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THE EFFECT OF LIGHT CONDITIONS ON LEAF INJURY IN UNDERBRUSH SHRUBS CAUSED BY LEAF-EATING INSECTS

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Abstract. Light conditions exert direct effects on metabolism, growth and development of plants, including their ability to defend against pests. In this study, we explored the impact of light conditions on response of six understory shrub species (*Sambucus nigra*, *Prunus serotina*, *Prunus padus*, *Cornus sanguinea*, *Frangula alnus* and *Corylus avellana*) to grazing by herbivore insects. Shrub species differed significantly in the level of foliar perforation by insects. Except for *C. avellana*, leaves of plants exposed to full sun were less affected by leaf-chewing insects than leaves from plants grown in low light. It is likely that shade-grown plants have higher host quality due to their lower content of secondary metabolites (soluble phenols and condensed tannins) and higher content of nonstructural carbohydrates and nitrogen. However, there were no significant relationships between interspecific susceptibility to grazing and leaf chemistry, indicating that other factors such as combined effect of host defense and herbivore abundance may be responsible for observed differences in foliar perforation.

Key words: insects, light, phenols, understory shrubs, tannins

INTRODUCTION

The understory shrub layer can have a considerable effect on the function and structure of forest communities. These shrubs contribute significantly to the maintenance of favourable water relations in the soil, accelerate the decomposition of litter and enrich the soil with nutrients [Szymański 2000]. They also play an important role in forest regeneration and at the forest border with other ecosystems (the ecotone zone) they protect the forest phytocenosis against degeneration [Balcerkiewicz and Kasprowicz 1989].

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Polish forests, similar to those in other European countries, have a considerable proportion of pine monocultures or mixed broadleaved forests, with pine predominating and a slight admixture of oak, beech or hornbeam. The predominance of pine can be a negative phenomenon, both from the point of view of forest economy and the ecological stability of stands. This may be counteracted by the introduction of an understory shrub layer composed of species such as black elder, hazel, euonymus, alder buckthorn, dogwood, viburnum, etc. or woody plants, which under normal conditions grow to become tall trees, while under adverse conditions their growth is retarded and development inhibited. The need to carry out research on shrubs in the forest underbrush results from the necessity to gain insight into the effect of this vegetation layer on stands.

Since light conditions have a significant effect on leaf structure and metabolite content, including those serving defense functions against the adverse effect of biotic factors (insect feeding, infestation by pathogenic fungi) [Jansen and Stamp 1997], it seems justified to include the effect of light conditions in this type of research. However, there is limited data available in the literature that would make it possible to test the hypothesis that plants growing at low light levels are more susceptible to insect herbivory than those growing at high light levels [Roberts and Paul 2006].

It is commonly proposed that several factors are responsible for the varied resistance of plants to feeding by leaf-eating insects. First of all it is believed that the degree of insect injury is dependent on the nutritive value of leaves [Awmack and Leather 2002]. In this case the primary cause of less intensive feeding by leaf-eating insects is chemical defense, either passive (pre-existing secondary metabolites such as simple phenolic acids, tannins, and flavonoids) in leaves, and/or induced (the capacity of enhanced synthesis of these compounds when fed on) [Oleksyn et al. 1998, Honkanen et al. 1999, Hemming and Lindroth 1999]. In contrast to this concept, some researchers are of the opinion that limited leaf feeding is not determined by contents of the above mentioned metabolites, but rather low nutritive value of leaves, characterized by low contents of nitrogen compounds and high lignin contents [Koricheva et al. 2004]. This hypothesis is opposed by some researchers, who are of the opinion that a consequence of low nutritive value of leaves is not a reduced insect injury, but on the contrary – an increase in the injury rates caused by insect feeding [Coley and Barone 1996]. It is indicated that low calorie content of plant tissue results in increased consumption, since otherwise it would be impossible for insects to complete their life cycles [Giertych et al. 2005]. According to this concept leaves containing more nitrogen compounds are less intensively eaten by larvae, since superior quality of food requires less intake.

The primary objective of the study was to determine the effect of leaf chemistry on variation in the degree of injury by leaf-eating insects, feeding on leaves of underbrush shrubs, depending on shrub species and light conditions under which they are growing.

The study was conducted on six species of underbrush shrubs, commonly found in Poland, differing in their light requirements and degree of defoliation caused by leaf-eating insects.

MATERIAL AND METHODS

Investigations were conducted in the Palędzie Forest District (52º23’ N, 16º40’ E, the Konstantynowo Forest Division). They were carried out on 6 shrub species of the forest underbrush: common elder (*Sambucus nigra* L.), black cherry (*Prunus serotina* Ehrb.), bird cherry (*Prunus padus* L.), common dogwood (*Cornus sanguinea* L.), alder buckthorn (*Frangula alnus* Mill.) and hazel (*Corylus avellana* L.). Six shrubs were selected of each species, three from each variant of light conditions (three shrubs growing under abundant light and three growing in shaded positions). When analysing the phenology and specific leaf area (SLA, the area of leaf projection per unit of its mass, $cm^2 \cdot g^{-1}$) the optimal date of leaf collection for the purpose of these analyses was established to be mid-August. The determination of SLA values makes it possible not only to establish the time of maximum leaf development, but also define their type in terms of light conditions. Within individual species leaves grown in shade have higher SLA values than those grown under relatively high light levels. The SLA value is a better indicator of the effect of light conditions than periodic measurements of light intensity, as it reflects light conditions found throughout the entire growth and development of a given plant [Elemans 2004]. The percentage of leaf perforation was estimated on the day of material collection. Leaves (20-40) gathered for the purpose of chemical analyses were either undamaged or injured to a minimal degree. This made it possible to eliminate the effect of feeding by leaf-eating insects on changes in contents of chemical compounds in leaves. After being dried at 65°C (40°C for tannins), leaves were analysed for their contents of defense compounds (total soluble phenols and tannins) as well as nutrients (nitrogen and non-structural sugars).

Contents of non-structural sugars (soluble sugars and starch) were determined using a modified method, as described by Haissig and Dickson [1979] and Hansen and Møller [1975]. Soluble sugars were assayed in methanol-chloroform-water extracts. The precipitate remaining after extraction was used to determine starch content. Starch analysis consisted of its transformation into glucose with amyloglucosidase and oxidation using the peroxidase-glucose oxidase complex. Contents of soluble sugars were measured at wavelength λ = 25 nm, following a colour reaction with anthranone, while contents of starch were measured at λ = 450 nm following the reaction with dianisidine. Contents of soluble sugars and starch (with glucose as a standard) were expressed in % dry weight.

Contents of total phenolics were measured according to Johnson and Schaal [1957], as modified by Singleton and Rossi [1965]. Total phenol content was determined using Folin Ciocalteu's Phenol Reagent (Sigma F – 9252) at wavelength λ = 660 nm, whereas results were expressed per μM chlorogenic acid in g^{-1} d.m.

Condensed (catechol) tannins, after extraction with absolute methanol, were determined by colorimetry using a colour reaction with vanillin in an acid medium [Price et al. 1978]. Readings of absorption were taken at λ = 500 nm, while results were converted into μM catechin g^{-1} d.m.

Nitrogen content was determined using an Elemental Combustion System CHNS-O 4010 analyzer (Costech Instruments, Italy/USA; http://www.costechanalytical.com).

Statistical analyses were conducted using JMP software (SAS Institute Inc.). Values presented on graphs are means calculated from 3 replications (shrubs) for each variant. Vertical segments on graphs marked values of standard error (SE) of means. A two-way analysis of variance was used to compare the degree of injury caused by insect feeding on leaves of investigated species with the other traits. The Tukey test was applied when dividing species in terms of leaf injury caused by insect feeding.

RESULTS

Results assessing the degree of leaf injury caused by insect feeding (Fig. 1) made it possible to classify the shrub species studied into 3 groups: 1) shrubs with low insect feeding rates – common elder, common dogwood, and alder buckthorn (feeding injury of 0.2, 1.2 and 1.2% – mean for both light condition variants of shrub growth), 2) shrubs with medium insect feeding injury rates – hazel, and black cherry (6.6 and 7.2%), and 3) shrubs with high leaf injury rates caused by insect feeding – bird cherry (15.0%).

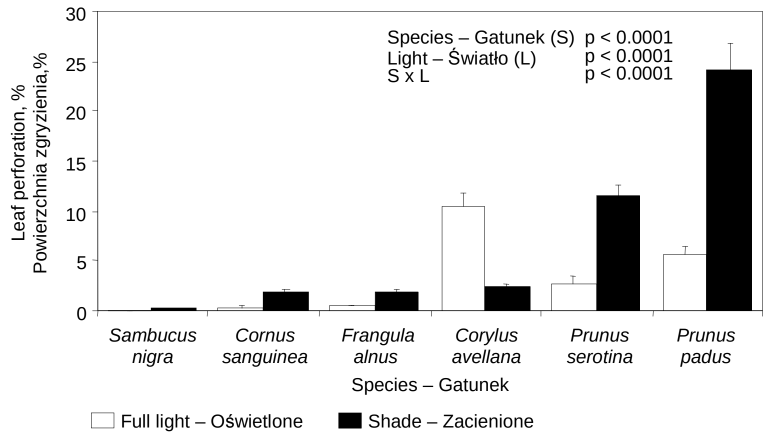

Fig. 1. Leaf perforation (+SE) of six shrub species in relation to long-term light level. In the left corner is a dendrogram of cluster groupings of species based on similarity of their response to insect herbivory

Rys. 1. Zgryzienia liści przez owady (+SE) sześciu gatunków krzewów w zależności od warunków świetlnych. W lewym rogu zamieszczono dendrogram grupowania krzewów o podobnym stopniu zgryzienia przez owady

Results showed a lack of significant dependence between the rate of insect feeding injury on leaves and their contents of analysed metabolites and nitrogen. A lower insect feeding rate on leaves in individual species (Fig. 1) was not correlated with a higher phenol content (Fig. 3), a lower nitrogen content (Fig. 5) or non-structural sugar contents (Fig. 6). Despite a lack of such correlations, some dependence was observed for the case of tannins (Fig. 4). Results indicated that tannin content in leaves of shrubs belonging to the groups of species with low insect feeding rates (common elder, dogwood, alder buckthorn) was almost seven times lower than that in shrubs with medium or high insect feeding rates (hazel, cherries).

In turn, we may observe a relationship between the degree of leaf injury and analysed factors, depending on light conditions within the same species. In five of the species investigated, leaves of shrubs growing in shaded positions were more intensively infested by leaf-eating insects than leaves of shrubs growing at full insolation (Fig. 1).

This was manifested most distinctly in bird cherry. Hazel was an exception to this rule. It was the only species analyzed in which leaves from high light shrubs were injured by

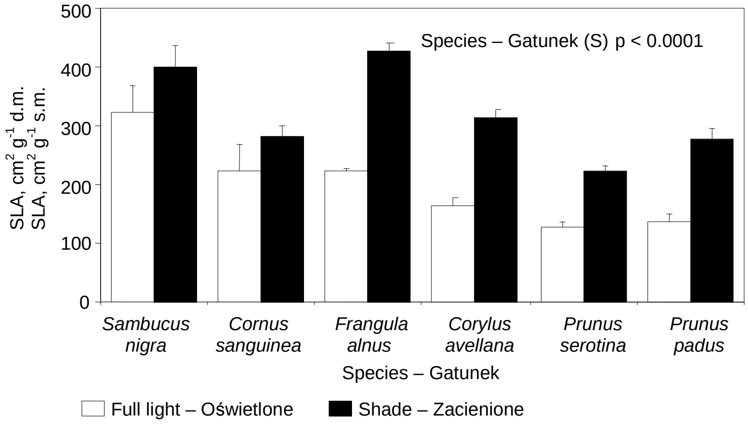

Fig. 2. Specific leaf area (+SE) of six shrub species in relation to long-term light level

Rys. 2. Specyficzna powierzchnia liści (+SE) sześciu gatunków krzewów w zależności od warunków świetlnych

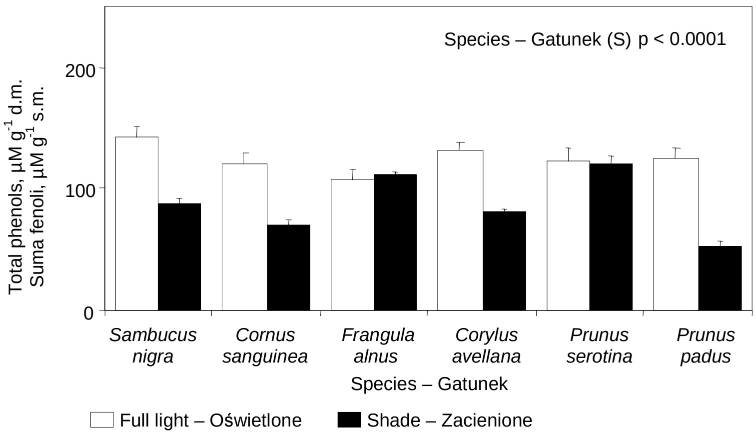

Fig. 3. Soluble phenolic concentration (+SE) expressed as chlorogenic acid in relation to long-term light level

Rys. 3. Zawartość rozpuszczalnych związków fenolowych (+SE), w przeliczeniu na kwas chlorogenowy, w liściach sześciu gatunków krzewów w zależności od warunków świetlnych

feeding insects more than leaves from shaded shrubs. For the shrub species in the study, SLA values (Fig. 2) were higher for leaves from shaded shrubs than high light shrubs, and total soluble phenols and condensed tannins were generally higher in leaves with lower SLA values (i.e. high light leaves, Figs 3, 4). Only alder buckthorn had a similar content of phenols in leaves from shrubs grown under different light conditions. Leaves of hazel grown under high light had higher contents of phenols and tannins, similar to

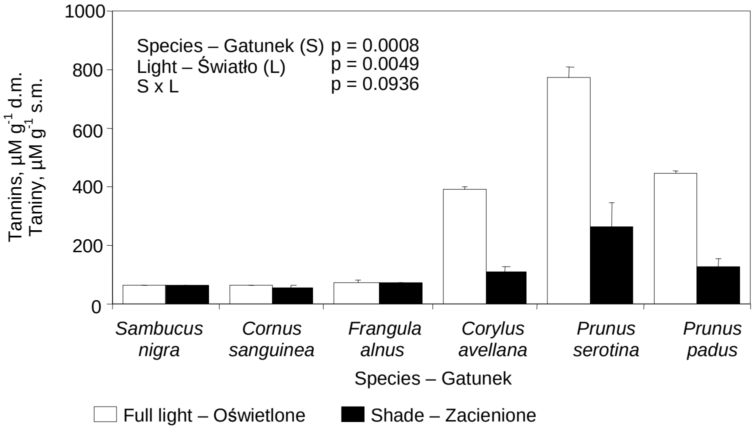

Fig. 4. Concentration of tannins (+SE) expressed as catechins in relation to long-term light level
Rys. 4. Zawartość skondensowanych tanin (+SE), w przeliczeniu na katechinę, w liściach sześciu gatunków krzewów w zależności od warunków świetlnych

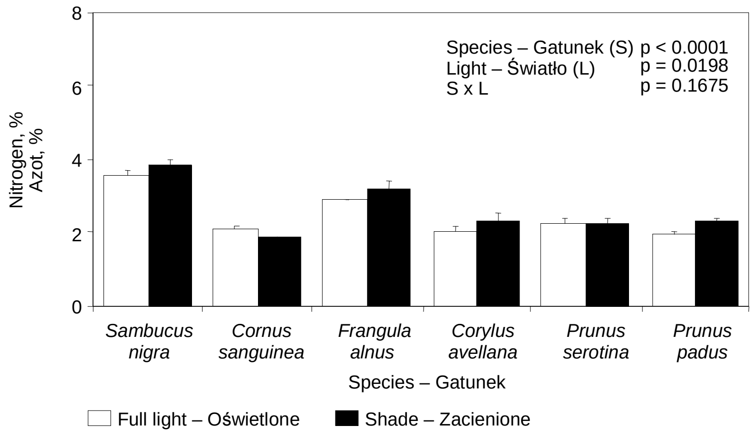

Fig. 5. Foliar nitrogen concentration (+SE) in relation to long-term light level
Rys. 5. Zawartość azotu (+SE) w liściach sześciu gatunków krzewów w zależności od warunków świetlnych

the other species, despite the fact that they were injured by leaf-eating insects to a higher degree than leaves from shaded shrubs. Also, contents of nutrients – nitrogen (Fig. 5) and non-structural sugars (Fig. 6), did not explain the difference in hazel leaf injury caused by feeding insects between leaves from the high and low light shrubs. In all these species, including hazel, contents of nitrogen and non-structural sugars were higher in leaves from shaded shrubs.

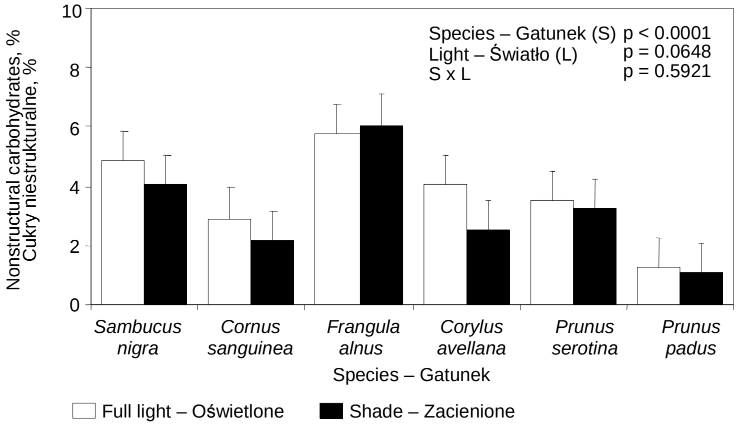

Fig. 6. Total nonstructural carbohydrates in leaves (+SE) in relation to long-term light level
Rys. 6. Zawartość cukrów niestrukturalnych (+SE) w liściach sześciu gatunków krzewów w zależności od warunków świetlnych

DISCUSSION

The six understory shrub species differed markedly in the average degree (for those grown under high and low light) of leaf blade injury caused by leaf-eating insects. Common elder, belonging to the group of species with the lowest degree of insect feeding injury [Atkinson and Atkinson 2002], did not show any or showed only a slight degree of such injury (Fig. 1). Other species, such as bird cherry, are subjected to considerable pressure from herbivorous insects [Kooi et al. 1991, Leather 1991] and frequently only the midribs of leaves remained on the shrub (observations recorded by the authors). Plants have developed several adaptations in defense against leaf-eating animals. Some species minimize damage caused by feeding insects due to increased regeneration and formation of new leaves [Honkanen et al. 1999], others (such as shrubs included in this study) use more of their resources for chemical defense of leaves than for regeneration after injury. The primary compounds involved in plant defense mechanisms are phenolic compounds [Kopcewicz and Lewak 2002]. However, results on total soluble phenolics in leaves of shrub species investigated in this study, do not explain differences in the degree of insect feeding injury. The results for tannins and insect feeding, namely low tannin contents in leaves of species with low insect feeding rates (approx. 65 $\mu M\ g^{-1}$ d.m. in elder, dogwood and alder buckthorn) and high contents in species with high insect feeding rates (350 $\mu M\ g^{-1}$ d.m. in bird cherry) may be explained in several ways [Harborne 1997]. Defense against leaf-eating insects involving tannins in shrubs with low insect feeding injury rates was limited in the course of evolution, since other defense mechanisms are sufficiently effective. Shrubs with medium and high insect feeding injury rates are subjected to such high pressure from leaf-eating insects that investing in tannin synthesis is necessary for the shrub to resist their infestation. A lack of dependencies between the degree of feeding injury and contents of defense compounds and nutrients recorded in this study, probably results from the presence of other defense compounds not analyzed. It is possible that particular shrub species are infested by highly specialized leaf-eating insect species, adapted to high contents of defense compounds or capable of utilizing fully even the smallest nutrient resources of plants. This problem may also be explained by the methodology of sampling itself. Leaves uninjured by insects were collected for chemical analyses. However, frequently it was impossible to find uninjured leaves of those shrub species intensively infested by leaf-eating insects. In such cases leaves least damaged by insects were gathered. It is possible that even under the influence of slight injury due to herbivore attack, a rapid tannin synthesis is triggered in leaves of these species. A similar phenomenon was observed by Nabeshima et al. [2001] who investigated the effect of leaf-eating insects (*Orthosia paromoea*, *Cosmia exigua*, *Telorta edentata*) on leaves of oak (*Quercus crispula*).

SLA values of leaves from shrubs growing in shaded positions were higher than those growing at full insolation, which is consistent with literature data [Coley and Barone 1996, McDonald et al. 1999]. The degree of injury caused by insect feeding was significantly affected by light conditions under which a given shrub was growing (Fig. 1), as was pointed out by Hemming and Lindroth [1999]. This is most frequently explained by different contents of phenolic compounds, which can have a repellent action against insects [Furlan et al. 2004, Akhtar and Isman 2004]. Generally leaves of shrubs growing at full insolation contain much higher contents of phenolic compounds than leaves of shrubs growing in shaded positions [Fig. 3, Bourgaud et al. 2001]. An opposite relationship was found between light conditions and nutrient contents (nitrogen, sugars). Leaves of the high light shrubs contained less nutrients than leaves from shrubs grown in the shade. Thus, leaves from shaded shrubs are eaten more frequently and to a higher degree by leaf-eating insects, than leaves of shrubs grown in the sun [Fortin and Mauffette 2002]. A similar relationship could be observed among shrub species analysed in our study. Hazel turned out to be an exception since its dependence was opposite that of the other five species. A similar exception to the rule that higher resistance to insect feeding injury occurs on plants grown with high insolation was reported for beech (*Fagus crenata*) by Yamasaki and Kikuzawa [2003], who also found that contents of defense compounds and nutrients in leaves did not explain the response to feeding by insects. The opposite correlation between the degree of insect feeding injury and the type of leaves in hazel compared to the other five shrub species may be due to the action of other chemical compounds (repellents or attractants) present in leaves or differences in the morphology and anatomy of the leaves themselves. It is possible that hazel has its own, specific fauna of leaf-eating insects adapted to feeding on leaves rich in phenolic compounds. Our observations also indicate that leaves of hazel from shaded positions have many more hairs than leaves of the insolated position type, and this could also help cause leaves from shade-grown shrubs to have more resistance than those from high light environments.

In future studies it will be advisable to investigate dynamics of changes in leaf characteristics throughout the entire growing season and to identify species of insects feeding on the leaves as well as their natural enemies.

CONCLUSIONS

1. The shrub species analysed differ significantly in their susceptibility to leaf consumption by leaf-eating insects. Three groups may be distinguished in this respect:
   – species with low insect feeding rates (common elder, common dogwood, alder buckthorn),
   – species with medium feeding rates (hazel, black cherry),
   – a species with a high feeding rate (bird cherry).

2. Variation in insect feeding rates on leaves among shrub species studied is not caused by differences in contents of the defense compounds and nutrients measured.

3. The considerably lower degree of feeding injury on leaves of shrubs growing in high light environments may be explained by varied levels of defense compounds and nitrogen within each species, except for hazel.

4. The different response of hazel to feeding by leaf-eating insects in comparison to that of other shrub species may not be explained by differences in levels of defense compounds and nutrients analysed.

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WPŁYW WARUNKÓW ŚWIETLNYCH NA USZKODZENIA LIŚCI KRZEWÓW PODSZYTU PRZEZ FOLIOFAGI

Streszczenie. Warunki świetlne wywierają bezpośredni wpływ na metabolizm, wzrost i rozwój roślin, w tym także na ich możliwości obronne przed szkodnikami. W badaniach określaliśmy wpływ warunków świetlnych na reakcję sześciu pospolitych gatunków krzewów podszytu (*Sambucus nigra*, *Prunus serotina*, *Prunus padus*, *Cornus sanguinea*, *Frangula alnus* i *Corylus avellana*) na żerowanie foliofagów. Gatunki różniły się istotnie w poziomie zgryzienia liści przez owady. Z wyjątkiem *C. avellana*, liście krzewów rosnących w warunkach pełnego nasłonecznienia były mniej zgryzione przez owady niż krzewy rosnące w cieniu. Należy sądzić, że wyższa jakość pokarmowa liści krzewów rosnących w cieniu jest związana z mniejszą zawartością w nich wtórnych metabolitów (rozpuszczalnych fenoli i skondensowanych tanin). Jednakże nie było istotnej zależności między wrażliwością gatunków na zgryzanie liści a ich chemizmem, co wskazuje, że zarówno reakcja obronna gospodarza, jak i liczebność foliofagów mogą być odpowiedzialne za obserwowane różnice w stopniu zgryzienia liści.

Słowa kluczowe: owady, światło, fenole, krzewy podszytowe, taniny

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