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Close Ties Between Undergrowth Plants and Insects

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The forest undergrowth is crucial for maintaining the humidity, soil fertility and stability of tree stands in a forest ecosystem. How do herbivorous insects interact with the undergrowth, and how will climate change affect these complex interactions?

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The forest undergrowth, or understory, is a layer of vegetation in the forest ecosystem made of shrubs and low trees up to 4 m high. In Poland, as well as in other European countries, a significant share of the tree stands are made up of pine mono-

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Fig. 1.
The American black cherry has taken over the undergrowth in many pine forests, such as this one

Fig. 2.
The invasiveness of the American black cherry is also a big problem for newly-planted forests

cultures or mixed forests, dominated by pine trees with an admixture of oak beech and hornbeam. This is not ideal when it comes to the ecological stability of stands, but it can be remedied by introducing undergrowth made up mainly of shrubs, such as bird cherry, hazel, euonymus, buckthorn, dogwood, rhamnus, etc. The understory has a great impact on the functioning of the entire forest ecosystem because it helps protect the soil against erosion, reduces the amount of water evaporated from the soil, and improves climate relations inside the stand by blocking the wind from penetrating into the forest. In addition, by shedding litter, which varies in terms of structure and chemical composition, undergrowth shrubs and trees can contribute to faster decomposition of dead organic matter, and by introducing various mineral compounds into circulation they can prevent soil degradation, thereby improving its structure and chemical composition.

In general, undergrowth shrubs play an important role in forestry. In contemporary forest management, much attention is paid to zones where a forest borders on open areas. Of particular importance is the proper shaping of transition zones (ecotones) in harmony with the natural vegetation – they protect the inside of the forest from the adverse effects of open areas as well as being a refugium for fauna, flora and biota of fungi. The forest border zone plays an important role in the ecotone. Forest phytocoenoses occurring along an open forest border, in other words without shrubs, are often subject to degeneration. In 1999, the Director General of the Polish State Forests issued an ordinance requiring forest-field and forest-water borders to have a 20–30 m wide protective strip, composed of shrubs and low trees and a loose upper story, as an ecotone zone.

Phytomelioration

Introducing undergrowth shrubs into tree stands themselves is also an important part of forest management efforts, namely in phytomelioration and in protecting trees from harmful insects. Phytomelioration involves introducing undergrowth into single-species stands to improve the circulation of nutrients. The choice of undergrowth species depends on such factors as their habitat requirements and whether or not they can occur among the natural vegetation. For example, years ago in Poland there were cases of inappropriate phytomelioration, where geographically alien species were used, leading to the spread of the American black cherry in Polish forests. Although this species is no longer being introduced into the undergrowth, it has been considered an invasive species due to its spontaneous rapid spread on a large scale. Its negative impact is very troublesome and clearly visible, especially in the case of newly-planted forest stands.

Protecting against harmful insects

Introducing the native undergrowth shrub species into a forest can also help protect trees against harmful herbivorous insects. This is one way of protecting monoculture coniferous stands against mass outbreaks of insects. In practice, this means introducing small clusters of undergrowth shrubs to impoverished forest ecosystems, especially those threatened by excessive numbers of leaf-eating insects (foliophages). Shrubs introduced into the forest environment can integrate the structural and functional features of the entire ecosystem, influencing the existence of other forest tree species.

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Fig. 3.
Common bird cherry leaves are widely consumed by foliophages

Fig. 4.
The broad-shouldered leaf beetle (of the Chrysomelidae family) on an American black cherry leaf

Undergrowth shrubs can to some extent provide a refuge for the leaf-eating insect pests that significantly affect important forest-forming tree species in Europe. This occurs mainly due to lack of food caused by large numbers (outbreaks) of harmful insects, or low availability of suitable food for consumption after sanitary spraying. In such cases, the undergrowth itself also suffers severely, as can be easily noticeable even to ordinary strollers walking through the woods. It is probably easiest to observe in the case of the bird cherry, whose leaves begin to develop very early and are eagerly consumed by leaf-eating insects. They often look like a sieve, because the insects first eat the tissue between the leaf veins. Other bushes and shrubs prone to herbivorous insect attacks are the American black cherry, elderberry, common hazel, dogwood and buckthorn.

Plant resistance to insects

The main reason why different leaves are consumed to differing degrees by herbivorous insects is their varied quality as food, both in terms of the nutrients they contain that are beneficial for the growth and development of the insects (proteins, carbohydrates, fats), as well as the defensive compounds meant to deter and discourage consumption. Chemical defense mechanisms help defend plants against herbivores: either constantly maintaining high levels of defense metabolites in the leaves, or having the ability to intensify and quickly synthesize these compounds in response to attacks from herbivores. Also, a low nutritional value of leaves, with low content of nitrogen compounds and energy-providing carbohydrate substances, can discourage foliophages from feeding. On the other hand, in the absence of other food, such low nutritional value of leaves will force herbivores to consume larger amounts of less caloric food, thus augmenting their attacks against plants. Some researchers believe that foliophages choose leaves for consumption based on a combination of their content of both nutritious and unfavorable ingredients. This can be understood by analogy to the spices we humans consume (salt, pepper, paprika, etc.), which are harmful to us in excess, but in small quantities are not only well-tolerated, but also considered desirable and useful.

Studies conducted on the resistance of various species of undergrowth shrubs to herbivorous insects, carried out at the PAS Institute of Dendrology, have shown that the native bird cherry (*Prunus padus*) and American black cherry (*Prunus serotina*) are among the species most often attacked. They are much larger than shrubs that are resistant to feeding insects, like the elderberry or dogwood, but also the hazel and buckthorn. We have found that the most significant pest attacking the leaves of all the shrub species we study is the broad-shouldered leaf beetle. The larvae of this insect do the greatest damage in the spring. For the bird cherry, the second most dangerous pest is the bird cherry ermine moth. Although it is a monophage (feeding almost exclusively on one plant species), we have observed that from year to year it is also increasingly frequently found feeding on the invasive American black cherry. Larvae of this insect destroy not only the leaves, but also inflorescences and fruits. Despite great difficulties, the ermine sometimes manages to live out its entire development cycle on this plant, from eggs, through larvae, to becoming an adult insect.

The content of compounds and substances harmful or beneficial for herbivorous insects is not the only factor decisive for the resistance of undergrowth

Fig. 5.
The butterfly of the bird cherry ermine on a bird cherry leaf

Fig. 6.
The caterpillars of the bird cherry ermine eat the leaves and destroy inflorescences of the American black cherry

bushes to herbivorous insects. For example, the American black cherry is more resistant to insect feeding than the native bird cherry due to differences in leaf structure. The leaves of the black cherry are thicker, stiffer and harder than those of the bird cherry, which makes it more difficult for herbivorous insects to feed on them.

Light's role in the plant–insect relationship

Often, greater differences in food quality can be found between shrubs of the same species growing in full sunlight (sun leaves) or in the shade under the canopy of tree crowns (shade leaves), than between different species of shrubs.

Undergrowth shrubs play an important role both in the depths of the forest, where there is great shading, and in sunny places, along roads, on the edges of forest clearings, and in the ecotone zone, i.e. on the border of the forest with open areas. Depending on light conditions, shrub leaves may be damaged by insects to varying degrees. The main reason for this is the effect of light on the chemical composition and structure of the leaves, and thus on their attractiveness as food. Shade leaves contain more nitrogen and fewer carbohydrates, but do not have as many substances protecting them from foraging insects as sun leaves. However, increased content of defensive compounds in the leaves is not always enough to repel insects. Certain monophages have adapted to feeding on leaves with a high content of defensive compounds.

One example is the flea beetle, *Altica brevicollis coryletorum*, which feeds mainly on well-sunlit shrubs. Most likely, in the course of this species' co-evolution with the common hazel, it developed effective mechanisms to overcome the chemical defense mechanisms of its host. For this insect, the ability to defend against predators is more important than the quality of food. Measurements of the jump length in this beetle species carried out in the field and in the lab indicate that light conditions are connected to their defensive reaction, or jumping. Hence the origin of this insect's name: the "flea beetle." The jumping length of this beetle has been found to be much greater in sunny places, where the temperature is higher than in the shade. This confirms that the light conditions of plant growth determine the size of leaf damage not only indirectly, by affecting the quality of the leaves as food, but also by affecting insects directly.

Climate change and forest undergrowth

Climate conditions affect the growth and development of undergrowth plants in two ways, directly and indirectly, through competition with other plant species. They can also affect them by interacting with organisms such as bacteria, parasitic and mycorrhizal fungi, as well as herbivorous insects.

Effect of temperature on undergrowth plants

The occurrence of particular plant species, their growth and condition depend to a large extent on their heat and humidity requirements. Poland's native bird cherry requires relatively fertile, and above all moist habitats. In contrast, the American black cherry does very well in dry areas with poor quality soil, where it spreads quickly, having no competition from other undergrowth species. It grows well both in the shade and in the sun. Prolonged drought and summer heat, which Poland has been experiencing for many years now, cause the groundwater level to drop, contributing to the poor condition and dying

Fig. 7.
The bird cherry ermine also destroys the bird cherry fruit

Fig. 8.
The flea beetle mainly forages on the sunlit leaves of the common hazel

out of the bird cherry, which is immediately replaced by the invasive black cherry. This happens very quickly, because this plant fruits much more abundantly than the bird cherry, and its seeds are widely spread by many bird species, which love to eat its fruit. This is why the American black cherry now dominates in many habitats where the common bird cherry once prevailed, with only single, older common bird cherry bushes or bushes that have developed a tree-like form, with a deeper root system, managing to remain. On the other hand, the American black cherry is much more demanding when it comes to thermal requirements than other shrub species, such as elderberry or dogwood. Global warming is therefore conducive to the spread of the black cherry and increasing its range to the north, which is detrimental to many other species of undergrowth. High temperatures and droughts cause leaves to age faster and fall prematurely, thus shortening the vegetation period of plants. In addition, such conditions disturb physiological processes and metabolism, which reduces the production of secondary defense metabolites. Thus, the defense capabilities of plants against insect feeding and the harmful effects of bacteria and pathogenic fungi are reduced.

Effect of temperature on herbivorous insects

Temperature affects plants not only directly but also indirectly – by affecting herbivorous insects, which in turn impact the plants. Temperature may also affect insects both directly and indirectly, such as by changing the chemical composition of the leaves they eat.

The rise in temperature affects numerous ecological systems, including the structure and functioning of forest ecosystems. Undoubtedly, in forests, climate change will affect the relationship between plants and herbivorous insects. It is widely assumed that the higher the temperature, the more the insects will feed. But this is not always the case and the problem is complex. Studies conducted at the PAS Institute of Dendrology indicate that high temperatures and the accompanying drought adversely affect the growth of undergrowth plants, but also the insects feeding on them. For example, the previously mentioned bird cherry ermine is also negatively affected by high temperatures, especially on hot summer days when it is in the pupa stage. It dries up, which affects the breeding of butterflies. The opposite is true when it comes to the flea beetle, which thrives in high temperatures, at least when it comes to defending itself against predators. It prefers very sunny bushes, where high temperatures prevail. Of course, everything has its limits and excessively high temperatures can also damage it. We tested this by conducting experiments on the effects of high temperatures under controlled conditions. In the case of this insect, it is expected that in natural conditions it will also begin to colonize shrubs growing in the shade, where the temperature is lower.

In general, we believe that elevated temperatures and periodic droughts associated with global warming will significantly affect the growth and reproduction of undergrowth, both directly and indirectly. This depends on many factors, from the thermal and humidity requirements of specific plants and their competition with other species, through the direct and indirect impact of high temperature on herbivorous insects. As a consequence, the degree of their feeding on the leaves will affect the functioning of their hosts, the plants. In such complex and dynamically changing systems, it is difficult to predict what will happen. What we do know is that any disturbance of the system, especially in nature, is unfavorable and needs time to stabilize. However, we must be aware that some changes may be irreversible.