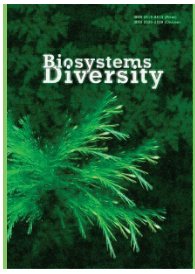

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Influence of tree-crown density on dominant plant species of the herb-shrub stratum in the zone of mixed forests

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Forest ecosystems are among the most complex and dynamic biological systems of our planet. They play an important role in sustaining biodiversity, regulating the climate, and preserving water resources. Furthermore, they serve as natural filters, improving the quality of soil and air, and also preventing erosive processes. Forests create unique conditions for life of various species of plants and animals, which contributes to maintenance of the natural biodiversity and supports the stability of the ecosystem. Likewise, forests are important for the carbon cycle. They absorb a large amount of carbon, thus hindering global warming. Therefore, forest ecosystems are of paramount ecological value and their preservation is crucial for a balanced functioning of the planet. Our studies were carried out in the forest ecosystems of the Desna-Starohutskyi National Park, which is in the Ukrainian Polissia. The materials and methods of the study included systematic collection of the data on density of tree crowns, and also records of diversity of plants of the herb-shrub stratum in the chosen forest areas. Those data were analyzed using statistical methods. The study results revealed that the crown density has a significant effect on diversity of herb-shrub plants in the lower forest strata. Increase in crown density correlated with decrease in the light availability in the herb-shrub stratum. Change in the crown density towards increase significantly altered the conditions for competition between herbaceous and shrub species. Decrease in light availability led to shift in the competition ratio between the species, promoting dominance of more shade-loving species. Increase in crown density, which often reached 100%, made the competition more severe, especially for key resources (light, water, and nutrients). Because of this, species diversity in the herb-shrub stratum of the forest ecosystems was observed to decrease, and less adapted species were extruded. In general, change in tree-crown density in the forest ecosystem had a significant effect on the dynamics of herbaceous and shrub species, changing competitive relations and the structure of those plant communities. The results we obtained expand the knowledge about interactions between crown density and the structure of herb-shrub stratum, which gives perspectives for more efficient management of forest resources, and can also improve scientific identification and implementation of measures for protection of forest ecosystems.

Keywords: forest ecosystems; ground cover; herbaceous plants; species diverse; forest communities; protected nature areas; biodiversity.

Introduction

In the general diversity of types of plant communities, forest phytocenoses have the most complex structure and the richest floristic composition (Estrada-Villegas et al., 2020; Coldea & Cristea, 2022). Oliynyk & Viter (2011) fairly pointed out that forests have a complex organization, interconnection of organisms and cenoses, unity of organisms and environment in this complex. This determines the complexity of functional relations that provide their stability and dynamics (Haggerty et al., 2019; Peng et al., 2020; Michalet et al., 2023). They are a unique unification of various live organisms (Omodior et al., 2021; Reese et al., 2022) and physical factors that interact inside the biosphere (Thyroff et al., 2019; Saulino et al., 2022). An important aspect of forest ecosystems is interaction between various levels of the herbaceous cover (Grabska & Socha, 2021) such as trees, shrubs, and herbaceous plants. Crown density of trees, their size and structure, play a fundamental role in the formation and functioning of the herb-shrub stratum of forest ecosystems.

The most important biological-ecological peculiarity of forest phytocenoses is their multi-stratum structure (Istomina et al., 2020). Typically, there are four strata: trees, shrubs, ground herbs, and mosses. In turn, in favourable soil-climatic conditions, the tree and shrub strata contain two layers each. This peculiarity makes the system of relations between plants of different forest phytocenoses especially complex. Trees that comprise the upper stratum of forest biotopes have multifaceted influence on the lower strata, including herb-shrub stratum (Long et al., 2021). One of the key effects trees have on the herbaceous stratum is change in the availability of sunlight (Zhang et al., 2022; Kriššáková et al., 2023). Decrease in insolation due to crown density makes plants compete for light, and therefore may have significant effects on their growth and development. Moreover, trees have effects on the chemical characteristics of the soil in the lower strata of forests (Zhu & Cheng, 2022). Foliage promotes soil mineralization and its enrichment with nutrients (Estiarte et al., 2023). However, long decay of the leaves and formation of foliage can also inhibit the light availability and resources for herbaceous plants (Pairo et al., 2021). Besides physical and chemical effects, some tree species are known to produce chemical compounds that influence the growth and development of plants in their surroundings (Zhi et al., 2023). This process is called allelopathy and is important for the structure and composition of herb stratum.

Therefore, each stratum in a phytocenosis has influence on plants of other strata and is subject to their influence at the same time. A strong factor is also anthropogenic loading on the forest ecosystems (Hedwall et al., 2019). Classic forest-science studies and modern specialists (Chevaux et al., 2022; Zlobin et al., 2022) identified that the main types of such effects of plants of one stratum on plants of another stratum are: a) effects of upper-stratum plants on the lower ones through light reduction, increased root competition for water and nutrients in the soil, formation of a specifically structured forest litter, and formation of a certain allelopathic biochemical environment (Schönbeck et al., 2021; Wu et al., 2023); b) influence of lower-stratum plants on the upper-stratum plants through reduction of potential niches of recovery of tree species and control of development of their undergrowth.

In the complex of ecological effects of the tree stratum on the stratum of herbs and shrubs, the leading factor in the formation of live ground cover is obviously the light at the soil level, for it controls the most important process in the life of plants – photosynthesis (Fowler et al., 2013). However, the literature data contain very few quantitative statistically significant data on patterns of formation of the herb-shrub stratum in forest phytocenoses depending on the degree to which tree crown intercepts sunlight. Based on accurate quantitative data, it was determined that in coniferous-deciduous forests, the mosaic of above-soil cover forms under the influence of the tree stand through changes in insolation (Helbach et al., 2022). Comparing quantitative parameters of the condition of the tree stand and live cover in boreal beech forests, Tatarnikov (2017) came to the conclusion that closure of the tree crown "leads to "borealization" of the lower strata: occurrence and abundance of light-loving and nemoral herb species sharply decrease in their compositions". Using Canonical Correspondence Analysis, Gillet et al. (1999) revealed that in *Larix* forests, the structure of above-soil herbaceous cover depends on the light level as a result of changes in photosynthesis productivity. In the deciduous Zhiguli forests, Sharyi et al. (2017) determined a positive correlation ($R^2 = 0.85$) between light and size of the green mass of herbaceous vegetation. Korablev (2018), using the method of gradient analysis and method of multidimensional scaling, revealed that in spruce forests, the structure of the tree stratum determined the species and ecological-cenotic composition of live above-soil cover in general. Shlapak et al. (2019) noted that high density of the tree stand leads to formation of lower strata by shade-tolerant and shade-loving plants, whereas low crown density by contrast leads to formation of the lower strata by light-loving plants.

Taking into account many factors influencing the interaction between trees and herbaceous plants, this article aimed to analyze the influence of the tree-crown density on the structure and functioning of the herb-shrub stratum. Analyzing condition of populations of plants of herb-shrub stratum in relation to the extent of tree-stand density is a relevant scientific problem, solving which would help identify reasons for differences in the composition and structure of populations of live above-soil cover in forests depending on light conditions. Understanding those interrelations is important for forestry, ecology, and management of forest resources, and also for preservation of biodiversity in forest ecosystems. The objective of the conducted study was identification of statistically significant differences in the condition of populations of 8 species of vegetative-mobile herbs and shrubs of live above-soil cover depending on the crown density of deciduous trees. The species we chose are typical for the live above-soil cover of deciduous forests of the Ukrainian Polissia, where – as it has been demonstrated earlier – cryptophytes account for over 60% (Kovalenko, 2018).

Materials and methods

The study was carried out in 2018–2022 in three types of forest phytocenoses of the Desna-Starohutskyi National Nature Park (52.3254º N, 33.7745º E), situated in the Ukrainian Polissia (Fig. 1). Specifics of forests of this region have been thoroughly described in the literature (Onyshchenko & Yuhlichek, 2010; Andrienko et al., 2015). To accomplish our objective and ensure the representativeness of the data in the territory of the Desna-Starohutskyi National Nature Park, we chose three structurally close forest phytocenoses, in which we made 160 complete geobatanical relevés. In 10 x 10 m plots, we recorded complete composition of plants for strata – from trees to herb-shrub species. We identified the density of tree stand for the tree stratum, and diversity for herb-shrub species. Density of tree canopy and abundance of plants in live above-soil cover were evaluated as percentages.

Growing location 1 is a forest structure with domination of *Quercus robur* L., with participation of *Populus tremula* L., *Acer platanoides* L., *Betula pendula* Roth, and other deciduous species in the tree stand. The stratum of live ground cover has been formed by *Convallaria majalis* L., *Asarum europaeum* L., *Aegopodium podagraria* L., *Carex pilosa* Scop., and *Stellaria holostea* L. According to the floristic classification, this forest structure is a *Mercurialo-Quercetum*-typicum subassociation.

Growing location 2 is a forest phytocenosis, also with domination of *Quercus robur* L., with composition of accompanying deciduous species that is similar to Growing Location 1. The basis of the herb-shrub stratum is comprised of *Convallaria majalis* L., *Carex pilosa* Scop., *Stellaria holostea* L., *Asarum europaeum* L., and *Mercurialis perennis* L. According to the floristic classification, this forest structure is a *Mercurialo-Quercetum calamagrostidetosum arundinaceae* subassociation.

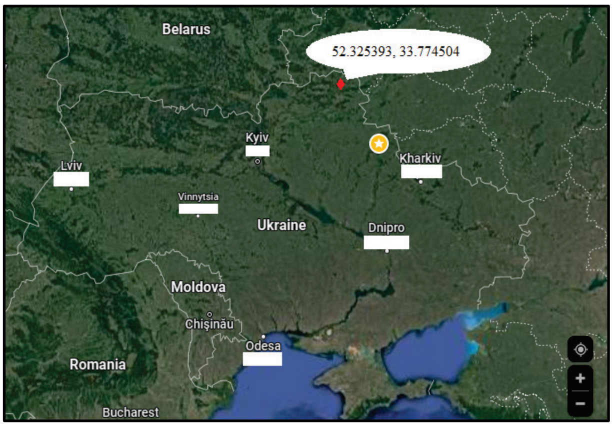

Fig. 1. Positions of the studied locations in Ukraine

Growing location 3 corresponds to subassociation *Mercurialo-Quercetum-corydaletosum cavae*. The phytocenosis has a two-stratum tree stand. The upper layer is formed of *Quercus robur* L., and the second stratum is dominated by *Acer platanoides* L. and *Tilia cordata* Mill. In the herbaceous stratum, the dominating species are *Carex pilosa* Scop., *Aegopodium podagraria* L., *Stellaria holostea* L., and *Mercurialis perennis* L.

According to the classification of Braun-Blanquet, the studied growing locations belong to class *Querceto-Fagetea* Br.-Bl. et Vlieger 1937, order *Fagetalia sylvaticae* Pawłowsky 1928, alliance *Querco roboris – Tilion cordatae* Bulokh. et Solom. 2003 (mixed oak-lime forests), and association *Mercurialo perennis-Quercetum roboris* Bulokhov et Solomeshch 2003. In-detail characteristics of the abovementioned subassociations have been given in the studies by Panchenko (2013, 2015). According to the dominant classification, the analyzed subassociations are formations of oak forests, typical in the Polissia in fresh suhrudok forests (suhrudok refers to an intermediate type of natural forest between subor (a forest with approximately equal amounts of coniferous and deciduous trees) and oak forest, i.e. such where broad-leaved oak trees play greater role than coniferous).

Abundance of species and density of the tree stand were quantified in percentages, separately for each accounted plot, where 100% was the maximum. To estimate the differences in the levels of species abundance depending on the tree-stand density, we used the single-factor disperse analysis (ANOVA) with the post Tukey test at $P < 0.05$ using the Statistica 10 software (Stat Soft, Inc., USA).

Results

Abundance of *Aegopodium podagraria* naturally decreases with increase in the tree-crown density (Fig. 2). This pattern, as indicated by the results of dispersion analysis, was statistically significant, at the level of $P < 0.05$ (Table 1). In the examined forest phytocenoses, abundance of *Asarum europaeum* increased with increase in the tree-stand density (Fig. 3). This dependence was statistically significant ($P = 0.0019$, Table 1). The optimal level for crown density of *A. europaeum* in the examined group of broad-leaved forests was found to be in the range between 70% and 79%. Those results emphasize the significance of accounting for the structure of forest biotope when analyzing phytocenoses and ecosystemic interactions.

In the conditions of Polissia, *Carex pilosa* is confined mainly to highly dense deciduous forests. A significant rise has been observed in the abundance of *C. pilosa* in the conditions of growing crown density (Fig. 4). This observation was not statistically supported by high significance level (P = 0.0524, Table 1). The optimal conditions for flourishing of *C. pilosa* were observed to be the deciduous forests with the crown density ranging 80–95%. Those results highlight the importance of structural characteristics of forest biotopes for identifying abundance and distribution of this species. Understanding the preferences of *C. pilosa* in growing locations is important for the protection and management of natural resources in this region.

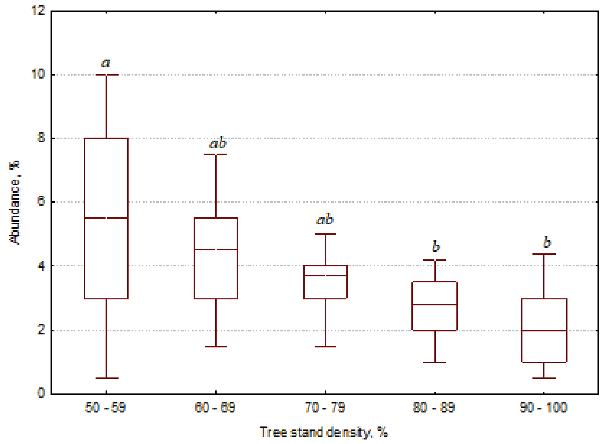

Fig. 2. Correlation of abundance of *Aegopodium podagraria* and tree-stand density of mixed forests of the Ukrainian Polissia: horizontal line in rectangles represents the median; margins of the rectangles represent the first and third quartiles; lines projecting out of the rectangles indicate minimal and maximal values; letters *a* and *b* indicate statistically significant differences in tree-crown density between the three growing locations (the Tukey test)

Table 1
Dependence of abundance of plants of the herb-shrub layer on the density of tree stand of mixed forests of the Ukrainian Polissia (2018–2022, n = 160)

Species	Mean ± SE	Fisher's criterion	P
Aegopodium podagraria L.	3.51 ± 0.80	0.52	0.0168
Asarum europaeum L.	2.60 ± 0.48	1.91	0.0019
Carex pilosa Scop.	12.08 ± 2.63	1.00	0.0524
Convallaria majalis L.	6.53 ± 1.52	3.96	0.0061
Glechoma hirsuta Waldst. & Kit.	2.23 ± 0.57	14.46	$0.2*10^{-5}$
Majanthemum bifolium (L.) F. W. Schmidt	5.57 ± 1.03	3.27	0.0845
Stellaria holostea L.	0.55 ± 0.62	8.83	0.0070
Vaccinium myrtillus L.	2.62 ± 0.71	17.02	0.0004

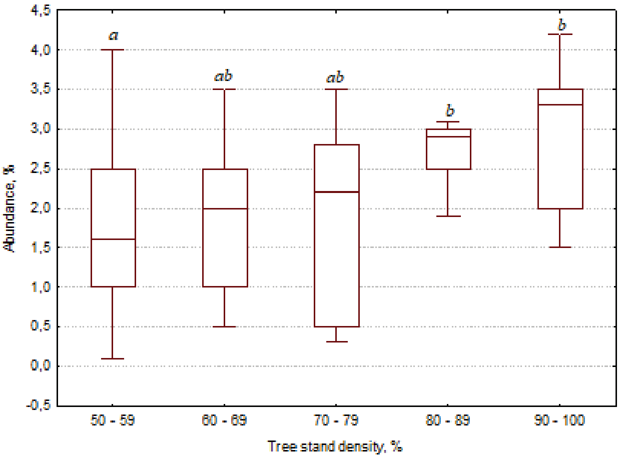

Fig. 3. Correlation between abundance of *Asarum europaeum* and tree-stand density of mixed forests of the Ukrainian Polissia: see Fig. 2

Abundance of *Convallaria majalis* in the examined growing location decreased sharply, by over 65%, with increased crown density (Fig. 5). Analysis of the data using dispersion analysis confirmed that this correlation was statistically significant, with the significance (P = 0.0061, Table 1). Those results indicate that *C. majalis* prefers more open forest biotopes with lower tree-crown density. Such conditions can provide this species with sufficient and available light and less competition for resources. The study we conducted highlights the importance of understanding how the structure of forest ecosystems influences abundance and distribution of *C. majalis*, which is important for preserving the populations of this species, as well as forest ecosystems in general.

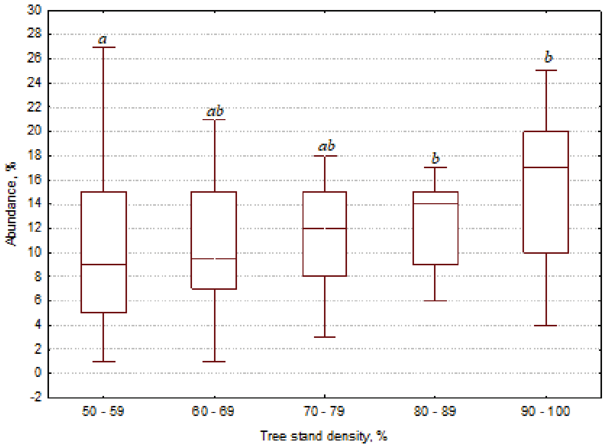

Fig. 4. Correlation between abundance of *Carex pilosa* and tree-stand density of mixed forests of the Ukrainian Polissia: see Fig. 2

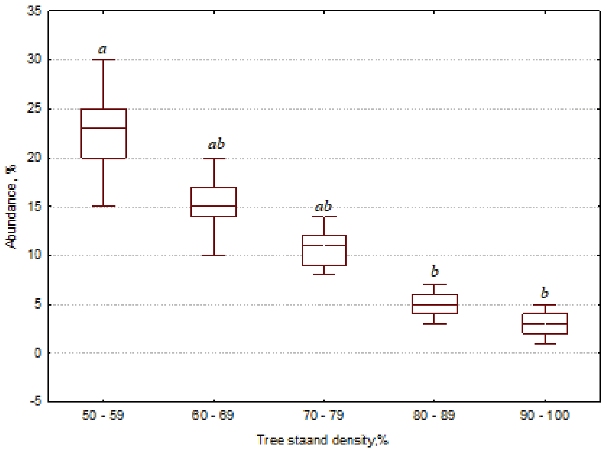

Fig. 5. Correlation between abundance of *Convallaria majalis* and tree-stand density of mixed forests of the Ukrainian Polissia: see Fig. 2

Abundance of *Glechoma hirsuta* increased with increase in the tree-crown density (Fig. 6). This correlation was statistically significant (P = 0.000002, Table 1). The optimal density level of deciduous tree stand for *G. hirsuta* was found to be in the range between 70% and 90%. Those results suggest that *G. hirsuta* prefers forest phytocenoses with denser tree stands. This may be due to the presence of certain microclimatic and resource conditions promoting growth and development of this species in forest ecosystems. The results expand our understanding of a group of factors influencing the spread of *G. hirsuta*, and also are practically important for management of forest biotopes and protection of biodiversity in the examined region.

With increasing tree-crown density (Fig. 7), abundance of *Maianthemum bifolium* increased, peaking when the tree stand ranged 80–90%. This trend has been confirmed statistically with the significance level of P = 0.084 (Table 1), indicating a close relationship of *M. bifolium* with shady broad-leaved and coniferous forests. The results of studies have demonstrated that *M. bifolium* prefers more shaded forest biotopes with high tree-stand density. Perhaps, such conditions provide this species with favourable microclimatic and resource conditions it needs to grow and develop.

We found that the dynamics of *Stellaria holostea* abundance depended on the level of tree-stand density in the interval of 50% to 90%. A tendency has been observed towards approximately 2% decrease in the abundance of this species in the conditions of increasing crown density

(Fig. 8). This trend was statistically significant (P = 0.007). *Stellaria holostea* preferred more open forest biotopes with lower tree-stand crown density. Perhaps, such conditions provide this species with access to enough light and resources to develop.

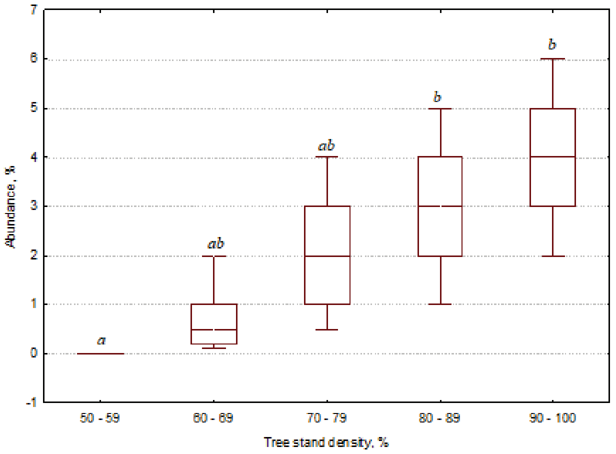

Fig. 6. Correlation between abundance of *Glechoma hirsuta* and tree-stand density of mixed forests of the Ukrainian Polissia: see Fig. 2

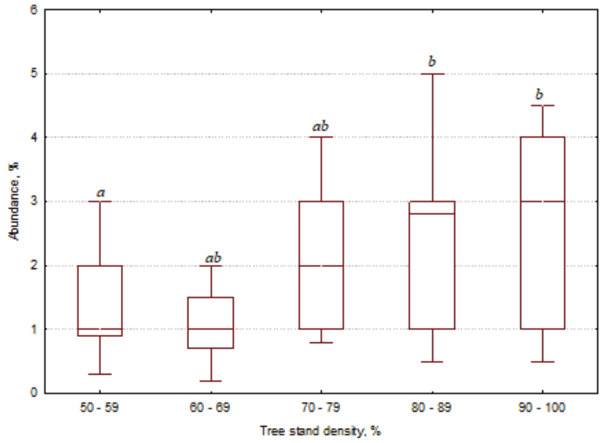

Fig. 7. Correlation between abundance of *Maianthemum bifolium* and tree-stand density of mixed forests of the Ukrainian Polissia: see Fig. 2

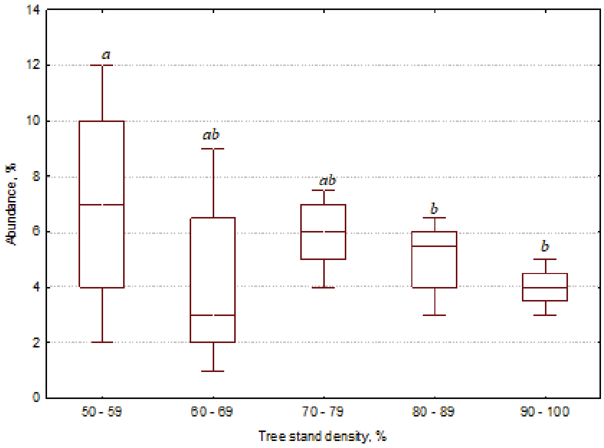

Fig. 8. Correlation between abundance of *Stellaria holostea* and tree-stand density of mixed forests of the Ukrainian Polissia: see Fig. 2

Abundance of *Vaccinium myrtillus* systematically increased with increase in the tree-crown density (Fig. 9). This trend was found to be statistically significant, with the significance level of P = 0.0004 (Table 1), indicating a close relationship between *V. myrtillus* and the structure of forest biotopes. Optimal crown density for *V. myrtillus* to flourish was in the range of 80–90%. The results demonstrate how important for this species are shade and the respective microclimate created by dense crowns.

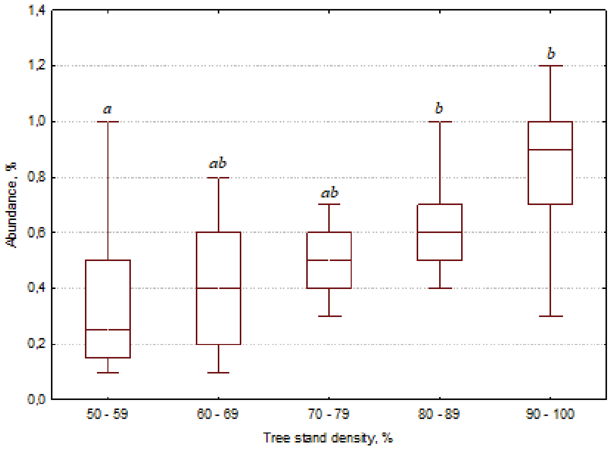

Fig. 9. Correlation between abundance of *Vaccinium myrtillus* and tree-stand density of mixed forests of the Ukrainian Polissia: see Fig. 2

Discussion

Aegopodium podagraria is a long-rhizome perennial. Hemicryptophyte. Mesophyte, megatroph. In relation to light regime, it is characterized as a shade-loving plant (Didukh, 2011). It has a number of economically beneficial properties (used as food, good honey-bearer, valuable forage species), and also exerted antirheumatic, diuretic, and wound-healing effects (Sher et al., 2021). According to ecological scales, it is considered a sciophyte – hemisciophyte (Didukh, 2011). The high sensitivity of *Ae. podagraria* to light conditions was confirmed by pronounced fluctuating asymmetry of the leaves depending on the light regime (Rakutko et al., 2018).

Asarum europaeum is a herbaceous evergreen long-rhizome rosette polycarpic, hemicryptophyte. The shoots are creeping, branching, and rooting. One shrub lives up to 9 years. Mesophyte (Didukh, 2011). It prefers loose, fertile soils, is moderately preferential to moisture and frost-tolerant. In relation to light regime, *A. europaeum* is considered a shade-tolerant plant with narrow ecological amplitude (3–5) (Didukh, 2011). The leaf size of *A. europaeum* does not depend on light (Evseev et al., 2008). It is used as raw material during biological synthesis of nanoparticles (Dobrucka, 2018).

Carex pilosa is a perennial herbaceous plant with long, underground creeping roots, which produce long thin woody shoots. Usually, it grows in deciduous forests (Kubov et al., 2019). Mesophyte, mesoeutropic, and shade-tolerant plant. It prefers clayey, loamy or sabulous, grey forest or rich sod-podzolized or chernozem soils. By the amplitude scale, the optimal light is 3 to 5. In overwintered and new leaves of *C. pilosa*, photosynthesis begin in spring before leaf unfolding. The plant spreads mainly by vegetative reproduction. In ash-linden oak forests, its number reaches 112–166 specim./m^2 (Andrushchenko et al., 2018). Thinning can contribute to increase in the general biomass, both above-ground and underground (Wang et al., 2021). According to Grime, *C. pilosa* realizes the CS strategy, being a stress-tolerant competitive species (Kovalenko, 2016).

Convallaria majalis is a perennial long-rhizome plant (Szöke et al., 2023). Horizontal rhizomes have long (4–9 cm) internodes and nodes, bearing lancet scale-like leaves and adventitious roots. It propagates by seeds and vegetatively with rhizomes and form clones. Geophyte, i.e. in winter, all above-ground parts of the plant die. Mesotrophic and mesophitic. *Convallaria majalis* is a moderate or weak acidophile. It grows in deciduous and pine forests, as well as mixed forests, forest clearings, and glades. It develops better in forest phytocenoses with good under-canopy light availability (Baranova et al., 2013). Depending on type of tree stand, the ontogenetic structure of *C. majalis* populations can range broadly (Penkovska, 2018). Shade-tolerant plant. In relation to light, it has a broad ecological amplitude ranging 2–7 (Didukh, 2011). In suhrudok forests, the optimal tree-stand density for *C. majalis* was 0.60–0.75 (Muzichenko, 2016). According genetic structure, diversity, and demographic history of *Convallaria* species, the study revealed (Lu et al., 2020) that seven of 19 loci exerted significant deviation from the Hardy–Weinberg equilibrium.

Glechoma hirsuta is a perennial herbaceous plant. The plant forms two types of shoots – orthotropic straight or slightly ascending, 30–80 cm tall, and numerous plagiotrophic, creeping shoot. It overwinters having green leaves that die off in spring after the new ones form. It propagates by seeds and rooting of the creeping shoots. A typical growing location of *G. hirsuta* is broad-leaved forests of different types. Mesophyte. The optimal light regime for *G. hirsuta*, according to the Didukh scale (Didukh, 2011), ranged 4 to 7, i.e. plants act as shade-tolerant species. Orthotropic vertical shoots of *G. hirsuta* are less tolerant to shade than plagiotrophic (Huber et al., 1997).

Maianthemum bifolium is a clone plant, which has a broad geographic range in Europe and Asia. It is also broadly distributed as an undergrowth species in acidic-soil beech forests in south Poland (Bierza, 2022). It is a perennial long-rhizome herbaceous plant. The rhizome is thin and creeping. The rhizomes do not branch. The adventitious roots, developed on the rhizome, do not lie deep, locating in the litter. Vegetative propagation dominates. Mesophyte, mesotroph, shade-tolerant plant. Seedlings are sensitive to moisture. *Maianthemum bifolium* is not demanding to soil richness. It prefers acidic soils (poorly acidic to strongly acidic), with pH ranging 3.1 to 4.1 (Didukh, 2011). It is common in coniferous and mixed forests. Phytocenotic optimum is in spruce forests – green-moss covered forests. Hemisciophyte.

Stellaria holostea is a perennial herbaceous plant, 10 to 30 cm tall, with thin creeping branching rhizome. The plant overwinters with green leaves, which die over the winter period. It mostly propagates vegetatively. The rates of vegetative growth of *S. holostea*, according to the data of Smirnova (1987), are 40–70 cm/h. Despite the large number of disseminating seeds, sprouts of *S. holostea* occur in forests rarely. It grows in humus, fresh humid and well ventilated forest soils. Mesophyte, often occurring in deciduous, coniferous, and coniferous-broad-leaved forests of different types, in sufficiently fertile soils. In relation to light regime, it is a hemisciophyte (Didukh, 2011).

Vaccinium myrtillus is a perennial summergreen shrub, 10–50 cm tall (Bussmann et al., 2020). The plant has a creeping rhizome, which produces a large number of shoots. It mainly propagates by roots, vegetatively. It forms clones of various structure. Mesophyte, oligotroph. *Vaccinium myrtillus* is sensitive to late-spring and early-summer frosts, especially during flowering. It is a shade-loving plant. According to the ecological scales, it is considered a sciophyte – subhemisciophyte with broad light amplitude, ranging 2 to 9. *Aegopodium podagraria* is a long-rhizome perennial. Hemicryptophyte. Mesophyte, eutrophic palnt (Didukh, 2011). Colak et al. (2018) have confirmed that wild specimens of *Vaccinium myrtillus* had almost twice the antioxidant ability of the Blucrop varieties. The results revealed that blueberry individuals can be a source of desirable genes for creating improved varieties that meet new market demands.

Of 5 species of plants the abundance of which increased in denser tree stands, 4 species were either evergreen or overwintering with green leaves, which allow them to perform active photosynthesis and growth during spring, when tree leaves have not yet unfolded. The reasons for changes in the abundance of forest herbs and shrubs during increase in tree-crown density are complex. The general structural characteristics of the entire tree stand are critical for restoration of undergrowth (Grabska & Socha, 2021). Increase in crown density first of all alters the conditions of photosynthesis, reducing the amount of light which reaches the soil, and in the conditions of deciduous forests the sunlight is even impoverished in photosynthetically active radiation (PAR) – rays of the red part of the spectrum, since it had been "filtrated" by the leaves of tree crowns. With increase in tree-stand density, changes occur in the availability of water and nutrients, and density and thickness of the litter, and the whole available competition in both above-ground and underground environments transforms. The content of nutrients, their ratio and transfer of macroelements from soil into the plant biomass are subject to changes during the vegetative period, which depends on phenological phases of the plants. Dynamics of nutrient content and macroelement accumulation in plant biomass are closely associated with their life form (Yang et al., 2023). Urbanization can have negative effects on a territory's ecology, but even small green spaces can be valuable shelters for rare and protected plant species (Bussmann et al., 2020). The larger such zones, the greater the effect. In broad-leaved forests, there functions an ecological-biological mechanism of regulation of composition and abundance of plants of herb-shrub stratum by changes in tree-crown density.

Conclusions

In forest phytocenoses of *Mercurialo perennis-Quercetum roboris* association in the Ukrainian Polissia, eight species of the herb-shrub stratum were observed to have significant changes in abundance as the crown density increased. It significantly decreased in *Aegopodium podagraria* and *Convallaria majalis*; had a pronounced tendency towards increase in *Asarum europaeum*, *Carex pilosa*, *Glechoma hirsuta*, *Maianthemum bifolium*, *Vaccinium myrtillus*; and remained almost the same in *Stellaria holostea*, varying only 3–5%.

The vertical zoning of tree stand leads to high non-uniformity in the forest microenvironment, which influences recovery of the undergrowth, as well as succession changes. For a deeper understanding of those processes in such forests, characterized by a complex vertical structure, it is necessary to perform more thorough studies, focusing on interrelations between the upper and lower layers of the forest community. This can make management of forest ecosystems more efficient, preserving their biodiversity by using forest resources, having accounted for their complex structure.

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