SUCCESSION OF XERIC CALCAREOUS GRASSLAND TOWARD THERMOPHILOUS OAK FOREST: THE CASE OF ABAVA VALLEY, WEST LATVIA

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The succession of semi-natural xeric calcareous grassland plant communities toward deciduous forest communities is poorly studied in Latvia. There is insufficient knowledge on the natural transformation of dry calcareous grasslands of Festuco-Brometea into thermophilous quasi-climax oak forest communities of Quercetea pubescentis that are very rare in Latvia. In this paper, a geobotanical study is presented that included studies of soils, tree age, spatial pattern of trees, vegetation composition of different succession stages, and analysis of environmental factors. The study was conducted in the Abava Valley, West Latvia, an area that is unique with species-rich xeric calcareous Festuco-Brometea grasslands, thermophilous oak forests dominated by Quercus robur, and intermediate secondary succession stages with young to medium-aged Juniperus communis and Pinus sylvestris formations.

Keywords: *Festuco-Brometea, Quercetea pubescentis, Juniperus communis stage, Pinus sylvestris stage, vegetation dynamics.*

INTRODUCTION

Thermophilous oak forests belonging to the class Quercetea pubescentis Doing-Kraft ex Scamoni 1959 (syn. Quercetea pubescenti-petraeae Jakucs 1960), order Quercetalia pubescenti-petraeae Klika 1933, have a wide distribution range and are found from the warm Mediterranean in South Europe to the cool temperature nemoral zone in Central Europe and East Europe. These are oak-dominated forests, usually dominated by *Quercus pubescens* or *Q. petraea*, rarely by *Q. robur*. They usually occur on south-facing base-rich slopes on limestone or dolomite bedrock. The shrub layer and herbaceous vegetation in such oak forests are rich in subcontinental species and often are rich in rare plant species. They include four alliances: Quercion petraeae Issler 1931, Quercion pubescenti-petraeae Br.-Bl 1932, Aceri tatarici-Quercion Zolyomi 1957, and Lathyro pisiformis-Quercion roboris Solomeshch et Grigoriev in Wilner et al. 2015 (Chytrý, 1997; Goncharenko et al., 2020).

The distribution of thermophilous oak forests was summarised by Goncharenko et al. (2020). Their distribution range

covers the Balkan and Apenine peninsulas, France, northern part of Spain, Czechia, Slovakia, Poland, Germany, Austria, Hungary, Romania, Belarus, Ukraine, steppe and forest steppe zone in Russia reaching the south-eastern part of Urals. In some parts of the range, they are abundant, while elsewhere, e.g., in West and Central Europe, they are considered relict and scattered and occur on meso-climatically and topographically confined areas (Chytrý, 1997; Bulokhov and Semenishchenkov, 2008; Goncharenko et al., 2020). Loss of these forests was caused by massive deforestation in the Neolithic Age (Rybniěková, 1985 in Chytrý, 1997). Presence and extent of this forest community in Eastern Europe (Belarus, Ukraine, Russia) is insufficiently studied and the syntaxonomy of the communities is not always clear. In scientific literature, Latvia falls out of the currently known range, as there is a lack of studies and published data.

However, the presence of Quercetea pubescentis forest communities in Latvia is mentioned as early as in 2001 by Jermacāne & Laiviņš (2001). Later, the community Lathyro nigri-Quercetum roboris (belonging to Quercetalia pubescenti-petraeae order) was recorded and described by

Laiviņš (2014; 2017), including the distribution map (Laiviņš, 2017), and incorporated into the list of rare habitat types in Latvia (*Lathyrus nigri-Quercetum roboris* association) (National Regulation of the Cabinet of Ministers No. 350, issued in 20.06.2017). Two other communities under *Quercetalia pubescenti-petreae* have been distinguished in Latvia: *Brachypodium pinnatum-Quercus robur* community and *Corylus avellana-Quercus robur* community (Jermacāne and Laiviņš, 2001; Laiviņš, 2014).

Such forests considerably differ from the oak communities belonging to the class *Querco-Fagetea* that are more frequent in Latvia and elsewhere in Eastern Europe outside the steppe and forest steppe zone. Thermophilous oak forests of *Quercetalia pubescentis* represent edaphic conditions and plant assemblages differing from the more frequent European temperate summer-green deciduous forests of *Querco-Fagetea*. Also, the succession and plant species composition of thermophilous oak communities, though sharing some similarities, are different from the communities of *Querco-Fagetea*.

The succession of xeric calcareous grassland plant communities toward deciduous oak forest communities is poorly studied in Latvia. Therefore, we conducted a geobotanical study to understand the complex of xeric calcareous grassland, scrub and thermophilous oak forest plant communities and their transformation process. The Abava Valley chosen as the study area is one of a few areas in Latvia where thermophilous oak forest communities of *Quercetalia pubescentis* have been recorded (Laiviņš, 2014). Thermophilous oak forests may be considered azonal vegetation in Latvia, i.e., occur outside the main range. This type of forest vegetation is very rare in Latvia, as suitable edaphic and local climate conditions are very rare.

The aim of the study was to identify and describe the succession stages of xeric semi-natural grassland (*Filipendula vulgaris*, *Helictotrichon pratense*) toward scrub facies and forest pioneer communities (*Juniperus communis*, *Pinus sylvestris*) that finally lead to a relatively stable quasi-climax forest community dominated by *Quercus robur*. The paper contributes to the overall understanding of the distribution of thermophilous oak forests and the succession from grassland to quasi-climax forest community.

MATERIALS AND METHODS

Study area. The Veģi study area lies in the Abava Valley (Fig. 1), West Latvia, in Veģi, 57°05'05.2" N, 22°28'30.9" E. According to the Köppen-Geiger climate classification (Peel *et al.*, 2007), the whole of Latvia is located in the warm-summer humid continental climate zone (*Dfb*). The study area occurs in the Abava Valley Nature Park, a protected nature area (Natura 2000).

The network of some largest rivers in Latvia is defined by regional tectonic faults in the pre-Quaternary bedrock with length of several dozen kilometres. Therefore, in river val-

Fig. 1. Study area and location of sample plots on an orthophoto map of 2019 (A) and 1994, shortly after abandonment (B). Circled numbers (yellow) – sample plots from 2020 (Vegi1–Vegi5); forest compartments (white numbers in italic): 1 – mature oak forest (random sample plots from 2003–2020), 2 – medium-aged aspen stand, 3 – medium-aged Scots pine-juniper stand (overgrowing semi-natural grassland), 4 – medium-aged Scots pine stand. The numbers of sample plots in Table 2 (results) are as follows: Vegi1 = 66, Vegi2 = 67, Vegi3 = 68, Vegi4 = 69, Vegi5 = 70; the others were randomly located in forest compartment 1. Background: orthophoto map by the Latvian Geospatial Information Agency, 1994 and 2019.

leys, often Devonian carbonatic bedrock, such as dolomite and dolomitic marlstone, may be exposed or lies close to the soil surface (Eberhards, 2013; Krievāns *et al.*, 2018). The Abava River Valley with its tributaries are among the few examples in West Latvia, where carbonatic bedrocks are exposed, which occur in a ca. 30-km long stretch between Kandava and Renda. In this stretch, the depth of the valley reaches up to 58 m, and dolomite is exposed or lies close to the soil surface on the terraced valley slopes.

The Abava River is a 134-km long medium-sized river. At its lower and upper reaches, the river valley is less pronounced, with gentle slopes, while the middle stretch of the valley has relatively steep, terraced slopes (relative height 30–58 m), oriented in an east-west direction. The valley was eroded in the pre-Quaternary period, and the slopes are formed by carbonatic rocks (dolomite, dolomitic marlstone, sandstone, carbonatic deposits with clay layers, etc.) exposed as cliffs in a few sites, but mostly covered with a shallow soil layer. On the slopes and terraces, the soils are eroded, rich in carbonates, shallow, laying on dolomite or dolomitic marlstone (Stinkulis and Sinkule, 2013; Strautnieks, 2020). This type of soil occurred also in the study area.

The shallow, carbonatic soils on dolomite and dolomitic marlstone and local climate have played important roles in the development of the particular flora and vegetation in the Abava Valley (Tabaka and Klavina, 1981; Priede, 2009). The dry, carbonatic soils host xeric calcareous plant communities, such as semi-natural grasslands with *Filipendula vulgaris*, *Helictotrichon pratensis*, and *Astragalus danicus*; forest fringe plant communities with *Geranium sanguineum*, *Laserpitium latifolium*, and *Origanum vulgare*; scrubs with *Juniperus communis*, *Corylus avellana*, *Rhamnus cathartica*, *Berberis vulgaris*, and *Prunus institia*; coniferous forests with *Pinus sylvestris*, *Brachypodium pinnatum*, *Festuca ovina*, *F. trachyphylla*, and *Primula veris*; and deciduous broadleaved forests with *Quercus robur*, *Lathyrus niger*, *Viola mirabilis*, and *Convallaria majalis*. In some areas with discharge of carbonate-rich groundwater, alkaline fens with *Schoenus ferrugineus* and *Carex davalliana* have developed (Tabaka and Klavina, 1981; Rūsiņa, 2007).

In the Abava Valley, the xeric calcareous plant communities (semi-natural grasslands, forests, and intermediate scrub facies) cover relatively small areas. Their mosaic-type spatial pattern is influenced by land use and land use intensity in the past; they represent various stages of succession. The transition zones between various succession stages are usually gradual, and therefore many of the characteristic species occur at different succession stages, thus forming a syntaxonomic continuum. The total number of plant species that form various communities is related to the succession stage and the mutual spatial and temporal relation with other phytocoenoses.

The river valley near Veģi, the study area, is 40 m in depth and asymmetric, as the relative height of the south-facing slope is larger in comparison to the gentler, lower north-facing slope (Krievāns *et al.*, 2018; Strautnieks, 2020). The study area (ca. 3 ha) is located on the upper part of the south-facing valley slope on dolomite rock close to the soil surface (50–60 cm below the soil surface, with 20–30% admixture of dolomite and dolomitic marlstone pebbles in the topsoil). At the study area, the slope inclination varies from 7 to 9 degrees, and exposition is 180 degrees. The altitude of the study area varies between 58 and 64 m a. s. l.

The climate in the region is relatively mild and moist with an average annual temperature of +6.3 °C (here and further the climate data from the period 1981–2021 are summarised from the nearest meteorological station in Stende, 7 km from the study area). The coldest month is February with –3.3 °C on average; the average temperature in July is +16.9 °C. The annual precipitation sum is 724 mm. The vegetation period is about 196 days (Briede, 2018). Overall, the micro-climate in the valley is more continental than in the surrounding areas. The south-facing slopes (including Veģi site) are more exposed to solar radiation and receive a larger amount of light and warmth than the north-facing slopes. On the slopes, there is increased runoff, enhanced moisture deficit in the soils and increased evaporation. The air temperatures tend to be lower on the valley floor and are higher in the upper part of the slopes; the difference in tem-

peratures can be even 7–8 °C (Temnikova, 1958; Strautnieks, 2020).

The valley is distinct with mosaic-type landscapes, richness of flora, especially flora related to dry calcareous grassland communities, thermophilous forest fringe and deciduous broad-leaved forest plant communities occurring on the slopes, terraces and floodplain of the valley (Tabaka and Klavina, 1981; Rūsiņa, 2007).

The study area (Fig. 1) represents a series of vegetation succession: (1) abandoned semi-natural xeric grassland partly overgrown with secondary, sparse tree cover dominated by common juniper *Juniperus communis* and Scots pine *Pinus sylvestris*; (2) young to medium-aged woodlands dominated by *Pinus sylvestris* and aspen *Populus tremula*; and (3) mature pedunculate oak *Quercus robur* forest.

The history of land use in the study site is not known in detail but can be partly reconstructed by “reading the landscape” and combining it with general knowledge on the land use history in Latvia and in the particular region and maps. The topographic maps of the early and mid-20th century depict the current oak forest patch in its contemporary borders. The grassland area may have been used as a hay meadow and pasture in the past (indicated by some residual fence fragments found during the fieldwork). It is highly probable that, similar to the common practice in the early 20th century Latvia (Lazdiņš, 1939; Dumpe, 1999), 80–100 years ago, the oak forest was grazed. Later, the grazing practice may have ceased; still, the forest may have been used for fuelwood collecting (e.g., removal of deadwood and fallen branches). Management of the grassland ceased at least 30 years ago.

According to the National Forest Register (State Forest Service, Latvia), the age of the oak forest is 135 years (in fact, it is older as shown further by our study results), whereas the younger forest on the transitional zone between the overgrowing grassland and the old-growth oak stand varies from 45 (aspen stand) to 65 (pine stand) years (Figure 1).

Vegetation sampling. In the study area, there are young forest stages of various age (< 100 years), in a mosaic with open grassland patches and a mature forest with *Quercus robur*. To characterise the succession stages from open grassland to oak forest, in June 2020 a transect with five sample plots was established (Vegi1, Vegi2, Vegi3, Vegi4, Vegi5) (Fig. 1). Four sample plots (Vegi1–Vegi4) were established in the young pine forest: circle-shaped plots with radius 10.0 m, area 314.0 m²; in the oak forest — a circle-shaped plot (Vegi5) with radius 15.0 m (area 706.5 m²). Different plot sizes were used to cover the diversity of spatial structures in the forest stand. The forest stand structure of younger forest stages typical for the area could be covered by a smaller plot size (314.0 m²) that provides more precise estimation of the cover of vegetation in all layers and individual species. A larger plot size (706.5 m²) was chosen to include a sufficient number of mature oaks, which

is essential to understand the spatial structure of the forest; otherwise the smaller size plots would include only 2–3 trees. Although usually in larger plots the accuracy of vegetation cover assessment is lower than in smaller plots, this was chosen as a compromise to be able to estimate the vegetation structure in all layers. The plot sizes were also defined by the size of the study area, i.e., the transect across the young forest stage did not exceed 200 m and included a series of succession stages that could not be well represented by larger sample plots, i.e., it was important to avoid partial overlapping of sample plots. The centre of each plot was marked with a wooden pole (1 m tall, diameter 5–10 cm).

All plant species and their cover (%) were recorded in each layer (E3 – trees, E2 – shrubs, E1 – herbs, E0 – bryophytes) (Dierschke, 1994). The cover was estimated visually by experienced surveyors.

To characterise the quasi-climax oak forest community, we used relevés from earlier years (2003–2010) from the same site, in total 15 (Fig. 1). Here, the vegetation was described using randomly located sample plots with sizes varying from 350 to 700 m² (the size for each plot is given in Table 2) and using the same vegetation recording method as described above. In contrast to the five above mentioned plots from 2020 (Vegi1–Vegi4), in the earlier sampled plots only vegetation was recorded, but no measurements of tree dimensions, annual rings or spatial distribution were done.

The nomenclature of taxa follows Gavrilova and Šulcs (1999) for vascular plants, Āboliņa *et al.* (2016) for mosses. The nomenclature of vegetation syntaxa follows regional vegetation reviews: Mucina *et al.* (1993), Rūsiņa (2003, 2007), Wilner and Grabherr (2007), Chytrý and Tichý (2008), Chytrý (ed.) (2013).

Measurements of tree dimensions, spatial pattern of trees and annual rings. In each sample plot within the transect Vegi1–Vegi5, each tree taller than 3 m (in the young pine forest) or 5 m (in the mature oak forest) was marked with a unique number. For each marked tree the following parameters were recorded:

- Diameter at breast height 1.30 m (measured using Hultafors Talmeter 3 m);
- The height of trees (measured using Vertex IV, Haglöf Sweden);
- Wood cores from each living tree within the sample plots Vegi1–Vegi5 were taken using a Presler border for analysis of annual rings and annual increment; the radial growth was measured using *LINTAB IV*, and data were processed by TSAP Win Scientific 0.55 and MS Excel software;
- The distance of each tree and its azimuth from the plot centre were measured using a Vertex IV and a Suunto compass. For each tree, considering its location within the sample plot, the nearest neighbour index (NNI) was

used. NNI is a tool to measure precisely the spatial distribution of a pattern and see if it is regular, random or clustered (intermediate patterns are possible). The distance to the nearest neighbour of each tree within the plot was measured using *ArcView 9.0* software. Then, the distribution of distances was tested using the z-score. At a 95% confidence level, a z-score within the interval –1.96 to 1.96 confirms the null hypothesis, i.e., the spatial distribution is random. If the z-score is > 1.96, the spatial pattern is regular, and if the z-score is < –1.96, the spatial distribution is clustered (Liepa, 1974).

Soil sampling and analysis. Soil was sampled from each of the transect plots Vegi1–Vegi5, but not in the earlier recorded relevés plots from 2003–2010. In the mature oak forest, the soil samples were collected only in Vegi5, as other sample plots were very similar to each other in vegetation pattern and composition. The soil data from Vegi5 were further extrapolated to the entire oak forest stand in the study area. The soil was taken at the depth of 1–15 cm and 15–30 cm (three sub-samples at each depth) and a mixed sample from each plot. The fine earth fraction of soils ($D < 2$ mm) was used for chemical analysis. Soil exchangeable acidity (pH) was determined using potassium chloride (1 M), the contents of adsorbed bases and base saturation was determined in 0.1 M hydrochloric acid solution using titrimetry, calcium (Ca), magnesium (Mg), potassium (K), iron (Fe) and manganese (Mn) was determined in 0.1 M hydrochloric acid solution using atomic emission or absorption spectroscopy.

During the fieldwork, all soil depths were examined by applying hydrochloric acid 10% HCl to detect the presence of free carbonates. Free carbonates were used as an additional indicator in characterisation of the soils.

Data analysis. The vegetation data were entered into the Turboveg database (Hennekens and Schaminée, 2001) and then exported for further analysis. The relevés were analysed using two-way cluster analysis in PC-ORD 6.0, and the clusters were distinguished using the flexible beta method, where the beta value was –0.25 (McCune and Mefford, 2002; 2011). To compare the similarity of relevés using plant cover as an indicator, the Sørensen coefficient was calculated.

Detrended Correspondence Analysis (DCA) (PC-ORD 6.0; McCune and Mefford, 2002; 2011) was applied (rescaling the axes without downweighting rare species). In detrending by segments the default option (26 segments) was applied. Kendall correlation coefficients between the environmental variables and the DCA Axes 1 and Axis 2 were calculated and used for descriptive purposes.

Vegetation data (20 relevés) were used as the first matrix, the Ellenberg indicator values (light, temperature, continentality, moisture, reaction, nitrogen) for Central Europe (Ellenberg *et al.*, 1992) were used as the second data matrix in the DCA ordination. Weighted averages of all indicator

values were calculated with weights determined by the abundance of each species in the relevé.

To analyse the mean values for each sample plot, standard error and standard deviation were calculated, and the confidence level of the variation among the sample plots was tested using t-test (MS Excel, Data Analysis tool).

RESULTS

Physical and chemical properties of soil. The physical and chemical properties of soil in the study area were characterised by granulometric composition, soil exchangeable acidity, base saturation, organic matter, and total nitrogen and macroelement concentration in two topsoil horizons (at the depth up to 15 cm and at depth of 15–30 cm). The variation in physical and chemical properties at all five soil sampling sites (Vegi1–Vegi5) was negligible (Table 1).

The examined soil layer contained three particle size fractions: medium sand (28.5–31.3%), fine and very fine sand (26.0–26.5%), and silt (30.0–30.6%). The topsoil (1–15 cm) had a higher proportion of medium sand than in the deeper layer (15–30 cm). However, it contained a lower proportion of large sand particles and clay particles indicating the intensity of dolomite weathering. There were equally high contents of very fine and fine sand and silt contents in the topsoil, while their proportion was lower at the deeper soil layer.

In both layers, the soil pH was weakly acidic (nearly neutral), the soil was highly saturated with exchangeable cations, rich in organic matter and with high total nitrogen content. The decomposition of organic matter and its turnover in the soil was intense (C/N was 15–18); accumulation of organic matter was not detected. The soil had high concentration of K, Ca, Mg. Increased concentration of K was found in the soil up to 15 cm depth where the plants have more significant role in its turnover, while the concentration of Ca and Mg was higher in the deeper layer close to the dolomite bedrock (Table 1). During the field studies, the application of hydrochloric acid 10% HCl caused low foam or little bubbling indicating the presence of carbonates. The soil contained a large concentration of Fe and Mn that may be related to a large amount of both elements in the bedrock.

Plant communities. The cluster analysis of 20 relevés resulted into three distinct groups that were named after the characteristic species: (1) *Filipendula vulgaris*-*Pinus sylvestris* community; (2) *Lathyrus niger*-*Quercus robur* community, and (3) *Corylus avellana* community. The description of the location of each sample plot, the main parameters of each vegetation layer and the covers are given in Table 2.

The DCA ordination (Fig. 2) shows a clear distinction of the above mentioned three plant community groups. The spatial pattern of the relevés in the ordination space is determined primarily by Axis 1 (eigenvalue = 0.82), with less explained variation of Axis 2 (eigenvalue = 0.20). The

Table 1. Granulometric fractions, physical and chemical properties of soil along the transect Vegi1–Vegi5

Soil parameters	Unit	Depth, cm	
		1–15	15–30
Soil texture	mm, %		
Coarse and very coarse sand	0.63–2.00	8.8 ± 0.4	9.8 ± 0.8
Medium sand	0.20–0.63	31.3 ± 1.8	28.5 ± 1.2
Fine and very fine sand	0.063–0.200	26.0 ± 0.6	26.5 ± 1.1
Silt	0.002–0.063	30.0 ± 2.4	30.6 ± 1.8
Clay	< 0.002	3.9 ± 0.3	4.6 ± 0.7
Acidity, carbon and nitrogen			
Exchangeable acidity, pH _{KCl}		6.5 ± 0.3	6.8 ± 0.1
Exchangeable bases	cmol·kg ⁻¹	49.5 ± 0.8	39.8 ± 7.7
Base saturation	%	97 ± 1	93 ± 4
Organic carbon, C _{org}	g·kg ⁻¹	38.1 ± 4.3	27.3 ± 7.7
Total nitrogen, N _{tot}	g·kg ⁻¹	2.1 ± 0.3	1.4 ± 0.2
C/N		18.1 ± 0.7	15.6 ± 3.2
Macroelements			
K	mg·kg ⁻¹	192 ± 12	113 ± 11
Mg	mg·kg ⁻¹	5854 ± 1470	8400 ± 3352
Ca	mg·kg ⁻¹	12543 ± 2875	17411 ± 6937
Fe	mg·kg ⁻¹	1178 ± 122	1074 ± 190
Mn	mg·kg ⁻¹	654 ± 121	840 ± 101

Fig. 2. DCA ordination of vegetation relevés. Abbreviations: L, light; T, temperature; C, continentality; M, moisture; N, nitrogen (Ellenberg indicator values). The numbers of relevés are given as in Table 2.

quasi-climax oak forest relevés occur in the lower left corner, while the relevés representing *Corylus avellana* community — at the upper left side of the ordination graph. The relevés of young forest pine forest stage and juniper facies occur on the right side. The groups are quite well distinguishable with a poorly pronounced intermediate stage that may be related to land use history, as suggested by the tree ages (see Discussion).

Table 2. Plant communities at the study site. The IDs of sample plots Vegi1–Vegi5 are modified to the numbers in the database, i.e., Vegi1 = 66, Vegi2 = 67, Vegi3 = 68, Vegi4 = 69, Vegi5 = 70

Species/Syntaxa	Layer	Plant communities																						
		Filipendula vulgaris-Pinus sylvestris community						Lathyrus niger-Quercus robur community										Corylus avellana community						
Relevé number		1	2	3	4	5	Frequency, %	6	7	8	9	10	11	12	13	14	15	Frequency, %	16	17	18	19	20	Frequency, %
Relevé number in data base		66	67	68	23	69		24	25	70	29	39	36	34	41	35	40		26	27	38	37	30	
Cover tree layer (%)		6	40	75	55	90	90	55	55	70	65	80	70	60	60	65	0	5	0	0	0			
Cover shrub layer (%)		5	20	10	15	5	30	30	80	45	70	65	65	60	60	90	85	90	95	95	90			
Cover herb layer (%)		99	80	80	75	40	65	65	40	55	70	35	75	70	70	50	70	55	40	20	65			
Cover moss layer (%)		0	20	70	5	10	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0			
Relevč area, m2		314	314	314	350	314	425	350	700	400	400	350	300	400	400	400	400	400	400	400	400			
Aspect, degrees		210	180	170	180	180	170	170	180	190	180	180	110	80	180	180	90	150	180	180	.			
Number of species		42	39	43	52	41	33	21	35	30	27	25	23	24	23	28	13	13	15	16	28			
Cl. Festuco-Brometea Br.-Bl et Tx. ex Soo 1947, All. Filipendulo vulgaris-Helictotrichon pratensis Dengler et Lobel in Dengler et al. 2003																								
Filipendula vulgaris	E1	20	15	6	5	+	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Carex flacca	E1	4	2	4	10	5	100	1	.	.	.	.	.	+	.	.	.	20	.	.	.	.	.	
Helictotrichon pratense	E1	25	8	6	3	+	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Galium boreale	E1	7	1	5	1	+	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Knautia arvensis	E1	+	.	2	+	+	80	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Brachypodium pinnatum	E1	.	12	10	8	15	80	.	.	.	.	+	.	.	.	.	.	10	.	.	.	.	.	
Pimpinella saxifraga	E1	+	3	1	.	.	60	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Inula salicina	E1	8	2	.	+	.	60	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Briza media	E1	10	5	.	+	.	60	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Daucus carota	E1	4	+	.	.	.	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Fragaria viridis	E1	3	+	.	.	.	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Carlina vulgaris	E1	1	3	.	.	.	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Leontodon hispidus	E1	+	+	.	.	.	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Poa angustifolia	E1	+	.	.	1	.	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Plantago lanceolata	E1	+	.	.	+	.	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Cirsium acaule	E1	.	5	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Sesleria caerulea	E1	.	.	.	1	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Viola hirta	E1	.	.	.	+	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Cl. Trifolio-Geranietea T. Muller 1962, All. Geranion sanguinei Tx. in T. Muller 1962																								
Origanum vulgare	E1	12	4	3	2	+	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Agrimonia eupatoria	E1	6	18	+	3	4	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Calamagrostis epigeios	E1	7	3	2	8	1	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Geranium sanguineum	E1	.	10	5	1	+	80	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Ranunculus polyanthemos	E1	+	.	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Astragalus glycyphyllos	E1	.	+	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Cl. Quercetea pubescentis Doing-Kraft ex Scamoni et Passarge 1959, All. Quercion pubescenti-petraeae Br.-Bl. nrm. mut.																								
Veronica teucrium	E1	5	3	1	1	+	100	.	.	.	.	+	.	.	.	.	.	10	.	.	.	.	.	
Rhamnus cathartica	E2	+	2	+	.	+	80	+	.	+	.	.	.	.	.	.	.	20	.	.	.	.	.	
Campanula persicifolia	E1	+	.	+	+	.	60	+	.	.	+	+	.	.	.	+	.	30	.	.	.	.	+	
Clinopodium vulgare	E1	+	1	.	1	.	60	.	.	.	.	.	.	.	.	.	+	10	.	.	.	.	.	
Laserpitium latifolium	E1	.	.	18	5	10	60	7	.	.	.	.	.	.	+	.	+	30	.	.	.	.	+	
Ligustrum vulgare	E2	1	5	.	.	.	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Melica nutans	E1	.	.	.	4	.	20	4	+	+	.	6	2	.	+	+	.	70	.	.	.	.	2	
Crataegus curvisepala	E2	+	.	.	.	.	20	.	+	2	.	.	.	+	+	+	.	50	.	.	.	.	.	
Rosa rubiginosa	E2	.	1	.	.	+	20	.	+	+	.	.	.	.	.	.	.	20	.	.	.	.	+	
Berberis vulgaris	E2	+	.	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Asoc. Lathyro nigri-Quercetum roboris Bulokhov et Solomechsh 2003 in Bulokhov et Solomechsh 2003																								
Viola mirabilis	E1	.	.	.	+	1	40	4	2	1	6	4	4	+	4	2	5	100	3	5	6	.	+	
Lathyrus niger	E1	.	.	8	1	1	60	4	+	2	+	8	2	1	+	3	2	100	.	.	.	.	3	
Primula veris	E1	3	8	5	6	2	100	4	.	+	8	4	6	.	.	.	2	60	.	.	.	.	+	
Convallaria majalis	E1	.	.	.	.	.	.	8	35	25	.	.	.	25	20	25	3	60	.	.	.	.	.	
Carex montana	E1	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	20	.	.	.	.	.	
Anemone nemorosa	E1	.	.	.	2	.	20	10	20	3	10	.	+	10	7	8	8	90	20	40	10	5	.	
Viburnum opulus	E2	.	+	.	.	+	40	+	.	1	.	+	+	+	+	+	+	80	.	+	+	+	+	
Tilia cordata	E3	.	.	.	.	.	.	.	.	.	5	5	.	5	5	.	.	40	.	.	.	.	.	
Tilia cordata	E2	.	.	.	.	.	.	.	.	.	3	5	2	+	5	.	+	60	+	+	+	.	.	
Paris quadrifolia	E1	.	.	.	.	.	.	3	+	+	+	+	.	.	.	+	60	2	+	+	+	+		
Aegopodium podagraria	E1	.	.	.	15	1	40	6	.	.	+	5	3	.	+	.	+	60	.	.	.	.	20	
Carex digitata	E1	.	.	.	.	+	20	+	.	+	+	.	+	.	.	+	+	60	.	.	.	.	.	
Euonymus europaea	E2	.	.	+	.	.	20	.	.	.	+	+	+	+	1	.	.	50	.	.	.	+	.	
Malus sylvestris	E3	.	.	.	.	5	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Malus sylvestris	E2	.	.	.	+	.	20	+	+	.	+	+	.	.	+	.	.	50	.	.	.	+	.	
Ranunculus cassubicus	E1	.	.	.	.	.	.	1	.	.	.	.	+	+	.	+	1	50	+	.	+	.	.	
Brachypodium sylvaticum	E1	.	.	.	.	.	.	.	.	.	+	8	4	.	.	1	.	40	.	.	.	1	2	
Galeobdolon luteum	E1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	.	10	.	.	.	.	8	
Geum urbanum	E1	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	10	+	+	+	+	+	
Daphne mezereum	E2	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	10	.	.	+	.	.	
Poa nemoralis	E1	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	10	.	.	.	.	.	
Lathyrus vernus	E1	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	10	.	.	.	.	.	
Actaea spicata	E1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	.	.	.	.	.	
Scrophularia nodosa	E1	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	10	.	.	.	.	.	

Table 2 (continued)

Species/Syntaxa	Layer	Plant communities																						
		<i>Filipendula vulgaris</i> - <i>Pinus sylvestris</i> community						Lathyrus niger- <i>Quercus robur</i> community										<i>Corylus avellana</i> community						
Relevé number		1	2	3	4	5	Frequency, %	6	7	8	9	10	11	12	13	14	15	Frequency, %	16	17	18	19	20	Frequency, %
Relevé number in data base		66	67	68	23	69		24	25	70	29	39	36	34	41	35	40		26	27	38	37	30	
Cover tree layer (%)		6	40	75	55	90		90	55	55	70	65	80	70	60	60	65		0	5	0	0	0	
Cover shrub layer (%)		5	20	10	15	5		30	30	80	45	70	65	65	60	60	90		85	90	95	95	90	
Cover herb layer (%)		99	80	80	75	40		65	65	40	55	70	35	75	70	70	50		70	55	40	20	65	
Cover moss layer (%)		0	20	70	5	10		1	0	0	0	0	1	0	0	1	1		0	0	0	0	0	
Relevé area, m2		314	314	314	350	314		425	350	700	400	400	350	300	400	400	400		400	400	400	400	400	
Aspect, degrees		210	180	170	180	180		170	170	180	190	180	180	110	80	180	180		90	150	180	180	.	
Number of species		42	39	43	52	41		33	21	35	30	27	25	23	24	23	28		13	13	15	16	28	
<i>Polygonatum multiflorum</i>	E1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	20	
<i>Lonicera xylosteum</i>	E2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	20	
<i>Pulmonaria obscura</i>	E1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	20	
<i>Cerasus avium</i>	E2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	20	
<i>Asarum europaeum</i>	E2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	20	
Other species																								
<i>Pinus sylvestris</i>	E3	6	40	60	20	40	100	+	.	5	.	.	.	5	+	.	.	40	.	.	.	.	.	.
<i>Pinus sylvestris</i>	E2	2	+	.	.	.	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Pinus sylvestris</i>	E1	.	+	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Juniperus communis</i>	E2	3	15	6	4	+	100	2	.	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.
<i>Juniperus communis</i>	E3	.	+	1	.	.	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Quercus robur</i>	E3	+	.	.	.	15	40	80	55	45	65	65	80	65	60	60	65	100	.	.	+	.	.	20
<i>Quercus robur</i>	E2	+	.	1	2	1	80	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	20
<i>Quercus robur</i>	E1	.	+	+	2	+	80	.	.	+	.	.	.	.	.	.	.	10	.	.	+	.	.	20
<i>Corylus avellana</i>	E2	.	.	+	8	3	60	25	25	25	35	60	60	65	50	55	65	100	85	90	90	95	85	100
<i>Sorbus aucuparia</i>	E2	.	+	+	+	2	80	.	+	+	5	3	1	+	+	+	+	90	.	.	+	.	1	40
<i>Padus avium</i>	E2	.	.	.	.	+	20	.	3	10	+	.	.	+	.	.	.	40	10	15	5	+	5	100
<i>Picea abies</i>	E2	.	.	.	2	+	40	2	2	+	+	+	.	+	+	.	+	80	.	.	.	.	.	.
<i>Picea abies</i>	E3	.	.	15	.	+	20	+	3	10	.	.	.	.	.	.	+	40	.	.	.	.	.	.
<i>Populus tremula</i>	E3	.	.	.	30	30	40	10	+	5	.	.	.	.	.	.	.	30	.	.	.	.	.	.
<i>Populus tremula</i>	E2	.	.	.	1	1	40	.	.	+	.	.	.	.	.	.	.	10	.	.	.	.	.	.
<i>Populus tremula</i>	E1	.	.	.	.	2	20	.	.	+	.	.	.	.	.	.	.	10	.	.	.	.	.	.
<i>Fraxinus excelsior</i>	E2	.	.	+	.	+	40	.	.	.	.	+	.	.	.	+	.	20	.	.	.	.	.	.
<i>Acer platanoides</i>	E2	.	.	+	.	.	20	.	.	+	+	.	.	+	1	+	+	60	.	+	.	.	.	20
<i>Acer platanoides</i>	E1	.	.	.	+	.	20	.	.	+	.	.	.	.	.	.	+	20	.	.	.	.	.	.
<i>Betula pendula</i>	E3	.	.	.	5	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Frangula alnus</i>	E2	.	+	.	+	.	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Ulmus glabra</i>	E2	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	10	.	.	.	.	+	20
<i>Ulmus glabra</i>	E1	.	.	+	.	+	40	.	.	+	.	.	.	.	.	.	.	10	.	.	.	.	.	.
<i>Geranium sylvaticum</i>	E1	.	.	.	.	.	.	1	+	1	.	3	1	2	5	1	2	90	.	.	+	.	3	40
<i>Chaerophyllum aromaticum</i>	E1	.	.	.	.	.	.	2	.	.	+	4	.	+	.	+	1	60	.	.	.	1	+	40
<i>Calamagrostis arundinacea</i>	E1	.	.	.	.	.	.	.	2	1	.	.	.	.	.	3	+	40	.	.	.	.	.	.
<i>Rubus saxatilis</i>	E1	.	.	.	.	.	.	+	.	+	.	.	.	+	+	.	.	40	.	.	.	.	.	.
<i>Maianthemum bifolium</i>	E1	.	.	.	.	.	20	.	+	.	1	.	.	+	.	.	+	40	.	.	.	.	.	.
<i>Ranunculus acris</i>	E1	.	.	.	+	.	20	.	.	.	+	+	+	.	.	.	+	40	.	.	.	.	.	.
<i>Pteridium aquilinum</i>	E1	.	.	.	2	.	20	2	.	.	+	.	+	.	+	.	.	40	.	.	.	+	.	20
<i>Melampyrum nemorosum</i>	E1	.	.	.	3	.	20	3	.	.	6	.	3	.	.	.	.	30	.	.	.	.	15	20
<i>Taraxacum officinale</i>	E1	.	.	.	+	.	20	.	.	+	.	.	.	.	.	.	.	20	.	.	.	+	+	40
<i>Luzula pilosa</i>	E1	.	.	.	+	.	20	+	.	.	.	.	.	.	.	.	+	20	.	.	.	.	.	.
<i>Solidago virgaurea</i>	E1	.	.	1	.	+	40	.	.	+	.	+	.	.	.	.	.	20	.	.	.	.	.	.
<i>Veronica chamaedrys</i>	E1	.	.	.	2	+	40	.	.	.	+	.	.	.	.	.	.	10	.	.	.	.	+	20
<i>Rhytidadelphus triquetrus</i>	E0	.	10	20	5	10	80	1	.	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.
<i>Fragaria vesca</i>	E1	.	.	2	3	3	60	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Galium album</i>	E1	2	+	1	3	1	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Dactylis glomerata</i>	E1	+	+	+	1	+	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Leucanthemum vulgare</i>	E1	+	1	+	.	.	60	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Vicia cracca</i>	E1	1	+	+	.	.	60	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Scorzonera humilis</i>	E1	.	.	+	.	1	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Brachythecium albicans</i>	E0	.	10	1	.	.	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Scleropodium purum</i>	E0	.	.	50	.	+	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Eurhynchium hians</i>	E0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	20	.	.	.	.	.	.
<i>Fragaria moschata</i>	E1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	10	+	+	.	.	.	40

Rare species:

Tree layer: *Alnus incana* 5(17); shrub layer: *Cerasus vulgaris* 4(3), *Ribes spicatum* +(8), +(9), *Alnus incana* +(17), +(19); herb layer: *Convolvulus arvensis* +(1), 1(2), *Lathyrus pratensis* +(1), *Centaurea jacea* 2(1), *Medicago lupulina* 2(1), *Silene vulgaris* 1(1), *Senecio jacobaea* +(1), *Phleum pratense* +(1), *Potentilla reptans* +(1), *Prunella vulgaris* +(2), *Agrostis tenuis* +(2), *Melampyrum polonicum* 1(3), +(5), *Leontodon autumnalis* +(3), *Ophioglossum vulgatum* 6(4), *Vicia sepium* 1(4), *Festuca pratensis* +(4), *Helictotrichon pubescens* +(4), *Ononis arvensis* +(4), *Carex hirta* +(6), *Rubus idaeus* +(7), +(20), *Hieracium vulgatum* +(8), *Carex contigua* +(8), *Rubus caesius* +(9), *Deschampsia cespitosa* +(10), +(15), *Melandrium dioicum* +(10), *Carex vaginata* +(11), *Stellaria media* +(11), *Anemone ranunculoides* 5(16), *Allium oleraceum* 1(19).

Among the environmental variables used in the ordination, continentality, moisture and nitrogen appeared to be the most significant (the tightest correlation with the axes), while others were of lower importance (Table 3). The young forest stage with pines and junipers had the highest proportion of light demanding continental and subcontinental grassland and forest edge species, while mature forest community was composed of shade tolerant species. Not surprisingly, the moisture and nutrient levels were higher in the mature forest stage than in the young forest stage. The number of species was higher in the young forest stage that follows semi-open xeric grassland (see also Table 2).

The number of character species of various phytosociological classes varied at different succession stages (Fig. 3).

The succession of semi-natural xeric calcareous grassland toward formation of mature oak forest was represented by five sample plots located in a transect across a representative area. The first three sample plots (Vegi1–Vegi3) represented young overgrowing stages with pine at the age of 10 to 25 years, while Vegi5 represented the quasi-climax succession stage with more than 200-year-old oak forest. The 40-year-old pine stand (Vegi4) represented the transition from medium-aged pine forest at the oak forest edge to mature oak forest.

At the youngest forest stage, 10- to 15-year-old pine stand, species of Festuco-Brometea grasslands dominated. In the 25-year-old pine stand the number of Festuco-Brometea species decreased by 2.3 times. The most resistant grassland species during the pine and juniper encroachment are *Filipendula vulgaris*, *Helictotrichon pratensis* and *Carex flacca* (frequency 60%). In the 40-year-old stand, there was high

Table 3. Kendall correlation coefficients of the DCA axes with the means of Ellenberg indicator values. Correlation coefficients > 0.50 are given in bold

Variables	DCA Axis 1	DCA Axis 2
Light (L)	0.607	–0.301
T (temperature)	0.127	–0.434
C (continentality)	0.758	–0.379
M (moisture)	–0.340	0.681
R (soil pH)	–0.358	–0.021
N (nitrogen)	–0.554	0.354
Number of species	0.759	–0.122

Fig. 3. Number of diagnostic species of phytosociological classes at various succession stages in the sample plots Vegi1–Vegi5.

occurrence of Trifolio-Geranieta species, from which *Geranium sanguineum*, *Origanum vulgare*, *Agrimonia eupatoria* and *Calamagrostis epigeios* were the most frequent (frequency 60%). In the mature oak forest, the species of Festuco-Brometea were absent.

The number of character species of thermophilous oak forests (*Quercetea pubescentis*) and suboceanic and subcontinental thermophilous scrub (the early stages of thermophilous oak forests) at various age of pine stands and the mature oak forest was relatively constant and, within the distinguished succession stages, varied from 4 to 7 species. The number of species in the overgrowing grassland (young pine stand) and forest fringe communities was similar. The most frequent species (frequency > 60%) were *Rhamnus cathartica*, *Veronica teucrium* and *Campanula persicifolia*.

At the same time, there was a reverse pattern of the character species of the class *Carpino-Fagetea sylvaticae* — they are almost absent in the young, 10-year-old and 14-year-old pine stands (Vegi1, where only one species (*Viburnum opulus*) was found, and Vegi2). Only two species of *Carpino-Fagetea sylvaticae* (*Hepatica nobilis* and *Euonymus europaeus*) were found in the 25-year-old stand (Vegi3). The most frequent diagnostic species of the class *Carpino-Fagetea sylvaticae* were *Mercurialis perennis*, *Hepatica nobilis*, *Anemone nemorosa* and *Tilia cordata* (frequency > 60%).

In the 40-year-old pine stand with an admixture of oaks (Vegi4), the number of diagnostic species of each represented phytosociological class varied from 4 to 6. This means that in the transition zone between the young pine forest and mature oak forest all vegetation classes found in the study site were equally represented (xeric calcareous grassland, thermophilous forest fringe, thermophilous oak forest, and mesic hornbeam-beech forest).

Remarkably, in the transition zone, in the pine-oak stand (Vegi4), there was a high admixture of *Populus tremula*, a species that is more suitable for a local climate with a high continentality degree, rather than widespread woody pioneer species of mesic conditions, such as *Betula pendula* and *Alnus incana*.

Fig. 4. Mean age of pine (with standard deviation) at various succession stages in the sample plots Vegi1–Vegi5.

Table 4. Parameters characterising each forest succession stage (sample plots Vegi1–Vegi5)

Woody species	Parameters	Sample plots				
		Vegi1	Vegi2	Vegi3	Vegi4	Vegi5
<i>Pinus sylvestris</i>	Ind/ha	701	540	1210	287	28
	Age, year	10 ± 1	14 ± 1	25 ± 1	40 ± 3	64 ± 3
	D, cm_mean	9.1 ± 0.7	10.7 ± 1.2	13.0 ± 1.2	31.0 ± 3.4	26.4 ± 6.1
	H, m_mean	5.0 ± 0.3	7.0 ± 0.5	11.7 ± 0.7	18.8 ± 1.5	18.6 ± 4.5
	S, m ² /ha	5.2	5.9	20.9	23.6	1.6
	V, m ³ /ha	17.6	26.7	152.9	223.4	15.6
<i>Juniperus communis</i>	Ind/ha		414	318		
	Age, year		24 ± 3	25 ± 2		
	D, cm_mean		4.90 ± 0.5	5.7 ± 0.6		
	H, m_mean		4.2 ± 0.3	4.7 ± 0.1		
	S, m ² /ha		0.9	0.9		
	V, m ³ /ha		3.1	3.1		
<i>Quercus robur</i>	Ind/ha	32			191	170
	Age, year	29			30 ± 2	203 ± 6
	D, cm_mean	10.1			8.5 ± 1.5	53.3 ± 5.6
	H, m_mean	4.6			8.1 ± 1.2	21.9 ± 1.5
	S, m ² /ha	0.3			1.3	42.5
	V, m ³ /ha	0.9			7.1	493.1
<i>Picea abies</i>	Ind/ha			159	64	99
	Age, year			20 ± 1	19	65 ± 9
	D, cm_mean			9.6 ± 2.2	5.2	12.3 ± 3.2
	H, m_mean			8.7 ± 1.7	4.6	10.2 ± 2.6
	S, m ² /ha			1.3	0.1	1.7
	V, m ³ /ha			7.6	0.3	13.6
<i>Populus tremula</i>	Ind/ha				541	14
	Age, year				25 ± 1	40
	D, cm_mean				6.9 ± 0.4	12.1 ± 2.9
	H, m_mean				9.3 ± 0.6	15.3 ± 4.2
	S, m ² /ha				2.1	0.2
	V, m ³ /ha				11.2	1.2
<i>Malus sylvestris</i>	Ind/ha				159	
	Age, year				17 ± 1	
	D, cm_mean				5.7 ± 0.6	
	H, m_mean				5.5 ± 0.9	
	S, m ² /ha				0.4	
	V, m ³ /ha				1.4	
<i>Sorbus aucuparia</i>	Ind/ha				64	
	Age, year				21	
	D, cm_mean				9.1 ± 0.2	
	H, m_mean				9.6 ± 0.3	
	S, m ² /ha				0.4	
	V, m ³ /ha				2.1	

Tree parameters. Four sample plots within the transect (Vegi1–Vegi4) represent *Pinus sylvestris* stands of various age — from 10-year-old overgrowing patchy xeric grassland to medium-aged, 40- to 45-year-old mixed pine-juniper stand (Vegi4) that borders with the mature oak forest (Vegi5) (Table 4, Fig. 4) where the age of pine reached 64 years (Fig. 4). The age of junipers was ca. 25 years (Vegi2, Vegi3). The age of oak varied from 29 in the young forest (Vegi1) to 203 in the mature forest (Vegi5).

The most intense growth of pine was detected in the youngest, 10- to 15-year-old stands (Vegi1, Vegi2), where the mean annual radial increment during the last ten years (2011–2020) varied from 3.8 mm (Vegi1) to 2.9 mm (Vegi2) ($p < 0.05$) (Fig. 5). The lowest radial increment was found in the 25-year-old stand, where it was 1.3 mm on average, which may be explained by the large tree density (1210 individuals per ha) and, consequently, high competition among the individuals. The radial increment in Vegi1

Fig. 5. Mean radial increment of pines (with standard deviation) during the last 10 years (2011–2020), in the sample plots Vegi1–Vegi5.

Fig. 6. Dynamics of the radial increment of pine in the sample plots Vegi1–Vegi5.

and Vegi2 was significantly lower ($p < 0.01$) than the radial increment in the neighbouring sample plots. Mean annual radial increment of the medium-aged pine in Vegi4 and Vegi5 plots during the last ten years was lower than 2 mm and did not significantly differ within the relevant tree age class ($p = 0.48$) (Fig. 5).

The radial increment in young to medium-aged pine stands varied over years (Fig. 6). During the last years, in all sample plots a trend toward slower growth was observed, espe-

Table 5. Spatial pattern of trees in the sample plots Vegi1–Vegi5

Sample plot	Species	Mean distance, m	Nearest neighbour index	Number of trees	Z-score	Spatial pattern of trees
Vegi1	In total	1.56	0.85	23	–1.41	Random
Vegi2	<i>Pinus sylvestris</i>	2.19	1.02	17	0.13	Random
	<i>Juniperus communis</i>	2.27	0.93	13	–0.5	Random
	In total	1.35	0.83	30	–1.72	Random
Vegi3	<i>Pinus sylvestris</i>	1.2	0.88	42	–1.49	Random
	<i>Picea abies</i>	4.14	1.05	5	0.19	Random
	<i>Juniperus communis</i>	0.53	0.19	10	–4.89	Random, with a tendency to clusters
	In total	0.99	0.85	57	–2.13	Random, with a tendency to clusters
Vegi4	<i>Populus tremula</i>	1.46	0.68	17	–2.51	Random, with a tendency to clusters
	<i>Crataegus spp.</i>	4.69	1.18	5	0.79	Random
	<i>Quercus robur</i>	2.56	0.71	6	–1.37	Random
	<i>Pinus sylvestris</i>	3.1	1.05	9	0.29	Random
	In total	1.12	0.81	41	–2.29	Random, with a tendency to clusters
Vegi5	<i>Picea abies</i>	4.85	0.97	7	–0.17	Random
	<i>Quercus robur</i>	5.51	1.44	12	2.89	Random, with a tendency to regular pattern
	In total	3.23	1.17	23	1.54	Random

Statistically significant values are marked in bold.

Fig. 7. Dynamics of radial increment of juniper in the sample plots Vegi2 and Vegi3.

cially in Vegi3, a pine stand with the highest tree density among the studied plots.

Individual pines at various succession stages of the formerly open grassland had different age; they differed in diameter and height, and their spatial pattern was random (Table 5). This means that, since the cessation of regular grassland management, their establishment and survival were driven by various factors. The differentiation of pine individuals by diameter and height usually occurs during the first years of tree colonisation in grasslands.

Also, overgrowing of the xeric grasslands with *Juniperus communis* takes place in the study site (recorded in Vegi2, Vegi3). Like pines, junipers had a random spatial pattern, rarely forming small clusters (as in Vegi3) (Table 5). In Vegi2, juniper trees were on average ten years older than pine trees (Table 4). The age of juniper varied from 17 to 37 years, while the age of pine varied from 8 to 25 years. During the last 20 years, the radial increment of juniper was synchronous ($p = 0.138$). Over the last decade, the average annual ring width of juniper in Vegi2 was 0.79 mm, and in Vegi3 it reached 0.85 mm (Fig. 7).

A few oak individuals were found in the overgrowing xeric grassland with the secondary pine forest, but the largest pro-

Fig. 8. Mean radial increment of oak (with standard deviation) during the last decade (2011–2020) in sample plots Veg1, Vegi4, and Vegi5.

Fig. 9. Dynamics of radial increment of oak in Vegi1 and Vegi4.

portion of them was recorded in the area adjacent to the mature oak forest (Vegi4). The radial increment of oak in the young to medium-aged pine forest varied from 1.6 to 1.7 mm annually. In the mature forest the oak increment was lower (1.1 mm annually) and significantly different ($p = 0.001$) from that of the oak individuals in the young to medium-aged pine forest (Fig. 8).

The spatial pattern of oak individuals in the entire study area was random. Regardless of the presence of dead oak trees in the stand (volume of dead oak wood was $15.2 \text{ m}^3 \cdot \text{ha}^{-1}$) and openings in the canopy, oak tended to have a regular spatial pattern (Table 5).

During the last decades, the radial increment of oak, to some extent also pine, has stabilised in the quasi-climax oak community (Fig. 9). The radial increment of pine and other woody species in the dynamic young succession stages was highly variable (Figs. 6, 7).

DISCUSSION

According to the literature (Mucina *et al.*, 1993; Rūsiņa, 2003; 2007; Wilner and Grabherr, 2007; Chytrý and Tichý, 2008; Chytrý, 2013), the character species of the following phytosociological classes and affiliated alliances, earlier recorded in Latvia, were identified in the Veģi study area: (1) class Festuco-Brometea: association Filipendulo vulgaris-Helictotrichon pratensis; (2) class Trifolio-Geranietea sanguinei, alliance Geranion sanguinei; and (3) class Quercetea pubescentis: alliance Quercion pubescenti-petraea, associations Carpino-Fagetea sylvaticae and Quercus robori-Tilion cordatae (nomenclature of the higher syntaxa follows Mucina *et al.* (2016)).

As stated by Rūsiņa (2007) and Szygendski and Brzeg (2015), the communities of Festuco-Brometea class have a dynamic connection with the plant communities of warm, dry forest fringes. Similar to a study from Poland (Szygendski and Brzeg, 2015), in Veģi in the later succession stage, the character species of xeric grasslands were accompanied by species of dry, warm forest fringes, such as *Geranium sanguineum*, *Agrimonia eupatoria*, *Origanum vulgare* and *Calamagrostis epigeios*. During the overgrowing of the grassland, encroachment of woody species of Crataegus-Prunetea, a scrub community of dry, warm sites, takes place. Here, the character species of scrub communities were woody species *Crataegus curvisepala*, *Rhamnus cathartica*, *Berberis vulgaris*, *Swida sanguinea*, *Rosa* ssp., and the non-native *Ligustrum vulgare*, as well as herbaceous species *Laserpitium latifolium*, *Veronica teucurium*, and *Campanula persicifolia* — character species of thermophilous oak forests and sparse pine woodlands of the class Quercetea pubescentis (Table 2).

The first relevé group distinguished in the study area, *Filipendula vulgaris*-*Pinus sylvestris* community, represents an overgrowing semi-natural xeric calcareous grassland that, after cessation of management, had been invaded by *Pinus sylvestris*. In Veģi, the dominant character species in the grassland were *Filipendula vulgaris* and *Helictotrichon pratensis* representing association Filipendulo vulgaris-Helictotrichetum pratensis of the class Festuco-Brometea (Rūsiņa, 2003; 2007). *Carex flacca*, *Pimpinella saxifraga*, *Brachypodium pinnatum* and *Knautia arvensis* were constant species in this community (Table 2).

The second group of relevés represented a *Quercus robur* dominated forest community with ground vegetation composed of *Viola mirabilis*, *Primula veris*, *Lathyrus niger* and *Convallaria majalis* (Table 2) — species with high frequency (60%). Also, *Carex montana*, a character species of thermophilous oak forests with *Lathyrus niger* (Roleček, 2007), was present in the ground vegetation.

Oak forest communities with the above mentioned constant species are affiliated to the thermophilous oak forest association Lathyro nigri-Quercetum roboris (Bolokhov and Solomeshch, 2003), earlier recorded in East Europe. Roleček (2007) has distinguished a similar forest community in Czechia: moderately thermophilous oak forests (as association Potentillo albae-Quercetum Libbert 1933). In Central Europe, such forests occur on deep, often heavy soils, with dominance of *Quercus petraea* and *Q. robur* that form open high stands. Although the syntaxonomical affiliation is rather unclear and controversial, similar thermophilous communities with *Q. robur*, the only *Quercus* species in Eastern Europe, occur in Ukraine and Russia (Goncharenko *et al.*, 2020). The vegetation and site conditions recorded in Veģi are like those described in Central Europe (Chytrý, 1997; Roleček, 2007), although numerous continental and subcontinental species, as well as some Mediterranean elements typical for the more southern located thermophilous oak forests, do not occur in Eastern Europe including Latvia (Goncharenko *et al.*, 2020). These

types of forest communities were recorded earlier also in Latvia, though they are very rare (Laiviņš, 2014).

Three character species of thermophilous oak forests (Chytrý, 1997; 2013; Chytrý and Tichý, 2008; Laiviņš, 2014), *Viola mirabilis*, *Primula veris* and *Lathyrus niger*, occur also in the partly overgrown xeric grassland of *Filipendulo vulgaris*-*Pinus sylvestris*, a forest pioneer stage. This points to the mutual connection of both forest communities, as they represent different subsequent succession stages, i.e., an overgrown Festuco-Brometea grassland gradually turns into a thermophilous oak community with *Quercus robur* and *Lathyrus niger*.

The presence of some species of light, warm forest fringes in the *Quercus robur* dominated forest, such as *Origanum vulgare*, *Laserpitium latifolium*, *Veronica teucrium*, *Campanula persicifolia* and *Primula veris* (Chytrý and Tichý, 2008; Laiviņš, 2014) indicates the successional relation to xeric calcareous grassland, as these species are remnants from the grassland succession stage. Currently, the frequency and abundance of these species in the oak forest is not high, as their primary habitat is warm, dry forest fringes, i.e., in Veģi they do not anymore occur in their optimum niche but can be considered as residuals of the earlier succession stage. Their presence in the oak forest suggests that in the past when the forest may have been grazed these species were perhaps present in higher abundance.

The third group of relevés described in Veģi was composed of *Corylus avellana* scrub that occupied some patches in the canopy openings of an oak stand. Openings in the tree layer have appeared after falling of some older oaks. The cover of *Corylus avellana* exceeded 85% of the shrub cover; the ground vegetation was relatively poor in species (17 species per sample plot on average), mostly composed of shade-tolerant species of Carpino-Fagetea sylvaticae (Chytrý and Tichý, 2008; Laiviņš, 2014), such as *Mercurialis perennis*, *Anemone nemorosa*, *Paris quadrifolia*, *Geum urbanum*, and *Viburnum opulus*. In such hazel-dominated openings, there is lack or negligible presence of character species of thermophilous oak forests and light, warm forest fringes. As suggested by studies in Poland and Ukraine, the colonisation of hazel that may lead to its dominance and decline of thermophilous oak forest communities, is largely related to cessation of traditional grazing in forests (Jakubowska-Gabara, 1996; Wolański *et al.*, 2021).

In the boreonemoral zone, young forest stages that develop after cessation of grassland management, similarly as during forest stabilisation after catastrophic events such as clearcuts, fires, windbreaks, are dominated by the pioneer woody species, e.g., birches, aspen, pine (Tullus *et al.*, 2013). The fast-growing, light-demanding pioneers are gradually being replaced by woody species that are more tolerant against shading and form more stable forest communities dominated by spruce and deciduous broadleaved tree species (Ruskule *et al.*, 2016). The vegetation shift in the study area in Veģi follows the same path.

The early stage of the secondary succession during the overgrowing of *Filipendulo vulgaris*-*Helictotrichon pratensis* grassland included the establishment of *Pinus sylvestris* and *Juniperus communis*. The change at landscape level can be detected by comparing the orthophoto maps of 1994 and 2019 (Fig. 1). In the mid-1990s (Fig. 1, B), the grassland was recently abandoned; some juniper and pine clusters had already established or survived during the last years when the area was still mowed or grazed.

Later, the young forest stage transformed into *Quercus robur* dominated forest, although *Q. robur* may also be present at earlier stages together with pines, junipers and other shrub species. In the study site, this succession is well presented by all the above-mentioned stages in a relatively small area that were represented by a transect 300 m in length and 20 m in width across the young forest and semi-open overgrowing grassland on one end and mature oak forest on the other end. As shown by the tree age studies, the stages represent a 200- to 250-year period. The four youngest pine forest stages, each represented by one sample plot (Table 3), represent the last 40- to 50-year period, while the oldest succession stage, the mature oak forest, reaches an age of at least 200 years. The difference between the youngest and the oldest forest stage in the succession series is about 100–150 years. However, in Veģi an intermediate stage between the young and mature forest was not found. Most probably, this is related to the land management until the mid-20th century, when the grasslands were intensively utilised for hay collecting and grazing (Lazdiņš, 1939; Dumpe, 1999). Thus, due to continuous grazing and mowing impact, there was no space for gradual forest development at the forest edges. Thus, it can be assumed that both the grassland and oak forest were grazed, i.e., there was regular grazing impact at the forest edge and very low chance of young tree survival. During the latest decades, cessation of grazing has, most probably, caused formation of dense hazel undergrowth in the oak forest openings that would not be possible under continuous grazing pressure (Wolański *et al.*, 2021).

The study results suggest that in xeric grasslands the encroachment of juniper may take place earlier than the establishment of pines, but later juniper is gradually replaced by pine. In the Vegi3 sample plot, some juniper individuals were a few years older than pine trees. Early establishment of juniper may be related to the grassland management practise before cessation of grazing, as some solitaire juniper individuals in pastures may survive as “non-browsable” shrubs. However, as the management history of the study area is not known, this is an assumption not supported by historical records of the particular site. The study results show that the shrub encroachment may start both with establishment of juniper (Vegi2, Vegi3), and establishment of pine (Vegi1).

In the oldest stages of pine woodland in the study area, other woody species such as *Picea abies*, *Populus tremula* and *Quercus robur* were recorded. The oldest spruce *Picea abies* was 23 years old and was found in a mixed pine-

juniper stand (Vegi3) established around the same time as most pines. Spruce creates extra shade and somewhat modifies the environment, making it more suitable for shade-tolerant species. In the later succession stage (Vegi4), the oldest spruce was 33 years old, while in the mature oak forest (Vegi5) the maximum age of spruce reached 65 years (Table 4). In all three sample plots (Vegi1–Vegi3) where the spruce was present, the *Picea abies* individuals had a sparse canopy and low vitality.

The intermediate stage between the medium-aged pine forest and mature oak forest (represented by Vegi4) was characterised by the presence of young (25 years) *Populus tremula* individuals. Due to low light availability in the forest stand, the aspen trees are spindly, their diameter at breast height was on average 6.9 cm, and some young aspen individuals were dead. Aspen individuals were also found in the mature oak forest, some of them dead.

The increment of trees, especially for pine, has not been linear and has varied considerably since their establishment, as it depends on different environmental drivers and the synergetic processes during woodland development.

Although confined to a small area, the study site can be considered as a representative example of the succession of xeric, thermophilous plant communities that are very rare in Latvia, as they occur in highly specific abiotic conditions. To understand the vegetation composition and its variation, as well as the succession pattern at a broader scale in Latvia, where the thermophilous oak forest communities were previously considered absent (Chytrý, 1997; Goncharenko *et al.*, 2020), further studies at other locations are necessary.

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SAUSU KAĻĶAINU ZĀLĀJU TRANSFORMĀCIJA TERMOFĪLOS OZOLU MEŽOS: ABAVAS SENIELEJAS PIEMĒRS

Sausu kaļķainu zālāju augu sabiedrību aizaugšana, dabiski pārveidojoties platlapju mežu sabiedrībās, Latvijā ir maz pētīta. Maz zināms par sausu kaļķainu Festuco-Brometea klasei piederošu zālāju sukcesijas gaitu, tiem aizaugot un pārveidojoties kvaziklimaksa termofīlo ozolu Quercetea pubescentis klasei piederošu ozolu mežu sabiedrībās. Šādas ozolu mežu sabiedrības Latvijā ir ļoti reti sastopamas. Rakstā atspoguļoti ģeobotāniska pētījuma rezultāti, kas ietvēra augsnes, koku vecuma un telpiskā izvietojuma, kā arī veģetācijas sugu sastāva un vides faktoru analīzi dažādās sukcesijas stadijās. Pētījums tika īstenots Abavas senielejā Rietumlatvijā — teritorijā, ko raksturo sugām bagāti sausi kaļķaini Festuco-Brometea klases zālāji, kā arī sastopamas termofīlo ozolu mežu sabiedrības ar parasto ozolu *Quercus robur*, bet starpstadijās sastopamas jaunas līdz vidēja vecuma kadiķu *Juniperus communis* un parastās priedes *Pinus sylvestris* audzes.