all phases of flower development. In the case of transmittance, negative relationship between the visible regions (with the exception of green) and anthocyanins and chlorophyll *a* and *b* was obtained in the developing phase, while UV-B–absorbing substances were more important in the flowering phase (Grašič et al. 2021 b).

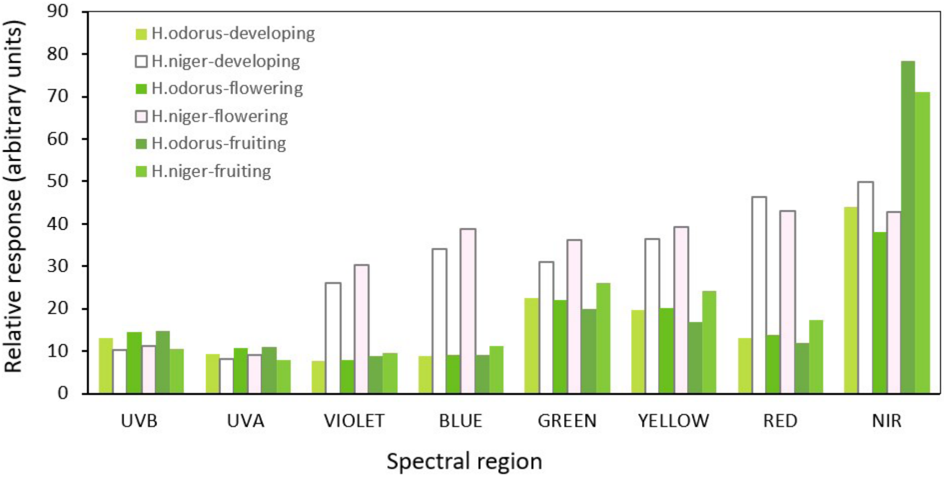

Figure 7: Mean reflectance of radiation in *Helleborus odorus* and *H. niger* sepals in the different spectral regions at different phases of flower development.

Slika 7: Povprečna odbojnost sevanja čašnih listov vrst *Helleborus odorus* in *H. niger* v različnih spektralnih območjih v različnih fazah razvoja cvetov.

In some genera, floral bracts serve as a protective structure and replace the lacking perianth by enclosing floral organs (von Balthazar et al. 1999). Their photosynthetic ability presumably increases the importance of bracts early in the season. Bracts are also extremely important for the attraction of pollinators in some species (Gagliardi et al. 2018) since in 25% of angiosperm flowers, the reflection of ultraviolet light represents important visual information for pollinators (Klomberg et al. 2019). An example of such plant species is *Hacquetia epipactis*, which develops leaves, flowers, and fruits before the canopy layer closes (Gilliam 2014). It has a narrow ecological range and it is sensitive to changes in light conditions and water availability (Ellenberg 1996). *H. epipactis* has umbels that are supported by green bracts (von Balthazar et al. 1999). The shape of the spectral curves of bract reflectance reveals spectra typical of green leaves with peaks in the green and NIR regions, and with low reflectance in the shorter wavelengths (Klančnik et al. 2012). During umbel development, the traits of these bracts change along with changes of the basal leaves, wherein the most evident difference in the reflectance spectra was observed in the UV range (Fig. 8), which increased with age for bracts, while it decreased with age for basal leaves (Grašič et al. 2021 a). Some similarity was observed for bracts of immature and flowering umbels, which may be of relevance for pollinators (Arnold et al. 2010).

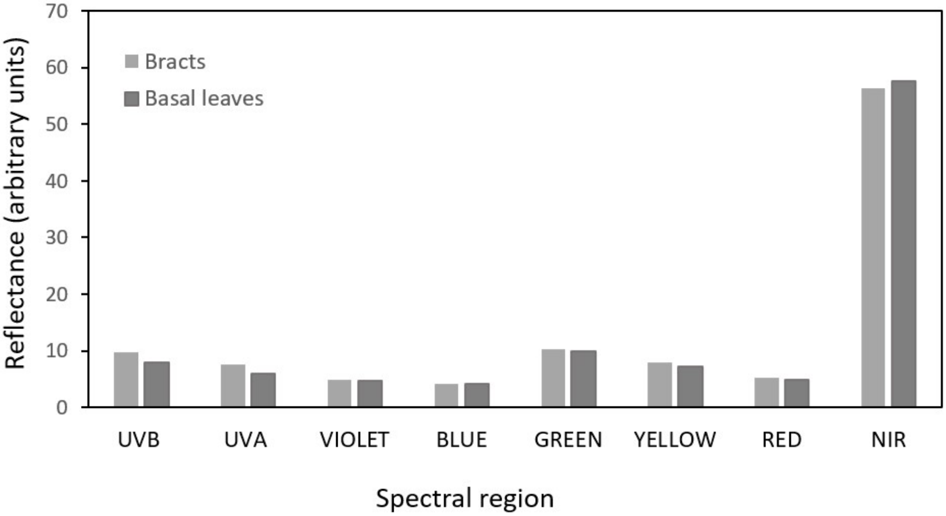

Figure 8: Mean reflectance of radiation in *Hacquetia epipactis* basal leaves and bracts in the different spectral regions.
Slika 8: Povprečna odbojnost sevanja bazalnih in podpornih listov *Hacquetia epipactis* v različnih območjih spektra.

Summary

Temperate deciduous and mixed forests are marked by annual dynamics of radiation level that is related to the vegetation cycle of forest trees. The amount of radiation on the forest floor at a certain time of the year is a consequence of the canopy structure. During winter and early spring, the understorey is exposed to full solar radiation, while later in the growing season radiation is limited due to the closing of the tree storey. In a fully foliated forest, light enters the system *via* gaps in the canopy forming sun flecks that are very variable regarding their quality, intensity, and duration. The radiation conditions in the understorey layer during the vegetation period define the functional traits of photosynthetic organs, including their optical properties, which support efficient light use. The present article presents the optical properties of different structures in some understorey plants species in temperate deciduous forests. The understanding of the functioning of these optical responses and the traits supporting them contributes to the understanding of the forest ecosystem and enables the maintenance of some of these plants in man-made environments, which usually differ significantly from those of the floor of deciduous forests. Plant traits are a result of the evolutionary process, which favours a variety of adaptations that enable an optimal response to specific environmental conditions. The adaptation to light depends on a trade-off in plant responses to other factors. However, plant plasticity that enables the development of specific traits may also enhance light harvesting. Different species in the forest understorey exhibit different levels of phenotypic plasticity. Plasticity may be expressed in different organs and at different levels of plant structure and function, and it also differs among different environments. The plasticity of leaf optical properties is directly related to their structural and biochemical phenotypic plasticity. Plant biochemical and morphological structure, including photosynthetic pigments and anthocyanins, plays an important role in the adaptive strategy of plants to the radiation environment in the forest understorey. Plant leaves are usually uniformly coloured. However, some understorey plants develop leaves in such a way that they have different colour patterns at their surface, optimising the use of both high and low light levels in the forest understorey. The higher light reflectance in

the light green leaf parts is mainly a consequence of the morphological differences and to a lesser extent of pigment contents. Some species may use structures other than leaves, such as bracts and sepals, for efficient energy harvesting.

Povzetek

Za zmerne listnate in mešane gozdove je značilna letna dinamika ravni sevanja, ki je povezana z vegetacijskim ciklom gozdnega drevja. Količina sevanja v gozdnih tleh skozi čas je posledica strukture krošnje. Pozimi in zgodaj spomladi je podrast izpostavljena polnemu sončnemu sevanju, kasneje v rastni dobi pa je sevanje omejeno zaradi zaprtja drevesnih krošenj. Sevanje v podrasti med vegetacijskim obdobjem vpliva na funkcionalne poteze fotosinteznih organov, med drugim tudi na njihove optične lastnosti, ki podpirajo učinkovito rabo svetlobe. Pričujoči članek predstavlja optične lastnosti različnih struktur nekaterih vrst rastlin podrasti v zmernem listnatem gozdu. Poznavanje optičnih odzivov in funkcionalnih potez, ki jih podpirajo, prispeva k razumevanju gozdnega ekosistema in omogoča ohranjanje določenih tovrstnih rastlin v umetnih okoljih, ki se običajno bistveno razlikujejo od razmer v gozdu. Funkcionalne poteze rastlin so rezultat procesa evolucije, ki daje prednost različnim prilagoditvam, ki omogočajo optimalen odziv na specifične okoljske razmere. Prilagajanje na svetlobo je kompromis med odzivom rastlin na vse dejavnike, medtem ko fenotipska plastičnost rastlin, ki omogoča razvoj specifičnih lastnosti, lahko izboljša tudi prestrezanje svetlobe. Različne vrste podrasti kažejo različno stopnjo fenotipske plastičnosti. Plastičnost se lahko izraža v različnih organih in na različnih ravneh zgradbe in delovanja rastline, razlikuje pa se tudi med različnimi okolji. Plastičnost optičnih lastnosti listov je neposredno povezana z njihovo strukturno in biokemijsko fenotipsko plastičnostjo. Biokemijska in morfološka zgradba rastlin, vključno s fotosinteznimi pigmenti in antocianini, ima pomembno vlogo v strategiji prilagajanja rastlin na sevalno okolje v gozdni podrasti. Listi rastlin so običajno enakomerno obarvani, vendar imajo nekatere rastline liste z različnimi barvnimi vzorci na površini, kar optimizira rabo tako visoke kot tudi nizke ravni svetlobe v podrasti. Večji odboj svetlobe v svetlozelenih delih listov je predvsem posledica morfoloških razlik in v manjši meri vsebnosti pigmentov. Nekatere vrste lahko za povečanje učinkovitosti prestrezanja svetlobe poleg listov uporabljajo tudi druge strukture, kot so podporni in čašni listi.

Acknowledgements

This work was supported by the Ministry of Education, Science and Sport, Republic of Slovenia, through the programme “Biology of plants” (P1-0212).

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