

## *Successional Pattern, Stand Structure and Regeneration of Forest Vegetation According to Local Environmental Gradients*

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**Abstract.** Despite the attempted botanical and ecological studies so far, integrated picture of successional and regenerative pattern of the forest vegetation in the studied area have not been achieved. Moreover, stand composition and development of these forests have never been studied in the context of environmental gradients. This study aims to integrate and clarify the accumulated knowledge about the successional pattern, stand structure and regeneration in the studied territory. It has also attempted to test some classical viewpoints about the forest vegetation pattern, placed in the context of environmental gradients. We hypothesized that most forest stands will follow the normal diameter distribution. Gradient-transect sampling procedure was used. Accumulated field samples were classified using TWINSpan clustering method. Obtained forest community types were tested for consistency. Distribution of stand stem number by diameter classes was tested with Shapiro-Wilk test for normality. Stand successional distribution followed its own trajectory and no convergence has been found. All stands had normal diameter distribution and compromised seed regeneration, i.e. they were in "stagnant" condition. Dominant trees also had normal stem distribution except beech stands from the most xeric habitats, but this was due to their sprouting regeneration. We hypothesized that this regeneration pattern is due to erroneous management and lack of major natural disturbances in the area during the last decades, which could have drew the stands from "stagnancy" and restart the seed regeneration. If this tendency is maintained we suppose that it will lead to continuing degradation of local forest vegetation.

**Keywords:** Balkans, succession, climax, diameter distribution, inversed J-curve, moisture gradient, stand structure, regeneration.

### **Introduction**

Vegetation literature often speaks of plant communities existing in climax condition, but data supporting this hypothesis for the compositional species populations seldom can be found. Vegetation managers traditionally accept the climax idea in theory as well as in practice, therefore identification of climax condition has a great practical significance. Demonstrating vegetation steady state in given community requires repeatable measurements over time greater or comparable with the complete turnover

period of all species populations. However, such measurements have been taken only for short-living plants. For the forest communities, dominated by long-living species, documenting of all species population dynamics for the whole turnover period is impossible. This is most frequently done only for a short period. Hence, for the climax condition of given vegetation it can only be supposed based on past and present characteristics of the compositional species populations (VEBLEN, 1992).

When the forest is in relatively steady-state condition it is characterized with

balanced mortality and regeneration rates. Forest stand, where there are numerous young individuals and lesser mature ones, is recognized as having an inverse *J*-curve diameter distribution (MEYER, 1952; LEAK, 1964, 1965; PEET, 1981). If mortality and birth rate of individuals from the different diameter classes is constant then diameter distribution can be described with negative exponential curve, which has the form of inversed *J*-curve. However, if mortality decreases steadily relative to size, diameter distribution is power function, which is more concave *J*-curve. Because the lower light levels under the canopy and the intense competition between the young individuals in most forests, species early mortality rate is higher (HETT, 1971; HETT & LOUCKS, 1971; PEET, 1981). Mortality slows down with the aging until senescence is reached. However, if senescence phase is included in the diameter class analysis then diameter distribution, more probably, has sigmoid curve form (GOFF & WEST, 1975). No matter what the model is or whether it is applied on diameter or age classes, the result, in principal, is inversed *J*-curve distribution, which indicates the presence of much more young individuals than mature ones (PEET, 1981). Diameter distribution in successional stands, however, has much more variable form. When disturbances destroy great part of the stand, many young individuals establish on the cleared place. With the stand aging, these saplings deplete the limiting resources and impede the new seedling establishment. In these cases diameter distribution curve most often has skewed bell-shaped form (BAILEY & DELL, 1973; BLISS & REINKER, 1964; DAY, 1972; ILVESSALO, 1937; NELSON, 1964; PEET, 1981). The height and breadth of the curve is influenced from the initial density and synchronization of the seedling establishment. The most important here is that the more favorable the habitat conditions are, and the more severe the competition is, the more intensive is the initial resource depletion. This process leads to sapling suppression and seedling elimination until mortality among the mature individuals relaxes the competition (PEET, 1981).

Considering these assumptions, for a stand with *J*-curved diameter distribution of principal tree species can be claimed that it is in relatively steady state. Deviations from this condition can be interpreted as evidence for weak reproduction or prior disturbance event (JACKSON & FALLER, 1973; JOHNSON & BELL, 1975; SCHMELZ & LINDSEY, 1965; PEET, 1981).

Three types of forest development under different habitat conditions are known (PEET, 1981), which are defined as points in the continuum of potentials possibilities. These have been applied to: 1) favorable sites, found on moderate elevation in the middle or moesic part of the moisture gradient; 2) unfavorable sites, found on higher elevation or in extremely xeric places on middle and lower elevation; and 3) episodic sites, distributed on lower elevation along the ecotone between forest and open habitats.

Environmental gradient classification results in group of stands with variable age, but with similar habitat conditions and potential for development, in which successive change of stand population structure can be established (PEET, 1981). Bell-shaped curves have been acknowledged (PEET, 1981) as an indicator for even-aged stands, where curve breadth is consequence of the establishment period duration, initial seedling density and habitat quality. The inversed *J*-curve is indication for successful regeneration and approximation of stand steady-state condition. Since the variation of habitat condition, seed arrival and disturbance history may influence successional rate, stand arrangement on the basis of diameter distribution makes them more comparable than their arrangement by age structure alone (PEET, 1981).

The three types of stand development are useful models and referent points in the continuum of stand structural variation. They can be used as frame for the interpretation of multiple aspects of forest ecology. Diversity, basal area, biomass, productivity and stability of forest communities are indicators, which are regulated by the dominant species population dynamics, which in their turn

react to the environmental conditions. Studying population dynamics during the forest succession should also be placed in the context of environmental gradients. Due to the extensive data required in the stand development studies, most of them fail in their attempt to bound obtained results with the environmental or successional characteristics (PEET, 1981).

Attempted botanical and ecological studies so far have not brought an integrated picture about the successional and regenerative pattern of the forest vegetation in the studied area. Moreover, stand composition and development of these forests have never been studied in the context of environmental gradients. This study is an attempt to expand and clarify the accumulated knowledge about the forest stand structure and regeneration. It has also attempted to test some classical viewpoints about the forest vegetation pattern, placed in the context of environmental gradients. We hypothesized that most forest stands will follow the normal diameter distribution. We also tried to predict the future successional trajectory of the studied forests as far as possible using this methodology. Accomplishing our tasks will improve vegetation understanding of the investigated territory, which in turn will ease undertaking forest management activities in the future.

### Study area

Vitosha Mountain is located in Western Bulgaria. Since it is a relatively young mountain (SHIPKOVA, 2005), it is characterized with compactness and well expressed elevation gradient. The mountain has steep slopes and variable expositions. Its vegetation has varied and rich species composition. Most of the mountain's territory is declared Nature Park by the Bulgarian legislation. The current study embraces the south slope of the mountain, covering all forested habitats. GPS coordinates of that territory are between N42°32' E23°09' and N42°26' E23°21'. This area covers 118 km<sup>2</sup>.

Vitosha Mountain is formed during the late Cretaceous and early Tertiary period.

The most widely distributed bedrocks are Paleozoic sediments and early Mesozoic sediments. The highest peak is Cherni peak reaching 2290 m (SHIPKOVA, 2005).

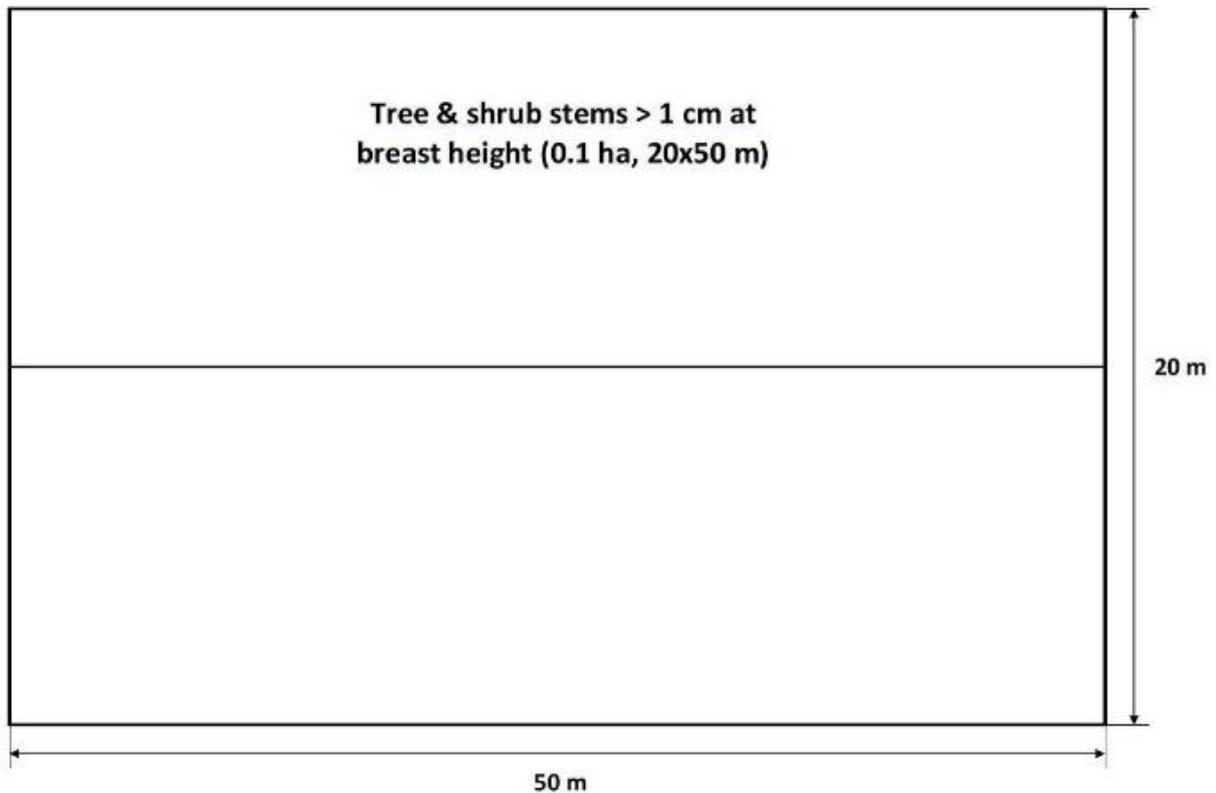
Mean annual rainfall is between 650-700 mm in the mountain base and around 1000 mm in the highest parts. Annual rainfall distribution has one peak and the most of the precipitation falls in the April-July period. The most arid period is late summer and early autumn. The highest parts of the mountain (above 1800 m) almost all year round are exposed to strong southwest and west winds, reaching up to 8m/sec (KOLEVA, 2005).

Vitosha Mountain has a great variety of soils. In the lowest mountainous parts dominate *Chromic Cambisols*. In the elevation belt 1400-1750 m the most widely distributed are *Cambisols*. In the highest parts of the mountain (1750-1900 m) prevail *Mollic Cambisols*. In the subalpine and alpine zones are formed *Umbrosols*. *Fluvisols* are present along the lower riverbeds (MALINOV, 2005).

Vitosha's natural vegetation was developed during the last ice age. According to palaeobotanical studies, the floristic composition of the territory has not changed essentially. Substantial vegetation alteration took place later, mainly due to human activity. During the 15-19 centuries, mining, primitive metallurgy and nomadic cattle breeding were developed in the region. The need of wood materials led to forest clearing over most of the mountain. Finding of pasture for the numerous herds necessitated setting of periodical fires in the high mountainous parts. This resulted in almost complete destruction of the natural vegetation. These factors, together with the steep relief and the heavy rain conditions, led to developing of erosion processes and the following degradation of the natural habitats (MESHINEV, 2005).

### Material and methods

*Sampling.* In the summers of 2008 and 2009, systematically, along a preliminary drawn vertical transects on the south slope of Vitosha Mountain, 114 0.1 ha (20×50 m) vegetation samples were taken (Fig. 1).



**Fig. 1.** Sampling plot, modified from WHITTAKER (1956, 1960). For more details on sampling procedure see the text.

Totally nine transects, following the main and intermediate Earth directions (E, EES, ES, SSE, S, SSW, SW, SWW, and W) were laid. Transects start at around 900 m and reach the tree line. Samples were taken at uniform distance of 50 m altitude along the vertical transect. Starting position of transects is randomly chosen after numbering of five possible starting points and pulling one of them. Sampling places are located in such a way so they can cover the maximum variety of expositions, slope inclinations, slope topography and elevations. The exact sampling sites are chosen visually keeping the requirement for vegetation homogeneity, i.e. they should not be located in the forest periphery or in large open forest patches. Forest communities under intensive human influence (intensive livestock grazing or logging) are avoided. In order to avoid spatial autocorrelation the distance between neighboring sampling plots is at least 200 m.

On the place chosen, 50 m plastic tape is laid on the ground, perpendicular to topographic horizontals. From the two ends

of the tape toward its two sides, perpendicular to it, 10 m distance is measured and metal stakes are fixed into the ground. Obtained in this way rectangular plot has 20×50 m sides (Fig. 1). First, total tree stratum cover is measured visually in percents. Then, diameter of all tree and shrub stems >1 cm at breast height ( $\approx 1.30$  cm) is recorded by species and grouped by diameter classes.

Undetermined on the field individuals were taken as herbarium specimens and transported to laboratory for species determination. Nomenclature and systematics follows JORDANOV (1989) and KOJUHAROV (1995). DELIPAVLOV (1992), JAVORKA (1975) and Flora Europaea (TUTIN *et al.*, 1968-1993) were also used.

*Classification and statistical tests.* In the current study TWINSpan classification (Two Way INDicator SPecies Analysis) (HILL & ŠMILAUER, 2005) was used. The basic idea in TWINSpan is that each group of samples can be identified based on indicator species, i.e. such species that prevail at the one side of the dichotomy. TWINSpan gives the

opportunity of processing qualitative and quantitative data. The software TWINSpan not only classify the samples but also produces two-way ordered data table (samples x species). In construction of TWINSpan table, two-way weighted average algorithm of Correspondence Analysis (CA) (HILL, 1973) was used. Combination of the two has made the method one of the most popular among the vegetation ecologists nowadays (VAN TONGEREN, 2004). Aiming to investigate in details dominant tree stand structure in the context of moisture gradient, all samples where *Fagus sylvatica* and *Pinus sylvestris* dominated were grouped in moisture ecological groups (WHITTAKER, 1956): moesic, submoesic, subxeric and xeric habitats.

Community types were tested for statistically significant difference with nonparametric ANOVA on Ranks, Dunn's method, because they had not normal distribution. Stem distributions for the different community types and moisture groups were checked for normality using Shapiro-Wilk normality test. If not noted otherwise, in all analyses the significance level is  $P \leq 0.05$ . The following specialized software products are used: STATISTICA, version 8.0 (STATSOFT, 2004), SigmaPlot for Windows, version 11.0 (SYSTAT SOFTWARE INC., 2008).

## Results

In the summers of 2008 and 2009 totally 114 0.1 ha samples were taken. These were classified using TWINSpan software, which results have been published in a previous paper (DYAKOV, 2012). The following analyses were done in the context of that classification scheme. As can be seen from Table 1, six of all forest communities were dominated by *Fagus sylvatica* L. In the other three community types *Pinus sylvestris* L., *Pinus nigra* Arn., *Quercus cerris* L., *Carpinus betulus* L., *Crataegus monogyna* Jacq. and *Cornus mas* L. were dominant. Arranged in this way, community types express the complex environmental gradient, resulting mainly by elevation and habitat moisture gradient interaction. In the very left part of the table, most moesic beech forests are

placed, followed by the submoesic beech communities, and then subxeric and xeric ones. In the very right table part are located the subxeric and xeric coniferous forests (plantations), and xeric mixed oak communities.

Forest community types were tested for significant differences in median stem number per 0.1 ha by all diameter classes. Results are shown in Table 1. Significant differences are few. In the thinner diameter classes (1-10 cm) *Fagus* communities are almost indistinguishable one another. Yet, we found significant differences between *Fagus sylvatica*-*Festuca drymeia* and *Fagus sylvatica*-*Gallium odoratum* in 5-10 cm diameter class. Another significant difference, between *Fagus sylvatica*-*Festuca drymeia* and coniferous forests (*Pinus sylvestris*-*Fragaria vesca* and *Pinus nigra*-*Crataegus monogyna*) in 5-10 cm diameter classes, was also found. Significantly, higher number of thinner stems in the former community is result of the sprouting mode of regeneration of these forests. Among the middle classes (10-25 cm) significant differences are also few. These are mainly among the coniferous plantations and submoesic beech communities, the former having significantly higher number of stems in 20-25 cm diameter class. The only significant difference among the *Fagus* types is between *Fagus sylvatica*-*Festuca drymeia* and *Fagus sylvatica*-*Gallium odoratum* in 5-10 cm diameter class and between *Fagus sylvatica*-*Gallium odoratum* and *Fagus sylvatica*-*Hepatica nobilis* in > 35 cm diameter class (Table 1).

Differences in the thickest classes are even lesser. These are between some beech forests and *Pinus nigra*-*Crataegus monogyna* community type, the later having significantly higher stem number in the 20-25 cm diameter class. Regarding the total stem number per 0.1 ha, forest communities are statistically indistinguishable (Table 1).

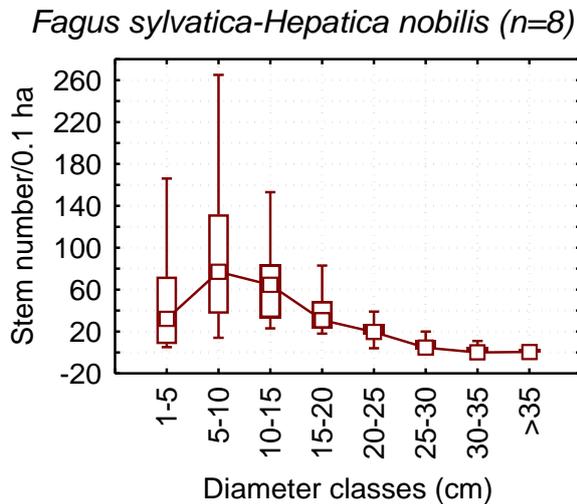
According to the obtained results from the statistical comparison of forest community types, we conclude that the forest communities in the studied area are

**Table 1.** Forest community types in the studied territory. Upper part of the table shows community type names (composed of the Latin names of dominant tree, shrub or herb species) and forest ecological groups. Lower part represents the median stem number by diameter class  $\pm$  quartile range. In the last row, the total stem number per 0.1 ha in forest communities is given. Stem number per 0.1 ha for the forest community types are tested for differences with ANOVA on Ranks, Dunn's method. Medians with different letters in the rows are significantly different at  $P \leq 0.05$  level.

Forest community types	Forest communities dominated by <i>Fagus sylvatica</i>					Mixed forest communities dominated by <i>Pinus</i> and <i>Quercus</i> genera			
	Moesic beech forests		Submoesic beech forests			Subxeric and xeric beech forests	Subxeric and xeric coniferous forests (plantations)	Mixed xeric oak forests	
	<i>Fagus sylvatica</i> - <i>Hepatica nobilis</i> (n = 8)	<i>Fagus sylvatica</i> - <i>Physospermum cornubiense</i> (n = 12)	<i>Fagus sylvatica</i> - <i>Galium odoratum</i> (n = 13)	<i>Fagus sylvatica</i> - <i>Luzula luzuloides</i> (n = 23)	<i>Fagus sylvatica</i> - <i>Festuca drymeja</i> (n = 17)	<i>Fagus sylvatica</i> - <i>Corylus avellana</i> - <i>Brachypodium pinnatum</i> (n = 15)	<i>Pinus sylvestris</i> - <i>Fragaria vesca</i> (n = 15)	<i>Pinus nigra</i> - <i>Crataegus monogyna</i> (n = 5)	<i>Quercus cerris</i> - <i>Cornus mas</i> (n = 6)
<b>Diameter classes (cm)</b> <b>(stem number per 0.1 ha)</b>									
1-5	12 $\pm$ 23	13 $\pm$ 13	17 $\pm$ 29	11 $\pm$ 27	20 $\pm$ 17	28 $\pm$ 25	7 $\pm$ 19	21 $\pm$ 14	32 $\pm$ 55
5-10	77 $\pm$ 95ab	44 $\pm$ 53ab	30 $\pm$ 49b	39 $\pm$ 60ab	80 $\pm$ 143a	68 $\pm$ 81ab	13 $\pm$ 39b	17 $\pm$ 12b	41 $\pm$ 97ab
10-15	65 $\pm$ 51	34 $\pm$ 69	19 $\pm$ 26	16 $\pm$ 46	69 $\pm$ 80	51 $\pm$ 74	29 $\pm$ 103	12 $\pm$ 16	49 $\pm$ 81
15-20	31 $\pm$ 26	29 $\pm$ 31	15 $\pm$ 14	15 $\pm$ 45	45 $\pm$ 39	27 $\pm$ 66	32 $\pm$ 103	34 $\pm$ 45	45 $\pm$ 13
20-25	20 $\pm$ 10ab	25 $\pm$ 14ab	12 $\pm$ 11a	15 $\pm$ 19a	25 $\pm$ 22ab	19 $\pm$ 24ab	39 $\pm$ 36b	59 $\pm$ 40b	25 $\pm$ 28ab
25-30	5 $\pm$ 8	11 $\pm$ 9	9 $\pm$ 9	10 $\pm$ 16	9 $\pm$ 15	9 $\pm$ 6	23 $\pm$ 32	40 $\pm$ 40	9 $\pm$ 6
30-35	-	9 $\pm$ 5	7 $\pm$ 5	5 $\pm$ 6	6 $\pm$ 10	4 $\pm$ 7	10 $\pm$ 20	12 $\pm$ 12	7 $\pm$ 7
>35	1 $\pm$ 4a	10 $\pm$ 12ab	16 $\pm$ 12b	10 $\pm$ 12ab	2 $\pm$ 6ab	6 $\pm$ 10ab	1 $\pm$ 7ab	-	1 $\pm$ 2ab
<b>Total</b>	<b>169 <math>\pm</math> 344</b>	<b>269 <math>\pm</math> 250</b>	<b>242 <math>\pm</math> 165</b>	<b>393 <math>\pm</math> 469</b>	<b>346 <math>\pm</math> 1015</b>	<b>338 <math>\pm</math> 666</b>	<b>336 <math>\pm</math> 502</b>	<b>77 <math>\pm</math> 110</b>	<b>173 <math>\pm</math> 325</b>

statistically indistinguishable by their stem diameter class distribution.

*Forest stand description.* Stem number distribution of *Fagus sylvatica*-*Hepatica nobilis* community type is shown in Fig. 2. Table 2 represents the normality test of stem distribution in the different forest communities.



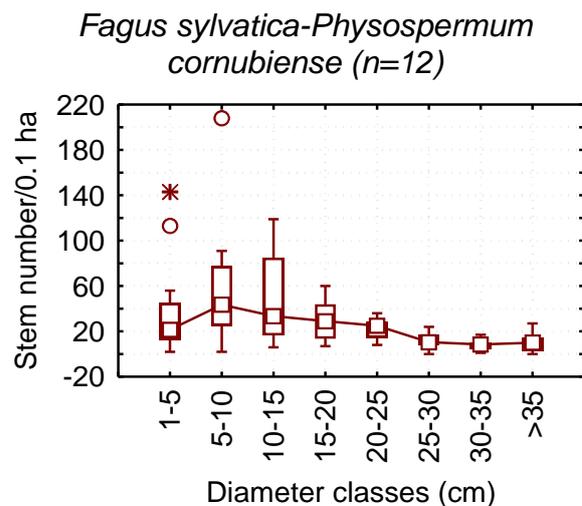
**Fig. 2.** *Fagus sylvatica*-*Hepatica nobilis* community type stem number distribution (> 1 cm at breast height  $\approx$  1.30 cm) of all trees and shrubs by diameter classes ( $\square$  Median  $\square$  25%-75%  $-$  Non-Outlier Range  $\circ$  Outliers  $*$  Extremes).

Stem distribution by diameter classes of the first community type is normal (Table 2) with greater variance in the small and middle classes (1-20 cm) (Fig. 2). Bell-shaped curve is resultant from the unsuccessful stand regeneration, and particularly of *Fagus sylvatica*.

Most abundant species in the thinner and middle diameter classes are sycamore *Acer platanoides* L., *Acer campestre* L., *Acer pseudoplatanus* L. and *Carpinus betulus*. Forest undergrowth is dominated by species like *Cornus mas*, *Sorbus aucuparia* L., *Corylus avellana* L., *Viburnum lantana* L., *Prunus avium* L. and *Crataegus monogyna*. With insignificant share in the small and middle diameter classes are *Ulmus glabra* Huds. and *Fraxinus ornus* L. Because of the weak regeneration of the beech in this community type, it is expected to compete for

dominance in the next decades with species like *Carpinus betulus*, *Acer platanoides*, *Acer campestre* and *Acer pseudoplatanus*. If the current tendency is retained, the transformation of these forests into coppice beech communities, despite the favorable habitat conditions, is unavoidable.

*Fagus sylvatica*-*Physospermum cornubiense* community type also has normal diameter class distribution (Fig. 3, Table 2) with greater variance among the thinner stems (1-15 cm).



**Fig. 3.** *Fagus sylvatica*-*Physospermum cornubiense* community type stem number distribution (> 1 cm at breast height  $\approx$  1.30 cm) of all trees and shrubs by diameter classes ( $\square$  Median  $\square$  25%-75%  $-$  Non-Outlier Range  $\circ$  Outliers  $*$  Extremes).

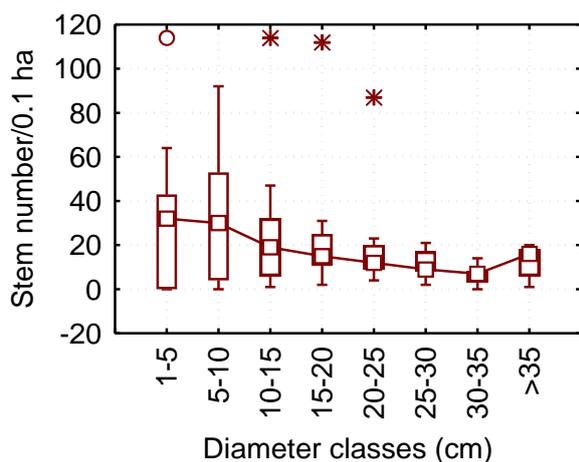
*Fagus sylvatica* dominates here too, but this is more clearly expressed in the thinner classes. In the diameter classes greater than 15 cm, *Tilia platyphyllos* Scop. prevailed. *Carpinus betulus* and *Acer campestre* are also well represented in the thinner and middle classes. Undergrowth composition is rather diversified, but with prevalence of species like *Corylus avellana*, *Picea abies* (L.) Karst., *Pinus sylvestris*, *Ulmus glabra*, *Prunus avium* and *Crataegus monogyna*. Here can often be found species like *Quercus petraea* (Matt.) Liebl. and *Sorbus aucuparia*, taking part mainly in the middle classes, and rarely in the thickest ones. However, in the thickest diameters only species like *Pinus nigra* n

*Populus tremula* L. take part. Exceptionally, in the middle and thicker diameter classes, species like *Fraxinus excelsior* L. and *Alnus glutinosa* (L.) Gaertn. can also be found.

Because of its dominance in the thinner diameter classes, mainly with sprouting regeneration, it is expected that *Fagus sylvatica* will dominate in the future successional stages together with species like *Carpinus betulus* and *Acer campestre*. *Tilia platyphyllos* almost completely lacks from the thinner classes, therefore, most probably, it will be excluded from the stand and will be replaced by *Fagus sylvatica* and *Carpinus betulus*.

Community type *Fagus sylvatica-Galium odoratum* looks similar to the previous one, except that the common beech has more weakly expressed dominance in the stand.

*Fagus sylvatica-Galium odoratum* (n=13)



**Fig. 4.** *Fagus sylvatica-Galium odoratum* community type stem number distribution (> 1 cm at breast height  $\approx$  1.30 cm) of all trees and shrubs by diameter classes (□ Median □ 25%-75% — Non-Outlier Range ◊ Outliers \* Extremes).

Stem distribution here is normal too (Fig. 4; Table 2). In the thinner classes (1-10 cm) dominate *Fagus sylvatica*, *Picea abies*, *Pinus sylvestris* and *Corylus avellana*. With weaker participation are species like *Fraxinus excelsior*, *Crataegus monogyna*, *Sorbus aucuparia* and *Prunus cerasifera* Ehrh. In the middle classes (10-25 cm), *Pinus*

*sylovestris* and *Tilia platyphyllos* prevailed, followed in dominance by *Fagus sylvatica*. With small percentage, here is *Picea abies*, but together with it can be found also species like *Betula pendula* Roth, *Salix caprea* L. and *Prunus cerasifera*. *Fagus sylvatica* and *Tilia platyphyllos*, together with *Pinus sylvestris*, dominate the thickest (25-35 cm) stem diameters. Here are also present *Betula pendula* and *Picea abies*. With negligible proportion are *Acer pseudoplatanus* and *Salix caprea*.

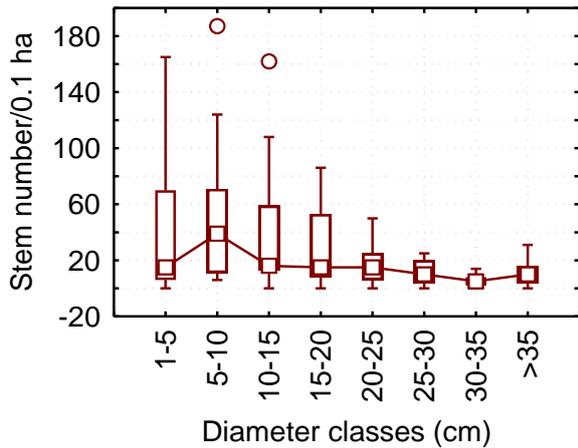
Considering the thinner stem composition, it can be asserted that with the successional progression *Pinus sylvestris* and *Tilia platyphyllos* will be eliminated from the forest stand. They, most probably, will be replaced by *Fagus sylvatica* and *Picea abies*, which have greater participation among the thinner stems.

Stem distribution by diameter classes in *Fagus sylvatica-Luzula luzuloides* type is normal (Fig. 5, Table 2). In this and the next community type, *Fagus sylvatica* reaches its greatest dominance, but the species number reaches its minimum. The beech dominates thinner classes exclusively with the weaker presence of species like *Picea abies*, *Carpinus betulus*, *Crataegus monogyna*, *Salix caprea* and *Prunus cerasifera*. In the middle diameters classes the two principal trees *Fagus sylvatica* and *Picea abies* prevailed too.

With lesser importance, here are species like *Pinus sylvestris* and *Sorbus aucuparia*. *Fagus sylvatica* and *Picea abies* dominate the thickest classes too, but here larger trees like *Betula pendula* can also be found, forming small groups in some more open sites in the stand. It is certain that for few decades, with the canopy closure, they will be excluded completely. It is doubtless that with the successional progression *Fagus sylvatica* dominance will persist, despite its exclusively sprouting regeneration. *Picea abies* will also have its role in the stand development of these forest communities in the next decades.

*Fagus sylvatica-Festuca drymeia* community type at greater extent resembles the previous one. Stem distribution of diameter classes of all species is normal (Fig. 6, Table 2).

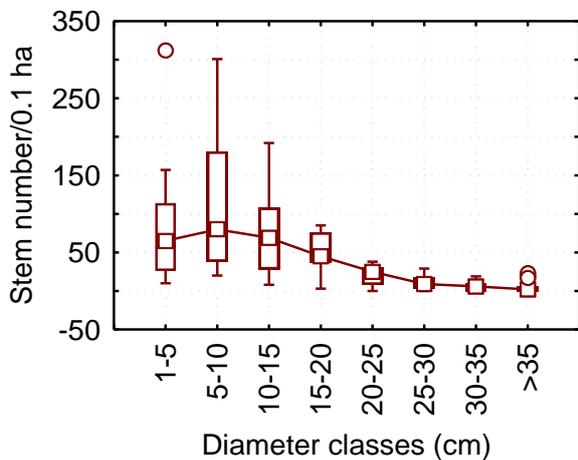
*Fagus sylvatica-Luzula luzuloides* (n=23)



**Fig. 5.** *Fagus sylvatica-Luzula luzuloides* community type stem number distribution (> 1 cm at breast height  $\approx$  1.30 cm) of all trees and shrubs by diameter classes (□ Median □ 25%-75% — Non-Outlier Range ○ Outliers\* Extremes).

*Fagus sylvatica* dominates the thinner classes exclusively. Here can be found only separate individuals from species like *Carpinus betulus*, *Sorbus aucuparia* и *Pinus sylvestris*.

*Fagus sylvatica-Festuca drymeja* (n=17)



**Fig. 6.** *Fagus sylvatica-Festuca drymeia* community type stem number distribution (> 1 cm at breast height  $\approx$  1.30 cm) of all trees and shrubs by diameter classes (□ Median □ 25%-75% — Non-Outlier Range ○ Outliers\* Extremes).

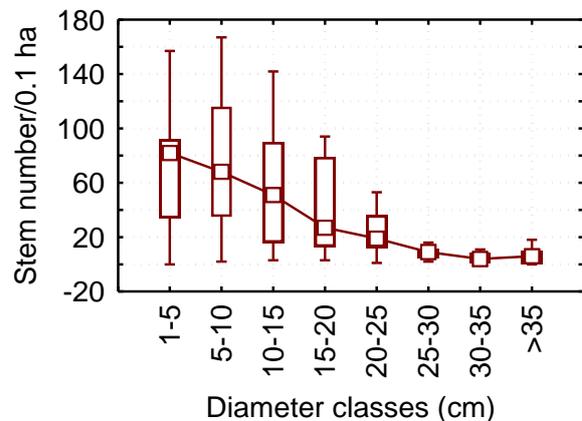
Species richness in these communities is extremely low, reaching only six tree and shrub species per 0.1 ha. Thicker stem

classes are dominated by three tree species, having almost equal importance. These are *Fagus sylvatica*, *Pinus nigra*, *Pinus sylvestris* as well as some individuals of *Betula pendula* can also be found.

Successional development of these forests will progress toward beech dominance and pure stand formation. This is so because from the late-successional species only the beech takes part in the thinner stem diameters. *Carpinus betulus* will also be present, but with negligible share. Here, like the former community type, the beech has completely sprouting regeneration.

*Fagus sylvatica-Corylus avellana-Brachypodium pinnatum* is the most xeric forest type, having greatest diversity of tree and shrub species. *Fagus sylvatica* and *Pinus sylvestris* dominate the stand. Stem diameter distribution is normal (Fig. 7, Table 2).

*Fagus sylvatica-Corylus avellana-Brachypodium pinnatum* (n=15)



**Fig. 7.** *Fagus sylvatica-Corylus avellana-Brachypodium pinnatum* community type stem number distribution (> 1 cm at breast height  $\approx$  1.30 cm) of all trees and shrubs by diameter classes (□ Median □ 25%-75% — Non-Outlier Range ○ Outliers\* Extremes).

Species composition among the thinner diameter classes is variable, but *Fagus sylvatica*, *Pinus sylvestris*, *Betula pendula*, *Corylus avellana* and *Picea abies* dominate. Less important are *Salix caprea*, *Prunus cerasifera*, *Crataegus monogyna*, *Cornus sanguinea* L., *Sorbus aria* (L.) Crantz, *Malus*

*sylvestris* Mill. and *Populus tremula*. In the middle diameter classes dominate *Pinus sylvestris* and *Fagus sylvatica* and less well represented are *Quercus cerris*, *Quercus petraea*, *Picea abies* and *Salix caprea*. With negligible share are *Carpinus betulus*, *Pyrus pyraeaster* Burgsd. and *Prunus cerasifera*. *Pinus sylvestris* and *Quercus cerris* prevailed in the thickest classes. *Fagus sylvatica* and *Quercus petraea* were more weakly represented. *Picea abies* and *Prunus avium* were also present, but with isolated individuals.

Because the variable composition of the thinner stems, it is impossible to predict the successional direction of these forests and their probable composition in the next decades. The most likely dominant is the beech, accompanied by the oaks and, at some places, for a short period of time, by *Betula pendula*. *Pinus sylvestris* will probably be eliminated completely from the stand.

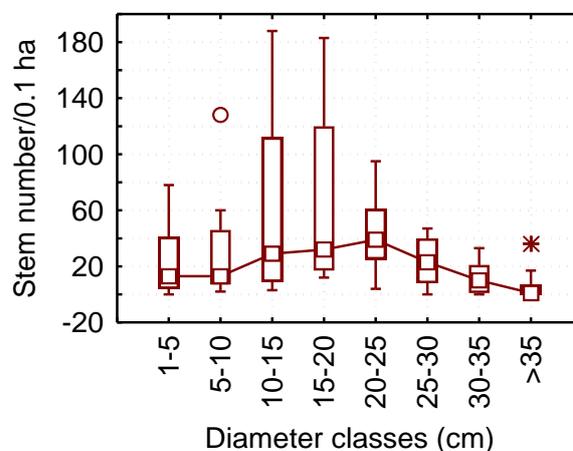
*Pinus sylvestris-Fragaria vesca* are co-dominated by *Pinus nigra* with greater stem number variance among the middle diameter classes. Stem distribution of all stems is normal (Fig. 8; Table 2). This forest type has artificial origin (i.e. plantation) and is extremely influenced by human activities – mainly from livestock grazing, insect attacks, forest fires and logging.

Thinner stem classes are dominated by *Fagus sylvatica* together with *Betula pendula*. *Rosa canina* L. has significant share. Because of the more opened canopy of the stand and the excess light reaching the forest floor, great number of shrubs like *Evonymus europaeus* L., *Crataegus monogyna* and *Prunus cerasifera* participate in the undergrowth. *Pinus sylvestris* and *Pinus nigra* sustain less numerous populations in this forest stratum as well as separate individuals of *Quercus petraea*, *Sorbus aucuparia* and *Acer pseudoplatanus* also can be found.

In the middle classes prevail the pines and, at lesser extent, *Betula pendula*. At some places, along temporal or permanent streams, isolated individuals of *Alnus glutinosa* survive. In the shadiest habitats, some individuals of *Fagus sylvatica* and *Tilia cordata* Mill. can be found. The thickest diameter classes are mainly dominated by the pines with the lesser participation of

*Tilia cordata* (in the moister and shadier places). Isolated individuals of *Fagus sylvatica* can also be found.

*Pinus sylvestris-Fragaria vesca* (n=15)



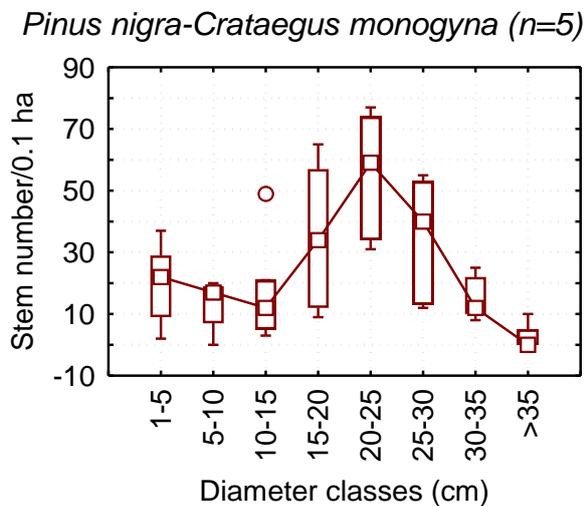
**Fig. 8.** *Pinus sylvestris-Fragaria vesca* community type stem number distribution (> 1 cm at breast height  $\approx$  1.30 cm) of all trees and shrubs by diameter classes (□ Median □ 25%-75% – Non-Outlier Range ◊ Outliers \* Extremes).

Because of their poor regeneration, successional development of these forests will be directed toward pine replacement by coppice beech communities. Probable reason for the unsuccessful regeneration of these communities, except unfavorable growth conditions, is the well-developed herb cover of the forest floor, precluding seedling survival. Unless new disturbances take place, this situation will prolong. *Betula pendula* will be probable companion of *Fagus sylvatica* for a few decades until its complete elimination from the stand. Otherwise, succession will be restarted or returned in earlier phase, precluding late-successional species of taking dominance.

*Pinus nigra-Crataegus monogyna* forests are more moesic, growing more frequently on shadier north-facing slopes. Stem distribution here is normal too (Fig. 9, Table 2).

Generally, *Pinus nigra* and *Pinus sylvestris* are the dominants, followed by *Fagus sylvatica*, which has mostly sprouting regeneration. In the thinner classes, there is

no clearly pronounced single dominant. However, with greater importance are species like *Quercus petraea*, *Carpinus betulus*, *Acer campestre*, *Crataegus monogyna* and *Fagus sylvatica*.



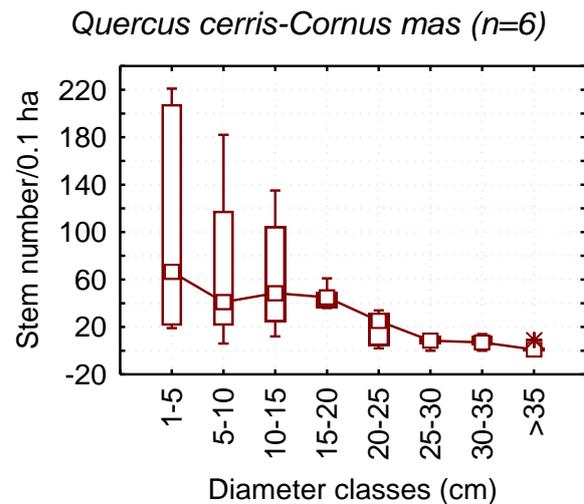
**Fig. 9.** *Pinus nigra-Crataegus monogyna* community type stem number distribution (> 1 cm at breast height  $\approx$  1.30 cm) of all trees and shrubs by diameter classes ( $\square$  Median  $\square$  25%-75%  $-$  Non-Outlier Range  $\circ$  Outliers  $*$  Extremes).

These forests are characterized with their relative heterogeneity, having multiple open patches in the stand and greater species diversity in the undergrowth. Species with negligible abundance among the thinner stems are *Viburnum lantana*, *Prunus cerasifera*, *Cornus sanguinea*, *Corylus avellana* and *Cornus mas*. In the middle classes oaks and pines dominate. These are *Pinus nigra*, *Pinus sylvestris*, *Quercus petraea*, *Quercus frainetto* Ten. and *Quercus cerris*. The pines prevail almost exclusively in the thickest diameter classes. Some individuals of the oaks also can be found.

Given the thinner and middle class stem composition, successional direction cannot be predicted at this stage. Most probable successional trajectory is toward elimination of the pines, because of their poor regeneration, their replacement by the beech and *Carpinus betulus*, but with the considerable participation of the oaks or even their dominance, especially of *Quercus petraea*. Because the lower elevation of their

distribution these forests are strongly influenced by the human activity (for example, livestock grazing and logging). This disturbance regime will be one of the principal factors, determining their future successional development.

*Quercus cerris-Cornus mas* communities have extremely diversified species composition and stand structure, due mainly to their disturbance regime and the poor habitat conditions.



**Fig. 10.** *Quercus cerris-Cornus mas* community type stem number distribution (> 1 cm at breast height  $\approx$  1.30 cm) of all trees and shrubs by diameter classes ( $\square$  Median  $\square$  25%-75%  $-$  Non-Outlier Range  $\circ$  Outliers  $*$  Extremes).

Tree stand is heterogeneous with multiple open patches, well developed herb layer, and numerous shrub species. Stem distribution of all species is normal (Fig. 10; Table 2). *Fagus sylvatica* is poorly represented and like the previous two forest types has exclusively sprouting regeneration. Greatest share among the thinner stems have *Carpinus betulus* and *Fraxinus ornus*. Other important species are *Quercus cerris*, *Quercus petraea*, *Cornus mas* and *Corylus avellana*. Weakly represented are species like *Cornus sanguinea*, *Crataegus monogyna*, *Fagus sylvatica*, *Ulmus minor* Mill., *Prunus cerasifera*, *Rosa canina*, *Malus sylvestris*, *Sorbus torminalis* (L.) Crantz and *Viburnum lantana*. In the middle diameter classes dominate *Quercus cerris*, *Quercus*

*petraea*, *Carpinus betulus* and *Quercus pubescens* Willd. *Acer campestre* is represented with separate individuals. Species like *Quercus cerris* and *Quercus petraea* completely dominate the thickest classes. Less important are *Carpinus betulus* and *Acer campestre*.

Successional trajectory of this forest type will be predetermined from the

heterogeneous stand composition, resulting from natural and anthropogenic disturbances, as well as from the poor and dry conditions of occupied habitats. These complex factors preclude one or few competitively superior species of assuming complete dominance over the rest and their elimination from the stand.

**Table 2.** Forest community stems distribution. *W* value shows the result of Shapiro-Wilk test of the hypothesis that tested variables have normal distribution. When  $P > 0.05$  the distribution is normal

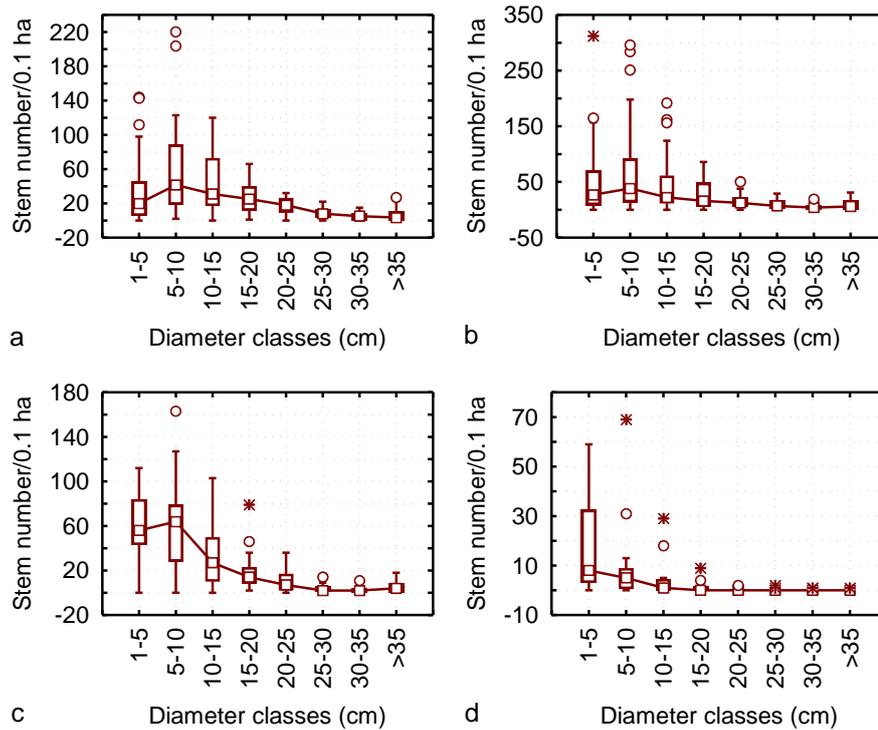
Variable (stem number per 0.1 ha)	Distribution	W (Shapiro-Wilk test for normality)	P
<i>Fagus sylvatica</i> - <i>Hepatica nobilis</i>	Normal	0.911	0.359
<i>Fagus sylvatica</i> - <i>Physospermum cornubiense</i>	Normal	0.924	0.467
<i>Fagus sylvatica</i> - <i>Galium odoratum</i>	Normal	0.943	0.639
<i>Fagus sylvatica</i> - <i>Luzula luzuloides</i>	Normal	0.930	0.516
<i>Fagus sylvatica</i> - <i>Festuca drymeia</i>	Normal	0.885	0.208
<i>Fagus sylvatica</i> - <i>Corylus avellana</i> - <i>Brachypodium pinnatum</i>	Normal	0.887	0.221
<i>Pinus sylvestris</i> - <i>Fragaria vesca</i>	Normal	0.933	0.545
<i>Pinus nigra</i> - <i>Crataegus monogyna</i>	Normal	0.934	0.552
<i>Quercus cerris</i> - <i>Cornus mas</i>	Normal	0.905	0.321

In order to analyze stand development tendency in more details, populations of the two principal tree species in the region (*Fagus sylvatica* and *Pinus sylvestris*) were examined separately. Beech forests from the poorest and driest habitats were separated in fourth group - xeric habitats. *Fagus sylvatica* population from the favorable and subxeric habitats (*sensu* PEET, 1981) is

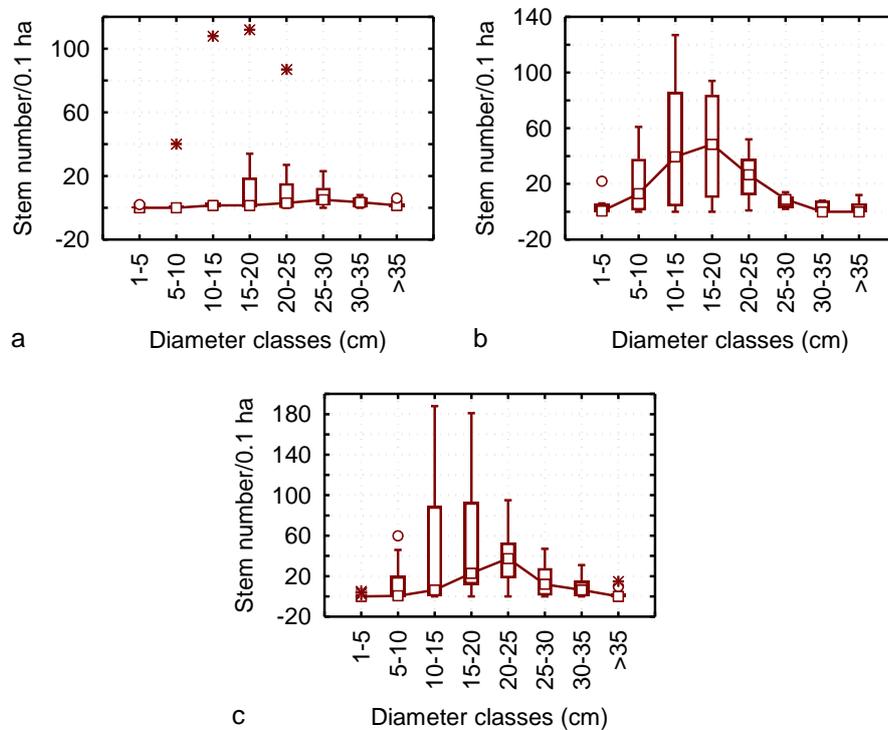
characterized with normal distribution. Only xeric habitats are with lognormal stem distribution. In the latter case, this distribution pattern is caused by the sprouting regeneration of the beech in these places and the numerous thinner stems, producing the inversed *J*-curve (Fig. 11, Table 3).

**Table 3.** *Fagus sylvatica* stem distribution in the four habitat types. *W* value shows the result of Shapiro-Wilk test of the hypothesis that tested variables have normal distribution. When  $P > 0.05$  the distribution is normal. Significant *P* values are marked with *italic*

Variable (stem number per 0.1 ha)	Distribution	W (Shapiro-Wilk test for normality)	P
Moesic habitats	Normal	0.920	0.427
Submoesic habitats	Normal	0.900	0.290
Subxeric habitats	Normal	0.853	0.101
Xeric habitats	Lognormal (inversed <i>J</i> -curve)	0.725	<i>0.004</i>



**Fig. 11.** *Fagus sylvatica* stem number per 0.1 ha (> 1 cm at breast height  $\approx$  1.30 cm) by diameter classes in four habitat types. a) Moesic habitats ( $n = 20$ ); b) Submoesic habitats ( $n = 52$ ); Subxeric habitats ( $n = 13$ ); d) Xeric habitats ( $n = 16$ ) ( $\square$  Median  $\square$  25%-75%  $-$  Non-Outlier Range  $\circ$  Outliers  $*$  Extremes).



**Fig. 12.** *Pinus sylvestris* stem number/0.1 ha (> 1 cm at breast height  $\approx$  1.30 cm) by diameter classes in three habitat types. a) Submoesic habitats; b) Subxeric habitats; c) Xeric habitats. ( $\square$  Median  $\square$  25%-75%  $-$  Non-Outlier Range  $\circ$  Outliers  $*$  Extremes).

**Table 4.** *Pinus sylvestris* stem distribution in the three habitat types. *W* value shows the result of Shapiro-Wilk test of the hypothesis that tested variables have normal distribution. When  $P > 0.05$  the distribution is normal.

Variable (mean stem number per 0.1 ha)	Distribution	W (Shapiro-Wilk test for normality)	P
Submoesic habitats	Normal	0.909	0.348
Subxeric habitats	Normal	0.835	0.068
Xeric habitats	Normal	0.890	0.235

The situation in the favorable places is different. Stems of all diameter classes are present here and the thinner ones prevail (Fig. 11), but this does not contribute for accomplishment of lognormal curve (Table 3).

Stem distribution of *Pinus sylvestris* was also analyzed. We have found normal stem distribution by diameter classes for this species in all habitats (Fig. 12, Table 4). These results also apply to the *Pinus nigra* stands in the region.

### Discussion

This study was designed to expand and integrate the accumulated knowledge of the vegetation stand structure and regeneration pattern in the studied area placed in the context of dominant local environmental gradients. It also aimed to investigate the stem diameter distribution of studied stands, which we hypothesized will follow normal distribution. We tried to predict the successional trajectory of forest vegetation in the area based on current stand stem structure.

Consistency of the described forest communities was statistically tested based on their stem number in the different diameter classes. Our results showed that, with few exceptions, forest communities, especially these dominated by the beech, are almost indistinguishable in the environmental space. This result supports the continuum concept of vegetation organization. Most stands that we have analyzed had normal stem diameter distribution as for the total stands as well as for the stem distribution of dominant tree species alone, with the exception of beech stem distribution from the most xeric habitats. This is assumed by

some authors to indicate difficulties in regeneration or prior human disturbance events (JACKSON & FALLER, 1973; JOHNSON & BELL, 1975; SCHMELZ & LINDSEY, 1965; PEET, 1981). We suppose that successful regeneration and human disturbances are connected. Possible reason for the unsuccessful seed regeneration is the prevailing even-aged and sprouting stand structure of most beech and pine communities resulting from the management practices (for example, clear-cutting), pushing local vegetation toward homogenization and "stagnancy" (*sensu* WHITTAKER, 1956). Another possible reason is the relative lack of severe natural disturbance (like windfall, for example) events in the area during the last decades, which could have made these forests more heterogeneous.

Beech stands from favorable (moesic) (*sensu* PEET 1981) places have higher stature and most stems are from seed origin. According to Whittaker (1956), the general tendency in the studied by him stands was height and diameter decrease along the moisture gradient from the moistest to the driest habitats. This tendency was in inverse correlation with the stem number per unit area, which increased in the same direction (ILVESSALO 1921, LUTZ 1932). In other words, the more unfavorable (xeric) was given habitat the less was the share of the thickest stems in the stand. Fig. 11 clearly shows the same tendency in our *Fagus sylvatica* stem distribution. PEET (1981) found inversed J-curve distribution for the most stands in the favorite habitats. However, we have found the opposite tendency in all habitats but the most xeric ones where regeneration comes only from sprouting. Canopy closure in the

both habitat types is high and the stands have not reached transitional successional phase. This is also evident from the extremely low number of tree and shrub species, which, according to PEET (1981), is minimal in the beginning of second phase. They are arrested in the thinning successional phase, preventing their transition into the transitional stage, characterized by canopy opening and seedling appearance.

Forest practices in the area lean to clear cutting, turning the forest into even-aged stand composed of numerous thin stems with only sprouting regeneration. Low intensity (the so called "regeneration logging") cuttings are also plasticized in the area. We suppose that the stand structural pattern is caused mainly by these activities. Unfavorable growth conditions (extremely dry summers in the last decade) in most places have also played a role for hampering seed regeneration. However, in some distant, inaccessible habitats (mainly moist deep ravines), where forest management is difficult, forest stands are heterogeneous with variable stem numbers from all diameter classes. Because these forest communities are spared from natural disturbances too, canopy opening and overcoming of stagnant forest state is impeded.

According to WHITTAKER (1956) regeneration of stagnant forests, most probably, happens periodically, following partial or complete stand destruction, allowing its replacement in irregular intervals. Unfortunately, forest stands in the studied by us territory, as mentioned above, are relatively spared from severe natural disturbances, which could change the stagnant situation.

In the more xeric habitats, lesser individuals reach the greater diameter classes, which leads to steeper distributional curves (WHITTAKER 1956). The situation in most stands investigated in this study is similar. WHITTAKER (1960) reported that lack of regeneration and normal stem diameter distribution can be result of fire disturbance too. However, we have not found data for severe fires that took place on the studied territory in the last decades.

Coniferous forests in the area have completely artificial origin. They have been planted in these habitats incongruous to the pine species ecology, which led to their even-aged structure and complete lack of regeneration. Stems from the middle diameter classes dominate the stands entirely in these plantations. This is most obvious in the subxeric habitats. The pine stands in the favorable places will be probably completely replaced in the future by the beech. However, in the more xeric habitats, sprouting beech communities together with other broadleaf species (e.g. oaks) will take over. In the most xeric sites, sprouting beech woodlands or/and more open mixed oak forests will dominate.

WHITTAKER (1953) recognized that climax forest can frequently be identified with inversed *J*-curve diameter or age distribution, but the successional one is characterized with discrepancy between the stand and understory composition in particular habitat. However, inversed *J*-curve can also be observed in successional stand or it can be untypical for the unstable climax forests.

Climax communities can be recognized by the regeneration type and by the species dominancy, whether it is stable or variable. Stands can regenerate constantly, regularly or cyclically. Each one of these variants can be seen in forests, where dominant species replaces itself. In other stands, dominant species can alternate cyclically or follow fluctuations and replace themselves irregularly (WHITTAKER 1953).

Similarity between distributional curves from the different moisture gradient parts as for the whole stands as well as for the individual species is regular phenomenon, which according to WHITTAKER (1956) is evidence that none of the stands changes toward another forest type. WHITTAKER (1956) perceived this as lack of convergence toward one climatic climax, with applies to our results too. There is potential for change of one community type to another in the studied territory and it concerns the coniferous plantations, which will be probably replaced by the beech and oaks in the near future. However, this is common

and does not constitute exclusion from the rule, given the artificial origin of these plantations.

### **Conclusion**

If the current forest practices continue to operate on this territory, given the xeric habitat condition and continued forest management, we suppose that the current vegetation will change toward more xeric and open one. It could be predicted that all stands, even those from the most mesic places, will be turned into more or less xeric sprouting beech forests. We also presume that in the driest habitats forest vegetation can even turn into woodland composed of sprouting beech or oak accompanied by xeric herb vegetation. Moreover, this structural transition is already obvious in some extremely disturbed and xeric habitats in the studied territory.

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