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Original Paper

Bryophytes under a moss "canopy" on the Stradch Mountain (Ukraine)

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The aim of this work was to investigate the ability of some mosses to grow under a "canopy" of larger life-forms of the other moss species, because at the moment this subject is poorly studied. On the northern slope of the Stradch Mountain (Yavoriv District, Lviv Region, Ukraine) in a 100-year old *Pinus sylvestris* planting, two moss species were identified under a moss "canopy": a common species of Ukrainian bryoflora *Plagiomnium rostratum* and rare *Buxbaumia viridis*. The latter one is included in European Red List of mosses in the category Least Concern but is a threatened species in Ukraine, where it is considered as vulnerable. On the investigated site, *B. viridis* grew exclusively on the ground adjacent to tree roots, with its gametophytes under the "canopy" of moss *Dicranella heteromalla*. *P. rostratum* occured freely on the ground or hidden under the "canopy" of wefts of *Pleurozium schreberi*, *Rhytidiadelphus squarrosus*, *Rhytidiadelphus triquetrus*, *Thuidium tamariscinum* or tufts of *Polytrichastrum longisetum*. Without a moss "canopy", *P. rostratum* occurred only on a quite shaded ground. On well-illuminated sites *P. rostratum* occurred exclusively being fully hidden. This study brings new information about the ecology of *B. viridis* and *P. rostratum*: the ability of their gametophytes to grow on the ground under a "canopy" of other moss species.

Keywords: life-forms, woody canopy openness, moss "canopy", slope, trampling

1 Introduction

Bryophytes are mostly found as groups of individuals having characteristic features of the species. Such groups are called life-forms. The life-forms may be modified under the influence of the environment (Mägdefrau, 1982). Thanks to mentioned property of bryophytes to create the life-forms, they store water considerably, protect from wind, sun and trampling, provide stable temperature and humidity in terrestrial conditions (Bates, 1993; Rice et al., 2001; Zotz & Kahler, 2007; Schirmel et al., 2010). Therefore terrestrial bryophytes are an attractive habitat for small organisms. The moss tissues contain repellents for herbivores, so they do not notable graze on mosses, except in highly cold regions (Glime, 2006). In above-mentioned ways mosses improve their own development as well as the one of vascular plants, which grow together with them (Sand-Jensen et al., 2015). Thus bryophytes serve as a shelter for different organisms from cyanobacteria, algae (Richardson, 1981), fungi (Davey & Currah, 2006) to invertebrates, including beetles and spiders (Schirmel et al., 2010) as well as also even some species of small vertebrates, for example frogs (Osborne, 1988). Not only small organisms can live under a moss "canopy". In tropic regions thanks to epiphytic (growing on tree bark) and epiphyllous (growing on leaves) bryophytes, whole large trees may be like under a bryophyte "canopy" (Karger et al., 2012).

It is known that the mutual interactions between different bryophyte species growing in mixtures are weak (McAlister, 1995) and characterized mostly by competitive inhibition (Scandrett, Gimingham, 1989). It is clearly that under a "canopy" of one moss species may find themselves individuals of the other bryophyte species. It may be as the consequence of the capturing a space occupied by a small species by a larger one (Bates, 1998). It was shown also that sporophytes of moss *Buxbaumia viridis* often grow through a carpet of moss *Hypnum cupressiforme* covering a dead wood, while their chloronemal gametophytes (*B. viridis* has not developed three-dimensional gametophyte – only small two-dimensional filamentous protonema) grow under the "canopy" of such a carpet (Amphlett, 2021).

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Thus, a question can be raised: is a good developed three dimensional moss gametophyte individual able to grow better all time being hidden under a "canopy" of a bigger life-form of another moss species than on the open air? If not in bogs, large moss cushions (dome-shaped colonies), tufts (loose cushions) or wefts (colonies with intertwining branched layers) usually occur on a sandy soil of a pine forest, which is well illuminated (the pine forest canopy is more open than of other forest types) and well drainaged (Hill et al., 2007). Such powerful life-forms are able to counteract enough to water losses and in the case of the positive answer on this question they could play a role of the shelter for the other tiny bryophytes, which could suffer on drought on the open air. The Stradch Mountain was chosen for the elucidation of this question because its sandy slopes have been planted by *Pinus sylvestris* about 100 years ago (Figures 1 and 2). Recently, blueberry and heath grow abundantly there with diverse epigeic bryophyte cover. Our goal was to investigate bryophytes diversity and the interiors of the life-forms growing on the ground of the Stradch Mountain.

2 Material and methods

2.1 Study site characteristics

The study site, the Stradch Mountain (a hill of 359 m a.s.l. consisting of Tortonian sandstone), is located in the village Stradch in Yavoriv district of Lviv region, Western Ukraine. A famous Ukrainian pilgrimage center, the Church of the Assumption of the Blessed Virgin Mary is located on the top of the Mountain (MSCU, 2019). Dwellings of the village Stradch are situated further to east on the inclined slope of the Stradch Mountain. The research was conducted on the northern slope on coordinates 49° 53′ 53″ N 23° 45′ 30″ E, where the inclination was about 30° (Figure 1). The average annual precipitation is 700 mm with maximum in June and July and minimum in January and February, the average temperature is +7,5 °C with maximum in July and minimum in January (JNNR, 2022). The lower canopy layer of the pine forest of the northern slope is occupied by several leafy deciduous species: *Carpinus betulus*, *Fagus sylvatica*, *Sorbus aucuparia*, *Ulmus glabra*, which are mostly grouped together in "leafy islands". The woody undergrowth consists of *Acer pseudoplatanus*, *Betula pendula*, *Calluna vulgaris*, *Carpinus betulus*, *Corylus avellana*, *Crataegus monogyna*, *Fagus sylvatica*, *Juglans regia*, *Pinus sylvestris*, *Quercus robur*, *Rubus caesius*, *Sambucus nigra*, *Sorbus aucuparia*, *Swida alba*, *Ulmus glabra*, *Vaccinium myrtillus*. Between mentioned "leafy islands" under the pine trees and the leafy undergrowth canopy there abundantly grow the large life-forms of different moss species. The northern slope is periodically trampled by pilgrims as well as berry collectors.

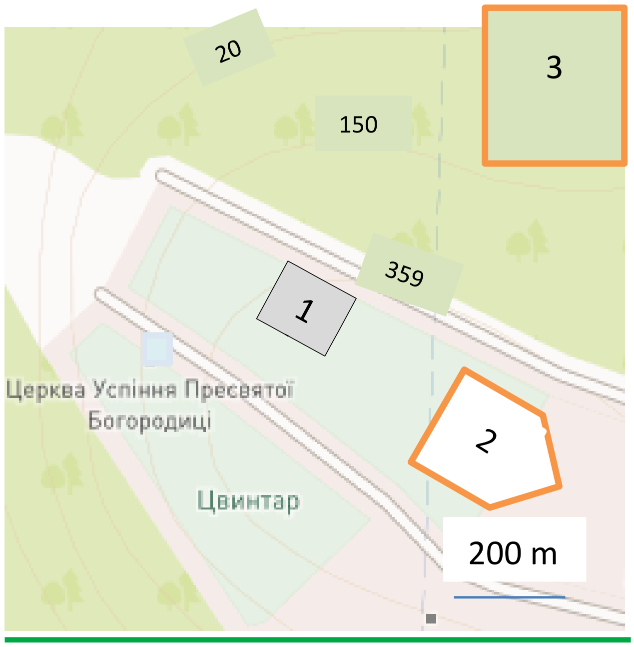

Figure 1 A map of the investigated site
1 – the Church of the Assumption of the Blessed Virgin Mary; 2 is the beginning of the village Stradch; 3 is the location of the investigated plots; 20, 150, 359 are isolines of elevation

2.2 Data sampling

The investigation was carried out in August, September, October, November and December 2022. Above mentioned northern slope of the Stradch Mountain within altitudes 20–150 m from the foot of the mountain (lower the soil was covered by dense blackberry bushes, higher it was highly shaded by dense leafy undergrowth) was investigated. Five plots were chosen of 100, 500, 200, 400 and 400 m^2 correspondingly on the investigated ground territory. The choice was made so that the slope (inclination of the soil surface), the woody canopy openness and the blueberry bushes density of each of mentioned plots were more or less evenly distributed (Figures 1 and 2, Table 1). The elevation increases with the number of a plot. All large moss life-forms growing within mentioned plots were opened and the occurrence of the other bryophyte species there was surveyed. The total surface areas (S_c) of each moss species and life-form were measured, including those under the moss "canopy" of each large life-form (i): S_{ci}. Then the percentages of each plot area occupied by any moss species and life-form were calculated:

$$P_c = \frac{S_c}{S_p} \cdot 100\%$$

where: S_p – a plot area as well as the percentages of each bryophyte species under the moss "canopy" of each large life-form:

$$P_{hi} = \frac{S_{ci}}{S_c} \cdot 100\%$$

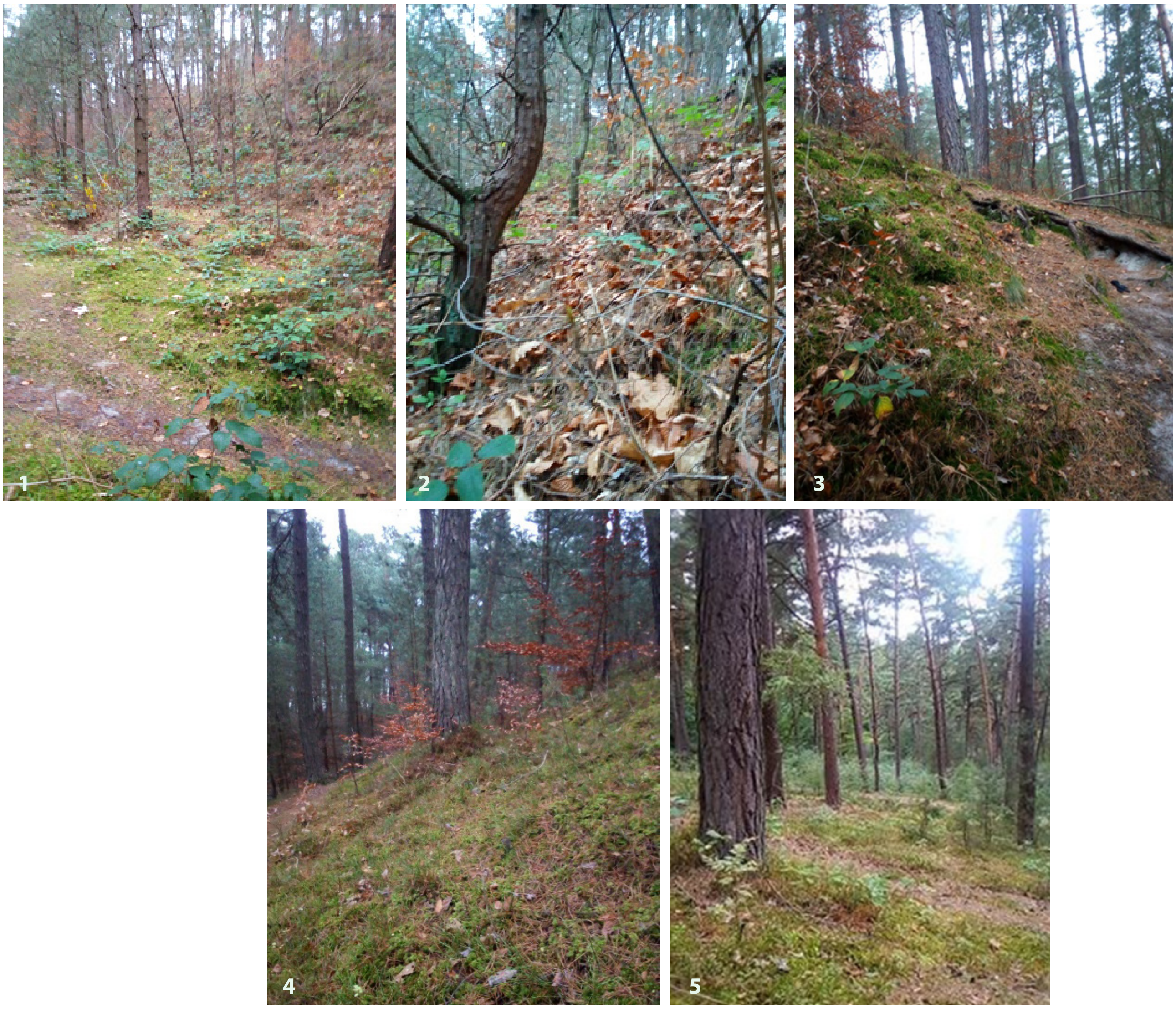

Figure 2 The plots on the investigated site – the numbering of the photos coincides with the numbering of the plots

The woody canopy openness of each plot (Volařík et al., 2017) was evaluated visually as the visibility of the sky through the canopy. The life-forms of bryophytes are defined according to Hill et al. (2007). The author names for identified bryophytes are provided according to Boiko (2014), while for woody plants according to Tasjenkevič (1998).

3 Results and discussion

The large life-forms (more than 3 cm of height) of mosses were noted on the ground of the study site. They occupied an area about 1 ha in total and consisted of: tufts of *Dicranum scoparium* and *Polytrichastrum longisetum*, cushions of *Leucobryum glaucum*, wefts of *Pleurozium schreberi*, *Pseudoscleropodium purum*,

Table 1 Common characteristics of the plots

Plots, №	The area of a plot (m^2)	The woody canopy openness (%)	Slope (°)	The density of blackberry bushes (ind.m^{-2})
1	100	35–45	15 – 20	–
2	500	15 – 20	55 – 65	4.3 ±0.1
3	200	15 – 30	25 – 35	12.0 ±0.1
4	400	20 – 30	25 – 35	19.0 ±0.1
5	400	60 – 70	25 – 35	17.0 ±0.1

ind – individuals

Rhytidiadelphus squarrosus, *Rhytidiadelphus triquetrus*, *Thuidium tamariscinum*. All those taxa are considered as common species of Ukraine bryoflora (Danylkiv et al., 2002; Boiko, 2014) as well as *Atrichum undulatum*, *Dicranella heteromalla*, *Fissidens bryoides*, *Hypnum pallescens*, *Plagiomnium rostratum*, which also occurred there, but not so abundantly (they occupied an area of less than 0.1 ha in total) and formed not so large (less than 2 cm of height) life-forms. *A. undulatum*, *D. heteromalla*, *F. bryoides*, *H. pallescens* and small tufts of *D. scoparium* grew mostly on the banks of trails or near the tree roots. On the investigated territory, each mentioned species created its pure life-form, where its individuals prevail (more than 90% of its individuals), but considerable area was occupied also by the life-forms consisting of different species mixtures. The most abundant mixed life-forms were wefts formed of *P. schreberi*, *R. triquetrus* and *T. tamariscinum* (mostly of different pairs of mentioned species in close proportions).

On the soil adjacent to the plot №3 near tree roots crossing a small trail, eleven sporophyte individuals of moss *Buxbaumia viridis* were revealed. Eight *B. viridis* sporophytes appeared in or before October (Figure 3, left), while three else appeared in November – December (Figure 3, right). All gametophytes of *B. viridis* (of area about 14 cm^2) grew under *Dicranella heteromalla* "canopy" (Figure 3). This finding of *B. viridis* is the first on the territory of Yavoriv district in Ukraine (compare to Boiko, 2019). *B. viridis* sporophytes neighbored also with small cushions of *L. glaucum* and tufts of *D. scoparium* (several square centimeters of area) and even smaller mats of moss *Hypnum cupressiforme* and liverwort *Lophocolea heterophylla*. Guillet et al. (2021) mentioned co-occurrence of *B. viridis* with *Dicranum scoparium*, *Hypnum andoi*, *Hypnum jutlandicum*, *Herzogiella seligeri*, *Brachythecium rutabulum*, and species of the genus *Cephalozia*. *B. viridis* belongs to epixylic mosses, which grow mostly on fallen highly decomposed dead wood. Recently sporophytes of this species are evaluated as Least Concern (LC) in the European Red List but they are threatened in many countries because of the lack of such a substrate type in managed forests. For example in Ukraine, Great Britain, Slovakia, Romania *B. viridis* is considered as vulnerable (Boiko, 2010; Ştefănuţ et al., 2023). The Stradch Mountain is not exclusion: dead wood there is cleaned up within several months after it's fallen. On the other hand, the appearance of *B. viridis* sporophytes on the ground is not new: it is known that they occur sporadically on humus of bare patches (Amphlett, 2021). However, often trampled (mostly each summer because of blackberry harvesting and two great pilgrimages) and well drainaged (sandy and inclined) ground is not preferable for such a tiny hygrophilous generation (Guillet et al., 2021). We found the woody canopy openness close to 20% on the investigated site, while Guillet et al. (2021) mentioned an appearance of *B. viridis* sporophytes at the mean canopy openness of 12.8 ±4.3% and the mean slope inclination of 32 ±30°. As mentioned above, our investigations took place on the northern slope of the Stradch Mountain, where local inclinations occupied by the sporophytes were within 60°–75°. Such steep slope inclinations highly decreased direct sun insolation. Thus unfavorably high for survival for *B. viridis* sporophytes the woody canopy openness was compensated. It can be assumed also that *D. heteromalla* "canopy" increased survival capacity of *B. viridis* gametophytes protecting them from the water losses bounded with so steep slope inclinations. Maybe it is the reason why *B. viridis* did not occur on the investigated territory without the moss "canopy". Thanks to high inclination, all noted *B. viridis* sites were situated not only near, but also under tree roots creating in such a situation an additional canopy.

Figure 3 Young sporophytes of moss *Buxbaumia viridis* growing through mats of moss *Dicranella heteromalla* in October (left) and in December (right) 2022

Figure 4 Occuring sites of *Buxbaumia viridis* protected from winter snow

Because of such a location the sites were protected from the trampling and winter snow (Figure 4), which allowed *B. viridis* gametophytes to form sporophytes also even in winter time. The appearance of rare species *B. viridis* on a site not favorable for survival of it allows us to assume that its spores or propagules were introduced here by tourists (on shoes or clothes), which visited the neighbor Nature Reserve "Roztochia" before. It also means that in the Nature Reserve "Roztochia" considerable and not yet discovered local population of *B. viridis* can exist.

Plagiomnium rostratum is considered as generalist and common species not only of Ukrainian, but also of British and European bryophlora (Hill et al., 2007; Boiko, 2014; Mišíková et al., 2020). On relatively shaded plots (№ 1, 2, 3, 4, the woody canopy openness of which was less than 45%), *P. rostratum* occurred being not fully under the moss "canopy" (it means it was visible, Figure 5). On well insulated plot № 5 (the woody canopy openness of which was within 60–70%), *P. rostratum* occurred being wholly hidden within moss wefts: all its shoots had been invisible until the wefts were not opened (Figure 6). *P. rostratum* shoots were there slightly or even strongly etiolated. Such a phenomenon cannot be bound only with the expansion of the large moss life-forms, which over time absorbed *P. rostratum* shoots. Certain quantity of *P. rostratum* individuals not hidden under the moss "canopy" would have stayed. Thus we can assume that such hidden moss individuals found a benefit: higher and stable humidity, which for numeral bryophytes outweighs reducing of insolation (Bates, 2006) causing in our case the etiolation. On the plot № 1, where the woody canopy openness was lesser (35–40%), only a part of *P. rostratum* shoots were hidden under the moss "canopy" (about 55% of the total area occupied by *P. rostratum*), the rest formed or the pure life-forms (about 15%), or grew in mixtures with visible *P. rostratum* individuals (about 30%). On the plots № 2, 3, 4, where the woody canopy openness is even less (15–30%), *P. rostratum* occurred only without the moss

Figure 5 *Plagiomnium rostratum* without the moss "canopy"

Figure 6 Wefts of moss *Rhytidiadelphus triquetrus*: untouched (left), open – it is visible a shoot of moss *Plagiomnium rostratum* being slightly etiolated (right)

"canopy". Thus we can conclude that the woody canopy openness mostly determines *P. rostratum* microhabitats distribution: under or without a moss "canopy". According to Tables 1 and 2, the density of blueberry bushes strongly influenced on the percentage of a plot area occupied by *P. rostratum*. On the plots № 1 and № 2, where blueberries were absent or were present in minimal quantities the percentage of a plot area occupied by *P. rostratum* was at least twice as large as on the plots № 3, 4, 5, where blueberries were abundant. The density of blueberry bushes determines the trampling by berries collectors (blueberries attract the collectors who are the main tramplers). Therefore we can say that *P. rostratum* is sensitive to trampling. High inclinations of the plot № 2 (55–65°) restricted the trampling and the percentage of a plot area occupied by *P. rostratum* was the largest among all sampled plots (100.0 ±0.5·10^{-3}%), although the blueberries density was not the most minimal there.

Table 2 Bryological characteristics of the plots

Plots, №	The percentage of a plot area occupied by *P. rostratum*		The percentage of pure *P. rostratum* mats area (%)		The number of taxa creating the moss "canopy" for *P. rostratum*	The percentage of *P. rostratum* area under the "moss" canopy	
	(P_c ±SE) (%)	*n*	(P_{hp} ±SE) (%)	*n*		(P_{hi} ±SE) (%)	*n*
1	99.8 ±1.1·10^{-3}	15	14.8 ±0.5	3	5	55.3 ±0.8	7
2	100.0 ±0.5·10^{-3}	71	57.3 ±0.3	33	0	0	0
3	4.0 ±0.2·10^{-4}	2	99.9 ±0.1	2	0	–	0
4	3.0 ±0.1·10^{-4}	3	99.9 ±0.1	3	0	–	0
5	4.0 ±0.1·10^{-3}	24	–	0	2	99.9 ±0.1	24

n – the measurements number; the percentage of a plot area occupied by *P. rostratum* (P_c) was calculated as: $P_c = S_c/S_p \cdot 100\%$, were S_c – the total surface of *P. rostratum* on a plot, S_p – a plot area; the percentage of pure *P. rostratum* mats area (P_{hp}) was calculated as: $P_{hp} = S_{cp}/S_c \cdot 100\%$, where S_{cp} – the total area of pure *P. rostratum* mats (where *P. rostratum* individuals make up not less than 90% of a mat); the percentage of *P. rostratum* area under the "moss" canopy (P_{hi}) was calculated as: $P_{hi} = S_{ci}/S_c \cdot 100\%$, where S_{ci} – the total surface area of *P. rostratum* under the moss "canopy" on a plot

Table 3 The list of surveyed taxa creating the moss "canopy" for *Plagiomnium rostratum*, followed by the plots characteristics

Plots, №	The moss "canopy"			The percentage of *P. rostratum* area under the "canopy" of a life-form on a plot		The percentage of a plot area occupied by large moss life-forms of other species not creating the "canopy" for *P. rostratum*		The taxa number of large moss life-forms not creating the "canopy" for *P. rostratum*
	taxa content of recorded life-forms	the percentage of a plot area occupied by a life-form						
		(P_{cl} ±SE) (%)	*n*	(P_{hil} ±SE) (%)	*n*	(P_{co} ±SE) (%)	*n*	
1	*Pleurozium schreberi*	11.2 ±0.1	21	8.5 ±0.3	1	–	0	0
	Polytrichastrum longisetum	7.5 ±0.1	18	5.6 ±0.3	1			
	Rhytidiadelphus squarrosus	9.4 ±0.1	17	6.5 ±0.3	1			
	Thuidium tamariscinum	33.6 ±0.2	64	27.2 ±0.5	3			
	Thuidium tamariscinum+ *Pleurozium schreberi*	10.3 ±0.1	17	7.5 ±0.3	1			
2	–	0	0	0	0	18.0 ±0.2	131	3
3	–	0	0	0	0	71.2 ±0.1	203	5
4	–	0	0	0	0	84,1 ±0.2	401	6
5	*Rhytidiadelphus triquetrus*	25.5 ±0.1	170	97.7 ±0.4	22	23.5 ±0.1	157	5
	Thuidium tamariscinum	20.5 ±0.1	131	2.2 ±0.4	2			

n – the measurements number; the percentage of a plot area occupied by a life-form (P_{cl}) was calculated as: $P_{cl} = S_{cl}/S_p \cdot 100\%$, where S_{cl} – the total area of a life-form on a plot, S_p is a plot area; the percentage of *P. rostratum* area under the "canopy" of a life-form on a plot (P_{hil}) was calculated as: $P_{hil} = S_{cil}/S_c \cdot 100\%$, where S_{cil} – the total surface area of *P. rostratum* under the moss "canopy" of a life-form on a plot; the percentage of a plot area occupied by large moss life-forms of other species not creating the "canopy" for *P. rostratum* (P_{co}) was calculated as: $P_{co} = S_{co}/S_p \cdot 100\%$, where S_{co} – the total area of large moss life-forms of other species not creating the "canopy" for *P. rostratum* on a plot

Probably large and well developed moss life-forms are able to protect tender *P. rostratum* shoots from trampling to some extent, because the percentage of a plot area occupied by *P. rostratum* on the plots № 3 and № 4 was considerably lesser (4.0 ±0.2·10^{-4}% and 3.0 ±0.1·10^{-4}% correspondingly) than that on the plot № 5 (4.0 ±0.1·10^{-3}%), where it was fully hidden (the densities of blueberry bushes on all mentioned plots were similar). According to Tables 1 and 3, the slope determined the diversity of species, under the "canopy" of which *P. rostratum* was hidden. The mosses diversity on considerably inclined ground of the plot № 5 (25–35°) was low including only two species. *P. rostratum* occurred there mostly inside of *R. triquetrus* and rarely in *T. tamariscinum* wefts. In contrary, the largest species richness was found on weakly inclined ground of the plot № 1 (15–20°), where five species were recorded. *P. rostratum* occurred there almost evenly under the "canopy" of *T. tamariscinum*, *R. squarrosus*, *P. longisetum* and *P. schreberi*. The ground inclination causes two contrary effects on the substrate: improves the drainage (which decreases the humidity) and decreases the direct insolation (concerning a northern slope). The life-forms of different moss species differently store water especially near soil surface (Bates, 1993). Such peculiarity is very important for the hygrophyte *P. rostratum* in the case, when it grows on highly inclined sites and thus the sites, which are more capable to drought ground. So, *P. rostratum* clearly preferred *R. triquetrus* wefts, which are capable to store water and dissolved ions considerably (Bates, 1993). It was shown also that *R. triquetrus* preserves the chemical content of the interior of its weft and grows fine even underventing moderate alkaline pollution. The other found bryophytes are characteristic mostly for non-polluted by alkalines sandy soil of a pine forest (Paal and Degtjarenko, 2015). Thus it may be assumed that they are not so good nutrition protectors as *R. triquetrus*. On weakly inclined ground, *P. rostratum* did not make any species preference (Tables 1, 3).

Thus the coverage by a moss "canopy" may positive affect on some bryophyte species (*Buxbaumia viridis* and *Plagiomnium rostratum* in our case) protecting them from the drought causing by excess woody canopy openness and substrate inclination in the conditions of considerable contemporal global climate changes expressing in the increasing of the amplitude of humidity fluctuations (Karl et al., 2003).

4 Conclusions

Bryophytes of the Stradch Mountain (Ukraine) under a moss "canopy" was investigated in 2022. Two species were recorded. Rare moss species *Buxbaumia viridis* occurring on highly inclined ground (60–75°) near pine roots was found for the first time on the northern slope of the Stradch Mountain. All eleven sporophytes of this species grew through *Dicranella heteromalla* carpets. Eight *B. viridis* sporophytes appeared in or before October, three of them appeared in November-December. We found that the woody canopy openness determined occurrence of common species of Ukrainian moss flora *Plagiomnium rostratum*: under or without a moss "canopy". Under the high woody canopy openness (60–70%) *P. rostratum* occurred only fully hidden under the moss "canopy", under medial one (35–45%) – such hiding was partial, while under small – the hiding was absent. The local density of blueberry bushes bounded with the trampling decreased the percentage of a plot area occupied by *P. rostratum*. The slope, which improves soil drainage, decreased the diversity of species, under the "canopy" of which *P. rostratum* was hidden. Obtained data contribute to the knowledge of the mosses ecology of *Buxbaumia viridis* and *Plagiomnium rostratum*. Their gametophytes are able to grow on the ground under a "canopy" of the other moss species: *B. viridis* – under the "canopy" of *D. heteromalla*, while *P. rostratum* under the "canopy" of several common species (*Polytrichastrum longisetum*, *Pleurozium schreberi*, *Rhytidiadelphus squarrosus*, *Rhytidiadelphus triquetrus*, *Thuidium tamariscinum*).

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