Fragm. Flor. Geobot. 45(1–2): 281–321, 2000

# Composition, structure and ecological aspects of Mesic Old Growth Carpathian Deciduous Forests of Slovakia, Southern Poland and the Western Ukraine

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MAYCOCK P. F., GUZIK J., JANKOVIC J., SHEVERA M. AND CARLETON T. J., 2000. Composition, structure and ecological aspects of Mesic Old Growth Carpathian Deciduous Forests of Slovakia, Southern Poland and the Western Ukraine. *Fragmenta Floristica et Geobotanica* 45(1–2): 281–321. Kraków. ISSN 0015–931x.

ABSTRACT: Scientists as well as the general public are slowly coming to realize the critical importance of preserving pristine examples of old growth forests. Their employment in the study of natural communities as ecological benchmarks for comparison to so many systems which have been degraded by human activities is of prime significance. The protection of the gene pool, inherent floristic and structural organization, in an undisturbed environment will become more and more useful as time passes. Their use in research, teaching and nature appreciation is of serious consequence and value. In this contribution quantitative data on the floristics, vegetational composition, structural organization as well as general environmental features are presented and related by means of analytical approaches of direct gradient analysis, as well as detrended correspondence analysis ordination. Aspects of biodiversity are included as well as comparison with other similar mesic old growth deciduous forests in other areas, but particularly with these systems as they are found in extreme Southern Ontario, Canada.

KEY WORDS: old growth, mesic deciduous forests, Slovakia, Poland, Ukraine, direct gradient ordination, DCA ordination.

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## INTRODUCTION

At this critical point in the development of human civilization when mankind is destroying the world environment at a more rapid rate than ever before, it is of the utmost importance that prime examples of natural ecosystems be purposely established as totally protected reserves so they are available for the critical scientific purposes of environmental monitoring, biodiversity preservation, comparative vegetational investigations and nature education. Undoubtedly, in time they will be required for additional scientific purposes which are not to this time fully understood. The continuance of the human race may well ultimately depend upon fully protected and representative nature reserve systems in critical geographical regions throughout the world. A system of biosphere reserves is an approach to this situation.

As a Canadian in the central province of Ontario, where the government has been slow to realize the inherent value of totally protected nature preserves and even slower in establishing such a system, the senior author has been very favourably impressed with the efforts of the governments of Poland, Slovakia and the Ukraine to establish nature protection areas, particularly forest reserves.

In 1996 through the auspices of the Szafer Institute of Botany in Cracow and the Director Prof. Dr. Leon Stuchlik as well as other colleagues, the senior and second author were assisted ably in field studies in mesic deciduous forest reserves throughout southwestern Poland. Then in 1997 and 1998, the senior and third author received very strong cooperation from the Forestry Institute in Zvolen and the Director Dr. Jan Ilavský, and other colleagues to undertake field studies in central and later far eastern Slovakia in these systems. Fortunately in 1997 the senior, second and fourth authors were assisted by colleagues and the Director of the Kholodny Botanical Institute in Kiev, to expand these field investigations into the Subcarpathian region of western Ukraine. During these relatively brief visits to these regions the authors succeeded in obtaining quantitative data on the composition, structure and general environmental conditions of 18 mesic old growth deciduous and deciduous-evergreen forests. Analysis of this body of data is presented here to advance the understanding of the composition, structure, reproduction and general ecology of these systems in the central area of Eastern Europe and make it available for quantitative comparison with similar systems in other regions of the North Temperate Zone. The data will also be useful in the study of the comparative biodiversity of these systems. Hopefully, this research will be a stimulus for an expansion of the conservation and preservation of old growth deciduous forest ecosystems, worldwide.

## Location and descriptions of the areas

The area including these forests stretches for more than seven degrees of longitude from the Boky Reserve, 3.5 km W. of Buda in the Slovakian Central Mountains ($19^{o}01'$E) and extending over a linear distance of more than 500 km to the forest 3 km S. of Ivankyvci, Khmelnitska Oblast’ SW Ukraine ($26^{o}15'$E). The latitudinal extent separating the stands is considerably less, approximately 100 km, passing from Ivankyvci at $49^{o}10'$N to Kostrza Mt., 3 km NE of Wilkowisko, former province Nowy Sącz in the Insular Beskid Mountains at $49^{o}46'$N in southern Poland. Thus the total area enclosing the stands is approximately 50000 sq. km.

The majority of the forests occur within or near the Subcarpathian regions either on the southern, northern or north western flanks of this great mountain system which so strongly influences all of Eastern Europe. A few stand locations are found on more level plains beyond the slope topography of the mountains specifically in the Central Slovak Mountains but scarcely beyond their environmental influences. These forests occur over a considerable range of elevation from 350 to 1000 m and some examples are found in every 100 m interval. The sites include considerable variation in degree of slope as well as aspect, include a range of soils except real sandy types, and some variation in microclimatic situation as well as soil pH.

In the region under study beech and beech and fir forest systems occur in the lower montane zones of the Carpathians and associated outlying mountains, such as the Beskids, Gorce, Bieszczady and the Central Slovakian Mountains. It is not possible to present detailed accounts of these mountain systems but suffice it to say that climatic and other environmental conditions particularly dependable moisture and humidity and a range of soils of relatively good fertility in these locations favours the development of broadleaved deciduous forests.

Beech forests are particularly well developed in the Southern Polish mountains in the lower montane zone from 600 to 1200 m. The slope sites appear to be highly favourable for these forests. In Poland these forests have long been the object of study (Pawłowski 1925; Rübel 1926; Medwecka-Kornaś 1955, 1960; Pancer-Kotejowa 1965). A host of research papers have enumerated the geographical variants of *Fagetum carpaticum* (Matuszkiewicz 1958; Dzwonko 1984).

In Slovakia Beech forests are found also in the lower montane zone from 400 to 800 m and Beech-Fir forests somewhat higher from 500 to 1000 m, zones with higher annual rainfall, higher humidity and somewhat lower temperatures than the lowlands. These forests have been the object of intense study by a succession of Slovak phytosociologists (Zlatník 1959; Randuška 1959; Korpel 1995; Vološčuk 1994). Paramount in these studies is the book *Pralesy Slovenska*, the virgin forests of Slovakia by Korpel (1989).

In the Transcarpathian region of southwestern Ukraine, in Polonine at elevations between 400 and 1280 m are found the optimum ecological conditions for the growth of beech forests, *Fagetea sylvaticae* of which some 40 variants have been carefully identified by Ukrainian phytosociologists (Grynj 1971; Fodor 1974; Kosets 1954; Popov 1949; Tasenkevich 1979; Stojko *et al*. 1991).

A listing of the locations of stands sampled is included in Table 1.

## METHODS

### Field methods

In each of the territories visited the local representative was responsible for determining the localities where old growth systems were to be found, mostly in National Parks but also in established nature reserves. Other knowledgeable colleagues were also consulted and were most helpful. On location these areas were often quite extensive and composed of many neighboring and interrelated natural systems. The general characteristics of mesic old growth forest systems were described to local keepers, foresters or knowledgeable forest custodians and workers and this greatly assisted in locating suitable stands for quantitative study. As much of these areas was traversed as possible in the search for suitable stands and

**Table 1.** Mesic Old Growth Deciduous Forests: Eastern Europe. Listing of locations where forest stands sampled occur.

| Country | Locality | Stand | Description |
|---|---|---|---|
| SLOVAKIA | Boky Reserve | EU 10 | 3.5 km W Budča, 8 km W Zvolen. Section 658, Forest Reserve of Technical University in Zvolen. Rich forest on bouldery terrain in valley bottom and adjacent lower slopes. Elevation 400 m. *Tilio-Carpinetum* transition. |
| | Badínsky Prales I | EU 12 | 6 km W Badín, 10 km SW Banska Bystricá. Section 803 in the reserve. Steep slope in Kremnické Mountains. Elevation 875 m. *Abieti-Fagetum*. |
| | Badínsky Prales II | EU 14 | 8.5 km W Badín, 10 km SW Banska Bystricá. Section 800 in Badínsky Prales Reserve. Ancient forest on steep to moderate N facing lower slope of Kremnické Mountains. Elevation 750 m. *Abieti-Fagetum*. |
| | Dobročský Prales | EU 13 | 3 km SSW Dobroč, Region Banska Bystricá, okres Brezno, Slovenski Rudohorie Mountains. Section 184, NE of Prales. Significant old growth mixed forest on moderate due N slope. Elevation 900 m. *Abieti-Fagetum*. |
| | Hrončokový grúň | EU 23 | 15 km SW Brezno, Region Banska Bystricá, okres Brezno, Slovenski Rudohorie Mountains. Very rich site. Old growth mesic forest beginning to deteriorate. On moderate NE slope. Elevation 875 m. Designated Biosphere Reserve. *Abieti-Fagetum*. |
| | Stužica | EU 24 | 5 km N Nová Sedlica, okres Snina, Vychodné Beskydy Mountains, extreme NE Slovakia. Plateau above creek valley on slight SW slope. Elevation 800 m. *Dentario glandulosae-Fagetum*. |
| POLAND | Babia Góra | EU 6 | 2 km SW Zawoja-Czatoża, Babia Góra National Park, Beskidy Zachodnie Mountains. Ancient deciduous-coniferous old growth on moderately steep N facing slope. Bedrock sandstone flysch. Elevation 1000 m. *Dentario glandulosae-Fagetum*. |
| | Poręba Wielka-Koninki | EU 7 | 3 km SSE Koninki, Turbaczyk Valley, Gorce National Park, former province Nowy Sącz, Beskid Żywiecki Mountains. Deciduous-coniferous old growth forest on steep SW facing slope. Elevation 900 m. *Dentario glandulosae-Fagetum*. |
| | Turbacz Creek Valley | EU 8 | 2 km SSE Koninki, E bank Turbacz Creek, Gorce National Park, former province Nowy Sącz, Beskid Żywiecki Mountains. Primarily deciduous old growth rich forest on sandstone flysch on steep WSW facing slope. Elevation 850 m. *Dentario glandulosae-Fagetum*. |
| | Kostrza Mt. | EU 5 | 3 km NE Wilkowisko, former province Nowy Sącz, Beskid Wyspowy Mountains. Primarily deciduous old growth forest on clay over sandstone flysch. Moderately steep NNW slope. Elevation 650 m. *Dentario glandulosae-Fagetum*. |
| | Kłodne nad Dunajcem Reserve | EU 9 | 0.5 km E Kłodne across the Dunajec River, Radziejowa Range, Beskid Sądecki Mountains, former province Nowy Sącz. Old growth deciduous forest on steep NNW facing slope. Clay over sandstone flysch. Elevation 500 m. *Dentario glandulosae-Fagetum*. |
| | Baniska Reserve | EU 4 | 6 km SW Rytro, Radziejowa Range, Beskid Sądecki Mountains, former province Nowy Sącz. Mixed deciduous-coniferous old growth forest on steep NE facing slope on clay over sandstone flysch. Elevation 875 m. *Dentario glandulosae-Fagetum*. |
| | Łabowiec Reserve | EU 3 | 5 km W Łabowiec, Jaworzyna Krynicka Range, Beskid Sądecki Mountains, former province Nowy Sącz. Remarkable mesic old growth deciduous-coniferous forest on modest but variable E facing slope. Clay over sandstone flysch. Elevation 900 m. *Dentario glandulosae-Fagetum*. |

**Table 1.** Continued.

| Country | Locality | Stand | Description |
|---|---|---|---|
| UKRAINE | Mala Ugolka | EU 18 | 2.5 km N Mala Ugolka, Ugolka-Shyrokoluzhankyi Massive, Tyachiv Region, Ukrainian Carpathian Mountains, Carpathian World Biosphere Reserve, Transcarpathia. Remarkable old growth deciduous forest on moderate S facing slope on somewhat flat terrain on sandy loam. Elevation 620 m. *Dentario glandulosae-Fagetum*. |
| | Ugolka Forestry | EU 16 | 3.0 km N Mala Ugolka, Shyrokoluzhanskyi Massive, Tyachiv Region, Ukrainian Carpathian Mountains, Carpathian World Biosphere Reserve, Transcarpathia. Old growth mesic deciduous forest in exemplary condition on moderate E facing slope on sandy loam soils. Elevation 760 m. *Dentario glandulosae-Fagetum*. |
| | Velyka Ugolka | EU 19 | 7 km N Velyka Ugolka, Ugolski Massive, Tyachiv Region, Ukrainian Carpathian Mountains, Carpathian World Biosphere Reserve, Transcarpathia. Old growth mesic deciduous forest in fine condition. Almost total *Fagus* dominance. On moderate W facing slope on clay soils over limestone bedrock. Elevation 550 m. |
| | Shyrokoluzhankyi Massive | EU 17 | 13 km NE Schiroki Lug, Tyachiv Region, Ukrainian Carpathian Mountains, Carpathian World Biosphere Reserve, Transcarpathia. Mesic old growth deciduous forest of great height and almost complete *Fagus* dominance. Moderate to steep S facing slope on sandstone bedrock. Elevation 700 m. *Dentario glandulosae-Fagetum*. |
| | Ivankyvci | EU 20 | 3 km S Ivankyvci, Khmelnitska Oblast', Gorodoski Region Satanów, Podolia. Mesic to wet-mesic old growth deciduous forest on flat plain. Elevation 350 m. *Tilio-Carpinetum* transition. |

often there was sufficient compositional variation between locations so that more than one could be selected. When chosen, the stand was carefully traversed noting general compositional features in terms of dominance patterns in the various vegetational layers and the extent and natural limits, so that a pattern of sampling could be decided upon. When the criteria of size (at least a hectare), homogeneity of general composition, absence of human disturbance, as well as noting larger areas of natural disturbance (extensive gaps or windfalls) which could be bypassed during sampling, were satisfied, the process could begin (Maycock 1963).

During exploratory examination a list of all vascular species observed was tallied, and this continued during the whole process of sampling. Unfortunately lack of time and expertise prevented the inclusion of mosses, lichens, liverworts and fungi. Any plants either difficult or impossible to identify were collected, later pressed, and subsequently identified by experts. Aspects of the environment were also noted, including topography, slope, aspect, general characteristics of synusia, dominance patterns, and any additional pertinent features.

An imaginary direction and line of sampling, conversant with stand configuration, was decided upon and random sampling points were established by pacing distances of 20 m. At each point a bisect at right angles to the direction of sampling was established which divided the stand into four quadrants. A meter square quadrat was laid using the bisect as two sides and presence and visual estimated cover of all shrubs, tree seedlings (those recently germinated and up to 2.4 cm diameter at breast height (1.5 m above ground) and herbs included, were recorded. The canopy cover in an area approximately four meter square overhead was tallied. Then in each quadrant, the tree (10 cm diameter, 77 square cm basal area or greater) nearest to the point was selected and the species, basal area, and distance from the point was recorded. As well the nearest sapling (woody stem, 2.5 cm diameter, 6.5 to 77 sq. cm basal area, capable of developing into a tree) was chosen and the species and distance from the point taken. This procedure was repeated for the nearest trees and saplings in the other three quadrants. When the measurements were concluded at the point another was established by pacing 20 m along the direction of sampling and the procedure then repeated. Quadrats for the recording of shrubs, tree seedlings and herbs were only recorded at every other point. Often the direction of sampling could be randomly changed so that a large rectangle or square, or a series of parallel lines could form the basis for the establishment of sample points. Usually a total of 30 points were sampled in each stand to provide quantitative data for 120 trees, 120 saplings and 15 m sq. quadrat records as well as 30 for canopy cover. At the termination one had traversed and observed many compositional, structural and ecological features of the stand. These aspects were precisely described by recording vegetational layers, maximum canopy and average heights, whether continuous or discontinuous, and their major recognizable dominants. An assessment of environmental aspects including slope, aspect, elevation, site moisture on a scale of dry, dry-mesic, mesic, wet-mesic and wet, microclimate, as normal, warmer or colder, natural disturbances; tree gaps, fallen logs and branch debris, wild boar damage, etc., was made. In a representative section, a soil pit was dug and the depths of $A_0$, $A_1$, $A_2$ and B were measured and the field pH of $A_1$ and B measured with a Cornell University Soil Kit.

## Laboratory procedures

In the laboratory all collected plant specimens were identified and added or corrected on the stand data. All specimens have been fully labelled and deposited in the herbarium of the Plant Ecology Laboratory, University of Toronto at Mississauga. The stand data were summarized using the following arithmetic procedures. For the trees, presence, frequency (points of occurrence for a species as a per cent of total points sampled), relative frequency (per cent frequency of a species of the sum of frequency for all tree species), relative density (number trees of a species as per cent of total number of all trees sampled), relative dominance (per cent total basal area of a species of total basal area for all species), and importance (sum of relative frequency, relative density and relative dominance), were calculated. The importance values for all tree species in the stand total 300 because each of relative frequency, relative density and relative dominance is 100%. If a tree was found in the stand but was not recorded at points, it was assigned a minimum importance of 1. For each sapling species a DF value, the sum of relative frequency and relative density was calculated. For the quadrat data, for each species, presence, frequency (percentage quadrats of occurrence) and average estimated cover (sum of cover in all quadrats divided by total quadrats recorded) was summarized. All of the canopy coverage estimates were averaged for all points recorded.

Additional general aspects of stand composition could be calculated from the measurements recorded in the field. The point to tree distances when averaged provided a basis for calculating the density of trees per hectare. This distance when squared and then divided into the total square meters per hectare, gives the number of trees per hectare (Cottam *et al*. 1955). Similarly the density of saplings per hectare were determined. When the density of trees per hectare is multiplied by the average basal area per tree in the stand, it provides a value-dominance per hectare or basal area per hectare, which is considered to approximate a measure of standing biomass per hectare. The additional contribution to biomass of saplings can be calculated by multiplying the mid point of sapling basal area (35.5 sq. cm) by the number of saplings per hectare.

## Analytic methods

Based on these calculations other aspects of forest composition could be determined. The patterns of leading tree dominance as well as understorey dominance are examples. Badinsky Prales I, in Slovakia had the following tree dominance sequence:

*Fagus sylvatica*$^{192}$ – *Abies alba*$^{65}$ – *Acer pseudoplatanus*$^{24}$ – *Ulmus laevis*$^{19}$ – *Fraxinus excelsior*$^{1}$ and the following understorey dominance sequence:

*Acer pseudoplatanus* seedlings$^{6.5}$ – *Fagus sylvatica* seedlings$^{4.9}$ – *Asperula odorata* $^{4.1}$ – *Rubus hirtus* $^{3.9}$ – *Dryopteris filix-mas*$^{3.1}$.

The values in the tree dominance sequence are importance, whereas those in the understorey dominance sequence are average per cent cover. The quantitative indices for species in each stand could also be employed in various types of quantitative analysis. These patterns were determined for all stands.

A simple life-form analysis was undertaken by assigning each plant species with a life-form designation – not only trees, shrubs, herbs, lianas but these general categories were further divided into trees of the upper canopy (utc), trees of the lower canopy (sct), trees mostly saplings of the subcanopy (lct), tree seedlings of the lower, understorey (tse), tall woody lianas (wlt), medium woody lianas (wlm), tall (ts), medium (ms) and low shrubs (ls), tall herbs (th), medium (mh) and low herbs (lh), tall (tf), medium (mf) and low ferns (lf), tall (o), medium (mg) and low (lg) graminoids, club mosses, saprophytes and parasites, according to heights (generally low – to 30 cm, medium 30–85 cm, tall 85–1m+). The life forms of individual stands were characterized and life-form relationships between forest stands determined.

A direct gradient ordination was established based on decreasing importance of the most significant tree species contributor to examine whether other species were related compositionally to this order.

Finally a two-dimensional ordination of stands using detrended correspondence analysis was attempted to relate stands in compositional space. Only the tree data was employed in this process but understorey elements could then be related to tree composition as well as to other species. The statistical package CANOCO for DOS was used for the ordination.

## Results

The composition of the 18 forest stands sampled and analyzed are provided in Table 2. The sample represents a small number but it must be emphasized that all were mesic or near mesic forests and represented only the compositional and ecological midpoint of deciduous forest variation in the regions concerned.

### Floristic composition

A total of 155 taxa in 54 families were recorded in the 18 mesic old growth forests. The largest families were Gramineae and Labiatae, each with eleven genera. Compositae included nine genera, Rosaceae and Dryopteridaceae seven, Liliaceae, six, Onagraceae, Cruciferae, Ranunculaceae and Cyperaceae, five, Boraginaceae, Caprifoliaceae and Umbelliferae four, Scrophulariaceae, Orchidaceae, Juncaceae, Caryophyllaceae, Corylaceae, Ulmaceae, and Campanulaceae, three. Another 15 families were represented by two genera and fully 19 had only a single genus.

At the generic level the two most significant were *Carex* and *Dryopteris* with five species each. Only *Galeopsis* included four species but *Acer*, *Ulmus*, *Circaea*, *Dentaria*, *Luzula* and *Stellaria* had three and *Rubus*, *Symphytum*, *Impatiens Sambucus*, *Epilobium*, *Viola*, *Lysimachia*, *Veronica*, *Polygonatum*, *Polystichum*, *Lonicera*, *Festuca*, *Ranunculus*, *Melica* and *Campanula* had two. Fully 92 of the genera involved in the composition of these stands were represented by just a single species.

At the specific level, 54 (35%) are represented in only a single stand and an additional 30 (19%) were in just two stands. Thus more than half of the taxa (54%) have very limited presence in these old growth forests.

It is a difficult task to recognize introduced species, and yet many have been transported from distant locations in America, tropical South America, central Asia, the steppes

**Table 2.** Mesic Old Growth Deciduous Forests: Eastern Europe. Compositional data – trees, tree seedlings, shrubs, herbs, environmental features.

| Stand number | | 17 | 19 | 9 | 16 | 5 | 18 | 24 | 14 | 6 | 3 | 8 | 7 | 20 | 12 | 13 | 4 | 10 | 23 | Sum I.V. | Av. I.V. | Constancy |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Country of origin | | U | U | P | U | P | U | S | S | P | P | P | P | U | S | S | P | S | S | | | |
| Location | | SCHYR | V. UGOL | KLOD | UGOL | KOST | M. UGOL | STUŽ | BAD II | BABIA | ŁABOW | TURB | PORĘ | IVANK | BAD I | DOBRO | BANIS | BOKY | HRONČ | | | |
| Latitude | | 48–18 | 48–13 | 49–28 | 48–12 | 49–46 | 48–12 | 49–05 | 48–40 | 49–36 | 49–28 | 49–35 | 49–34 | 48–10 | 48–40 | 48–11 | 49–27 | 48–35 | 48–43 | | | |
| Longitude | | 23–51 | 23–39 | 20–27 | 23–38 | 20–17 | 23–38 | 22–32 | 19–02 | 19–29 | 20–50 | 20–06 | 20–06 | 26–15 | 19–02 | 19–12 | 20–37 | 19–01 | 19–35 | | | |
| Elevation [m] | | 700 | 550 | 550 | 760 | 650 | 620 | 800 | 750 | 1000 | 900 | 850 | 900 | 350 | 875 | 900 | 875 | 400 | 875 | | | |
| Topography: | | | | | | | | | | | | | | | | | | | | | | |
| slope $^{o}$ | | 25 | 20 | 35 | 15 | 22 | 15 | 5 | 25 | 25 | 15 | 35 | 30 | 0 | 25 | 15 | 35 | 30 | 15 | | | |
| Aspect | | S | W | NNW | E | NNW | S | SW | N | N | E | WSW | SW | – | NNE | N | NE | SSE | NE | | | |
| Microclimate | | W | W | C | C | C | W | NC | C | C | C | W | W | N | C | C | C | W | C | | | |
| Substrate | | C | C | C | L | C | L | L | L | C | C | C | C | C | C | L | L | L | L | | | |
| Field pH $A_1$ | | 4.8 | 4.9 | 5.4 | 5.6 | 5.2 | 5.6 | 5.4 | 5.7 | 5.0 | 5.4 | 5.1 | 5.2 | 6.1 | 5.6 | 5.3 | 5.2 | 5.6 | 6.0 | | | |
| % Canopy | | 92 | 89 | 88 | 91 | 90 | 91 | 94 | 97 | 92 | 93 | 88 | 95 | 91 | 96 | 87 | 91 | 92 | 89 | | | |
| Tree density/ha | | 383 | 400 | 277 | 272 | 395 | 218 | 423 | 338 | 295 | 236 | 377 | 364 | 340 | 332 | 395 | 220 | 318 | 274 | | | |
| Tree dominance /ha(×1000) | | 743 | 951 | 395 | 816 | 679 | 704 | 814 | 623 | 683 | 531 | 472 | 571 | 498 | 679 | 695 | 673 | 473 | 844 | | | |
| Sapling density/ha | | 368 | 386 | 66 | 157 | 11 | 272 | 166 | 1374 | 537 | 181 | 84 | 72 | 11 | 264 | 383 | 229 | 219 | 15 | | | |
| Tree class to 516 sq. cm | | 27 | 28 | 24 | 21 | 4 | 11 | 37 | 39 | 17 | 20 | 24 | 30 | 13 | 41 | 57 | 25 | 36 | 5 | | | |
| Tree class to 2064 sq. cm | | 34 | 24 | 57 | 24 | 53 | 33 | 30 | 23 | 34 | 39 | 62 | 48 | 65 | 27 | 13 | 25 | 40 | 30 | | | |
| Tree class to 8258 sq. cm | | 38 | 46 | 19 | 71 | 23 | 51 | 32 | 38 | 46 | 41 | 14 | 21 | 22 | 30 | 27 | 46 | 23 | 62 | | | |
| Tree class 8259+ | | 1 | 2 | – | 4 | – | 5 | 1 | – | 3 | – | – | 1 | – | 2 | 3 | 4 | 1 | 3 | | | |
| Upper canopy height [m] | | 42 | 40 | 30 | 43 | 30 | 42 | 45 | 45 | 40 | 30 | 35 | 32 | 28 | 40 | 45 | 30 | 30 | 45 | | | |
| *Fagus sylvatica* | utc | 300 | 300 | 300 | 287 | 287 | 286 | 265 | 249 | 226 | 225 | 219 | 208 | 199 | 192 | 181 | 172 | 140 | 107 | 4143 | 230 | 100 |
| *Abies alba* | utc | 1 | | 1 | | 13 | | 35 | 48 | 64 | 75 | 81 | 63 | | 65 | 50 | 95 | | 32 | 623 | 35 | 72 |
| *Acer pseudoplatanus* | utc | 1 | 1 | 1 | 1 | 1 | 7 | 1 | 1 | 1 | 1 | | 4 | 1 | 24 | 37 | 33 | 7 | 35 | 157 | 9 | 94 |
| *Sorbus aucuparia* | sct | | 1 | | | 1 | | 1 | 1 | 1 | 1 | | 1 | | 1 | 1 | 1 | | | 10 | 1 | 56 |
| *Carpinus betulus* | utc | | | 1 | | | | | | | | | | 89 | | | | 54 | | 144 | 8 | 17 |
| *Tilia cordata* | utc | | | 1 | | | | | | | | | | 5 | | | | 30 | | 36 | 2 | 17 |
| *Fraxinus excelsior* | utc | | | 1 | 1 | 1 | 1 | | 1 | | 1 | | | | 1 | 3 | | 6 | 82 | 98 | 5 | 56 |
| *Populus tremula* | utc | | | 1 | | | | | | | | | | | | | | | | 1 | – | 5 |
| *Acer platanoides* | utc | | | | 13 | | 7 | | | | | | | 1 | | 11 | | 27 | 8 | 67 | 4 | 33 |

| | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ulmus laevis* | utc | | | | 1 | | | | | | | | | | 19 | | | | | | | | 20 | 1 | 11 |
| *Prunus avium* | utc | | | | 1 | | 1 | | | | | | | 1 | | | | 1 | | | | | 4 | – | 22 |
| *Ulmus montana* | utc | | | | | | | | 3 | | | | 6 | | | | | 11 | 4 | | | | 24 | 1 | 22 |
| *Picea excelsa* | utc | | | | | | | | | 9 | 1 | 1 | 20 | | | 19 | 1 | | 32 | | | | 83 | 5 | 39 |
| *Betula pendula* | utc | | | | | | | | | | | | | 7 | | | | | | | | | 7 | – | 5 |
| *Quercus petraea* | utc | | | | | | | | | | | | | | | | | 19 | | | | | 19 | 1 | 5 |
| *Acer campestre* | sct | | | | | | | | | | | | | | | | | 7 | | | | | 7 | – | 5 |
| *Ulmus carpinifolia* | utc | | | | | | | | | | | | | | | | | 1 | | | | | 1 | – | 5 |
| | | | | | | | | | | | | | | | | | | | | Stand cover | F | Totale cov | Av. cov. | % Av. est. cov. | |
| *Acer pseudoplatanus* (seedlings) | tse | 0.2 | 0.3 | | 0.3 | | 1.6 | 0.4 | | 0.1 | 0.1 | | 0.2 | | 6.5 | 3.1 | 2.7 | | 1.9 | 12 | 67 | 17.4 | 1.0 | 1.9 | |
| *Fagus sylvatica* (seedlings) | tse | 20.3 | 8.5 | 0.1 | 5.5 | 1.0 | 19.6 | 10.0 | 3.5 | 7.6 | 8.9 | 12.7 | 7.7 | 11.0 | 4.9 | 0.1 | 1.9 | 2.2 | 2.8 | 18 | 100 | 138.3 | 7.7 | 14.4 | |
| *Asperula odorata* | mh | 1.3 | 0.5 | 1.2 | 14.2 | 3.7 | 6.9 | 0.1 | 0.1 | | 6.8 | 0.3 | 8.0 | 2.7 | 4.1 | 7.7 | 2.1 | 8.4 | 21.5 | 17 | 94 | 89.6 | 5.0 | 9.4 | |
| *Oxalis acetosella* | lh | 1.5 | 0.1 | 2.3 | 0.1 | 2.1 | 0.1 | 0.6 | 0.2 | 11.2 | 3.7 | 9.1 | 11.4 | | 1.5 | 4.4 | 1.4 | | 5.4 | 16 | 89 | 55.1 | 3.1 | 5.8 | |
| *Rubus hirtus* | ts | 3.0 | 0.1 | 0.4 | 1.3 | 1.2 | 7.5 | 37.1 | 0.1 | 5.0 | 14.8 | 6.9 | 9.3 | 0.1 | 3.9 | | 14.1 | | | 15 | 83 | 104.8 | 5.8 | 10.9 | |
| *Rubus idaeus* | ms | 0.1 | | 0.5 | | 8.5 | 0.1 | | 0.1 | 9.2 | 0.1 | 2.4 | 1.9 | 0.1 | 0.1 | 0.1 | 0.9 | | | 13 | 72 | 24.1 | 1.3 | 2.4 | |
| *Symphytum cordatum* | mh | 0.1 | | 0.1 | | | | | | | 0.1 | 0.1 | 0.5 | | | | 0.5 | | | 6 | 33 | 1.4 | – | | |
| *Dryopteris filix-mas* | mf | 0.1 | 0.1 | | 0.1 | | 0.1 | 0.1 | 0.5 | | | | | 0.1 | 3.1 | 3.9 | | 0.3 | 36.5 | 11 | 61 | 44.9 | 2.5 | 4.7 | |
| *Circaea lutetiana* | mh | 0.1 | | | 0.1 | | 0.1 | | | | | | | 0.1 | 0.1 | | | 0.1 | 0.1 | 7 | 39 | 0.7 | – | | |
| *Dryopteris austriaca* | mf | 0.1 | 0.1 | 2.0 | | 9.0 | | 0.1 | 0.1 | 1.2 | 0.5 | 1.5 | 0.1 | 0.1 | 0.7 | | 0.1 | | 0.1 | 14 | 78 | 15.7 | 0.9 | 1.7 | |
| *Impatiens noli-tangere* | mh | 0.1 | 0.1 | | 0.1 | 2.7 | 0.2 | 0.1 | | 0.1 | 3.0 | 0.8 | 17.2 | | 0.1 | 8.6 | 1.2 | | 26.7 | 14 | 78 | 61.0 | 3.4 | 6.4 | |
| *Athyrium filix-femina* | mf | 0.1 | 0.1 | 9.1 | 0.1 | 30.5 | 0.1 | 0.1 | 1.3 | 7.0 | 2.3 | 6.0 | 12.2 | 0.1 | 2.0 | 13.6 | 3.7 | 2.2 | 1.3 | 18 | 100 | 91.8 | 5.1 | 9.6 | |
| *Dentaria glandulosa* | lh | 0.3 | 0.1 | 0.2 | 0.1 | 2.7 | 0.1 | 0.1 | | 0.6 | 0.6 | 0.7 | 1.2 | | | 0.1 | 1.5 | | | 13 | 72 | 8.3 | 0.5 | 0.9 | |
| *Galeobdolon luteum* | lh | 0.1 | | 3.3 | 0.1 | 4.2 | 0.1 | 0.3 | | 0.2 | 0.1 | 0.6 | 4.5 | 8.2 | 0.7 | 5.1 | 1.4 | 10.9 | 0.7 | 16 | 89 | 40.5 | 2.3 | 4.3 | |
| *Glechoma hirsuta* | lh | 0.1 | | | | | 0.4 | | | | | | | | | | | | | 2 | 11 | 0.5 | – | | |
| *Daphne mezereum* | ms | 0.1 | | | | | | | | | | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Urtica dioica* | th | 0.1 | 0.1 | 0.5 | 0.1 | | 0.1 | 0.1 | | 0.1 | 0.1 | 0.1 | 0.2 | 0.1 | 0.1 | 1.7 | 0.7 | 0.1 | 19.0 | 16 | 89 | 23.2 | 1.3 | 2.4 | |
| *Prenanthes purpurea* | th | 0.1 | | | | | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.8 | 0.1 | | 0.1 | 0.1 | 0.1 | | | 11 | 61 | 1.8 | 0.1 | 0.2 | |
| *Monotropa hypopitys* | lsa | 0.1 | | | | | | | 0.1 | | | | | | 0.1 | | | | | 3 | 17 | 0.3 | – | | |
| *Sambucus racemosa* | ts | 0.1 | 0.1 | | 0.1 | 0.1 | 0.1 | | 0.1 | | | 0.1 | 0.1 | | 0.1 | | | | | 9 | 50 | 0.9 | 0.1 | 0.2 | |
| *Epilobium angustifolium* | th | 0.1 | | | | | | | | | | | | | | | | | 0.1 | 2 | 11 | 0.2 | – | | |
| *Circaea alpina* | lh | 0.1 | | | | | | | | 0.1 | 0.1 | | 0.1 | | | | 0.1 | | 0.1 | 6 | 33 | 0.6 | – | | |
| *Actaea spicata* | mh | 0.1 | | 0.1 | | 0.1 | | | | | 0.1 | 0.1 | 0.1 | | 0.1 | 0.1 | 0.3 | | 0.1 | 10 | 56 | 1.2 | 0.1 | 0.2 | |

*(cont.)*

**Table 2**. Continued.

| Stand number | | 17 | 19 | 9 | 16 | 5 | 18 | 24 | 14 | 6 | 3 | 8 | 7 | 20 | 12 | 13 | 4 | 10 | 23 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Epilobium montanum* | mh | | 0.1 | 0.1 | | | 0.1 | | | | | 0.1 | | 0.1 | | | 0.1 | 0.1 | 0.1 | 8 | 44 | 0.8 | – | | |
| *Scrophularia nodosa* | mh | | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | | | | | | | 0.2 | 0.1 | | | | | 7 | 39 | 0.8 | – | | |
| *Viola riviniana* | lh | | 0.1 | 0.1 | 0.1 | 0.2 | 0.6 | | | | 0.1 | 0.1 | 0.2 | | | 0.7 | | | 0.2 | 10 | 56 | 2.4 | 0.1 | 0.2 | |
| *Epipactis helleborine* | mh | | 0.1 | | 0.1 | | 0.1 | | 0.1 | | | | | | 0.1 | | | | | 5 | 28 | 0.5 | – | | |
| *Dryopteris disjuncta* | lf | | 0.1 | 7.0 | 0.1 | 0.1 | 0.1 | 2.7 | 0.1 | 0.4 | | 0.1 | | | | 1.3 | 0.1 | | | 11 | 61 | 12.1 | 0.7 | 1.3 | |
| *Galeopsis speciosa* | mh | | 0.1 | | | 0.1 | | | | | 0.1 | 0.8 | | | | | 0.2 | | 0.1 | 6 | 33 | 1.4 | 0.1 | 0.2 | |
| *Lactuca muralis* | mh | | 0.1 | | 0.1 | 0.7 | 0.1 | | | | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.4 | 0.1 | 13 | 72 | 2.2 | 0.1 | 0.2 | |
| *Mercurialis perennis* | mh | | 0.1 | 0.3 | 1.0 | 0.1 | 0.1 | | | 0.1 | 0.1 | 1.7 | 3.3 | | 0.1 | 1.0 | 1.6 | | 24.2 | 13 | 72 | 33.7 | 1.9 | 3.6 | |
| *Sambucus nigra* | ts | | 0.1 | 0.5 | | 0.1 | 2.5 | | 0.1 | 0.1 | 0.1 | 0.2 | 0.1 | 0.3 | 0.1 | | 0.1 | 0.1 | | 13 | 72 | 4.4 | 0.2 | 0.4 | |
| *Luzula pilosa* | lg | | 0.1 | | | | | | | | | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Neottia nidus-avis* | mp | | 0.1 | | 0.1 | | | | 0.1 | | | | | | 0.1 | | | | | 4 | 22 | 0.4 | – | | |
| *Asarum europaeum* | lh | | | 2.5 | | | | | 0.1 | | | 0.5 | 0.1 | 1.1 | 0.3 | 0.1 | 0.3 | 0.1 | | 9 | 50 | 5.1 | 0.3 | 0.6 | |
| *Circaea intermedia* | lh | | | 0.5 | | 0.1 | | | | | 1.0 | | 0.1 | | | | 0.1 | | | 5 | 28 | 1.8 | 0.1 | 0.2 | |
| *Impatiens parviflora* | mh | | | 4.2 | | | | | 0.1 | | | | | | 0.1 | | 0.1 | 5.6 | | 5 | 28 | 10.1 | 0.6 | 1.1 | |
| *Senecio fuchsii* | th | | | 0.1 | | 3.4 | | | 0.1 | 0.3 | 0.1 | 2.2 | 0.1 | | 0.1 | 0.4 | 0.3 | | 2.6 | 11 | 61 | 9.7 | 0.5 | 0.9 | |
| *Salvia glutinosa* | th | | | 0.1 | | 0.1 | | | | | 0.1 | 0.5 | 0.1 | | 0.1 | 1.6 | 3.7 | 0.5 | 2.5 | 10 | 56 | 9.3 | 0.5 | 0.9 | |
| *Stellaria media* | lh | | | 0.1 | | | | | | | | | | 0.1 | | | | | | 2 | 11 | 0.2 | – | | |
| *Dentaria bulbifera* | mh | | | 1.1 | | 2.3 | 0.1 | | 0.1 | 0.1 | 0.6 | 0.2 | 0.3 | | 0.9 | 0.1 | 3.6 | | 0.5 | 12 | 67 | 10.0 | 0.6 | 1.1 | |
| *Paris quadrifolia* | lh | | | 0.1 | | 0.1 | 0.1 | | | 0.1 | 0.1 | 0.1 | 0.1 | | 0.1 | 0.1 | 0.1 | | | 10 | 56 | 1.0 | 0.1 | 0.2 | |
| *Pulmonaria obscura* | lh | | | 0.1 | | 0.1 | 0.1 | | | | | | 0.1 | | 0.1 | 0.1 | 0.1 | | | 7 | 39 | 0.7 | – | | |
| *Stachys sylvatica* | th | | | 2.2 | 0.1 | 0.1 | | | 0.1 | | 0.1 | | 1.0 | | 0.1 | 0.1 | 0.1 | 0.1 | 1.0 | 11 | 61 | 5.0 | 0.3 | 0.6 | |
| *Geranium robertianum* | lh | | | 0.1 | 0.1 | | 0.1 | | | 0.1 | 0.3 | | 0.3 | 0.1 | 3.5 | 2.2 | 0.1 | 0.2 | 3.7 | 12 | 67 | 10.8 | 0.6 | 1.1 | |
| *Dryopteris phegopteris* | lf | | | 0.1 | 0.1 | | | 0.1 | | 0.1 | 0.1 | 0.1 | 0.1 | | | | 0.1 | | | 8 | 44 | 0.8 | – | | |
| *Euphorbia amygdaloides* | mh | | | 0.1 | 0.1 | 1.0 | | | | | 0.1 | | 0.1 | | 0.1 | | 0.2 | 0.1 | | 8 | 44 | 1.8 | 0.1 | 0.2 | |
| *Luzula nemorosa* | lg | | | 0.1 | | 0.1 | | | | | | | | 0.1 | | | 0.1 | | | 4 | 22 | 0.4 | – | | |
| *Maianthemum bifolium* | lh | | | 0.1 | | | | | | | | | 0.1 | 1.0 | | | | | | 3 | 17 | 1.2 | 0.1 | 0.2 | |
| *Carex sylvatica* | mg | | | 0.1 | | 0.1 | 0.1 | | | | 0.1 | 0.1 | 0.1 | 0.1 | | | 0.1 | | | 8 | 44 | 0.8 | – | | |
| *Lysimachia nemorum* | mh | | | 0.1 | | 1.2 | | | | 0.5 | 0.1 | 0.1 | 0.1 | | | | 0.1 | | | 7 | 39 | 2.2 | 0.1 | 0.2 | |
| *Corylus avellana* | ts | | | 0.1 | | | 0.1 | | 0.1 | | | | | | 0.1 | | | 0.1 | | 5 | 28 | 0.5 | – | | |
| *Dryopteris spinulosa* | mf | | | 0.7 | | | | | | 5.1 | | | 1.5 | | | 0.6 | | | | 4 | 22 | 7.9 | 0.4 | 0.8 | |
| *Veronica montana* | lh | | | 0.1 | 0.1 | 0.1 | 0.1 | | | | 0.9 | 0.1 | | | | | 0.1 | | | 7 | 39 | 1.5 | 0.1 | 0.2 | |
| *Petasites albus* | mh | | | 0.1 | | | | | 0.1 | 0.1 | 0.1 | 0.1 | | | 0.1 | | 0.1 | | 5.5 | 8 | 44 | 6.2 | 0.3 | 0.6 | |

| | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Sanicula europaea* | lh | | | | 0.1 | 0.1 | | | | | | | | 0.4 | 0.1 | 0.7 | 0.1 | | 2.0 | 7 | 39 | 3.5 | 0.2 | 0.4 | |
| *Atropa bella-donna* | th | | | | 0.1 | | | | | | | | | | 0.1 | | | | | 2 | 11 | 0.2 | – | | |
| *Polygonatum multiflorum* | mh | | | | 0.1 | 0.2 | 0.1 | | | | | 0.1 | | 0.1 | 0.1 | | | | | 6 | 33 | 0.7 | – | | |
| *Solanum dulcamara* | wlm | | | | 0.1 | | 0.1 | | | | | | | | | | | | | 2 | 11 | 0.2 | – | | |
| *Hedera helix* | wlt | | | | 0.1 | | | | | | | | | 0.5 | | | | 0.5 | | 3 | 17 | 1.1 | 0.1 | 0.2 | |
| *Anemone nemorosa* | lh | | | | 0.1 | 0.1 | | | | | | 0.1 | | | | | | | | 3 | 17 | 0.3 | – | | |
| *Acer platanoides* (seedlings) | tse | | | | 1.0 | | 1.7 | | | | | | | | | | | 2.0 | | 3 | 17 | 4.7 | 0.1 | 0.2 | |
| *Prunus avium* (seedlings) | tse | | | | 0.1 | | | | | | | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Ulmus laevis* (seedlings) | tse | | | | 0.1 | | | | | | | | | | 0.5 | | | 0.3 | | 3 | 17 | 0.9 | – | | |
| *Fraxinus excelsior* (seedlings) | tse | | | | | 0.5 | 0.1 | 1 | 0.1 | | 0.1 | | | | 0.2 | 2.0 | | 0.4 | 6.1 | 8 | 44 | 9.5 | 0.5 | 0.9 | |
| *Polypodium vulgare* | lf | | | | | 0.1 | | | | | | 0.1 | | | | | | | | 2 | 11 | 0.2 | – | | |
| *Galeopsis bifida* | mh | | | | | 0.1 | | | | | | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Galeopsis tetrahit* | mh | | | | | 0.1 | | | | | | | | | 0.1 | | | | | 2 | 11 | 0.2 | – | | |
| *Vaccinium myrtillus* | ms | | | | | 0.1 | | | | 4.5 | | | | | | | | | | 2 | 11 | 4.6 | 0.3 | 0.6 | |
| *Carex leporina* | mg | | | | | 0.1 | | | | | | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Deschampsia caespitosa* | mg | | | | | 0.2 | | | | 0.1 | | | | | | | | | | 2 | 11 | 0.3 | – | | |
| *Allium ursinum* | mh | | | | | 0.1 | | | | 4.8 | | | | | | | | | | 2 | 11 | 4.9 | 0.3 | 0.6 | |
| *Stellaria nemorum* | mh | | | | | 1.0 | | | | | 0.1 | | | | | 0.3 | 0.1 | 0.9 | 3.4 | 6 | 33 | 5.8 | 0.3 | 0.6 | |
| *Lunaria rediviva* | th | | | | | 0.1 | | | | | | | | | | | | | 5.1 | 2 | 11 | 5.2 | 0.3 | 0.6 | |
| *Moehringia trinervia* | lh | | | | | 0.1 | | | | | | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Lamium maculatum* | mh | | | | | 0.1 | | | | | | | | | | | | 2.5 | 0.3 | 3 | 17 | 2.9 | 0.2 | 0.4 | |
| *Lilium martagon* | th | | | | | 0.1 | | | | | | 0.1 | 0.1 | | | | 0.1 | | | 4 | 22 | 0.4 | – | | |
| *Calamagrostis arundinacea* | tg | | | | | 0.1 | | | | | | 10.3 | | | | | | | | 2 | 11 | 10.4 | 0.6 | 1.1 | |
| *Rhamnus frangula* | ts | | | | | 0.1 | | | | | | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Milium effusum* | mg | | | | | 0.1 | | | | | 0.1 | | 0.1 | | | | | | | 3 | 17 | 0.3 | – | | |
| *Poa nemoralis* | mg | | | | | 0.1 | | | | | | | | | | | | 0.1 | | 2 | 11 | 0.2 | | | |
| *Polystichum lobatum* | tf | | | | | 7.3 | | | | | 2.0 | 0.5 | 0.5 | | | | 10.5 | | | 4 | 22 | 13.5 | 0.8 | 1.5 | |
| *Aegopodium podagraria* | mh | | | | | | 0.1 | | | | 0.1 | | 0.1 | | | | | | 2.1 | 4 | 22 | 2.4 | 0.1 | 0.2 | |
| *Galium schultesii* | mh | | | | | | 0.1 | | | | | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Pteridium aquilinum* | tf | | | | | | 0.1 | | | | | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Cephalanthera longifolia* | mh | | | | | | 0.1 | | | | | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Abies alba* (seedlings) | tse | | | | | | | 1.9 | 0.1 | 0.1 | 0.4 | 0.4 | 0.3 | | 0.5 | 0.1 | | | | 8 | 44 | 3.8 | 0.2 | 0.4 | |
| *Carex pilosa* (?) | lg | | | | | | | 0.1 | | | | | | | | | | 0.4 | | 2 | 11 | 0.5 | – | | |

*(cont.)*

**Table 2**. Continued.

| Stand number | | 17 | 19 | 9 | 16 | 5 | 18 | 24 | 14 | 6 | 3 | 8 | 7 | 20 | 12 | 13 | 4 | 10 | 23 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Polygonatum verticillatum* | mh | | | | | | | 0.3 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | | 0.4 | 0.1 | 0.1 | | | 9 | 50 | 1.4 | – | | |
| *Dentaria enneaphyllos* | lh | | | | | | | | 0.8 | | | | | | 0.4 | 0.5 | | | | 3 | 17 | 1.7 | 0.1 | 0.2 | |
| *Sorbus aucuparia* (seedlings) | tse | | | | | | | | | 0.1 | 0.1 | | | | 0.1 | 0.1 | | | | 4 | 22 | 0.4 | – | | |
| *Hieracium murorum* | mh | | | | | | | | | 0.1 | | 0.1 | | | | | | | | 2 | 11 | 0.2 | – | | |
| *Lycopodium selago* | lze | | | | | | | | | 0.1 | | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Polystichum braunii* | mf | | | | | | | | | 0.1 | 0.1 | 1.5 | 0.6 | | | | | | | 4 | 22 | 1.3 | 0.1 | 0.2 | |
| *Lonicera nigra* | ts | | | | | | | | | 0.1 | | 0.1 | | | | | | | | 2 | 11 | 0.2 | – | | |
| *Luzula maxima* | mg | | | | | | | | | 0.1 | | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Thalictrum aquilegiifolium* | th | | | | | | | | | 0.1 | | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Symphytum tuberosum* | mh | | | | | | | | | 0.1 | | | 1.5 | | | | | 0.2 | | 3 | 17 | 0.8 | – | | |
| *Blechnum spicant* | mf | | | | | | | | | 0.1 | | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Picea excelsa* (seedlings) | tse | | | | | | | | | | 0.1 | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Ajuga reptans* | lh | | | | | | | | | | 0.1 | | | 0.1 | 0.1 | 0.1 | 0.1 | | | 5 | 28 | 0.5 | – | | |
| *Adoxa moschatellina* | lh | | | | | | | | | | 0.1 | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Chrysosplenium alternifolium* | lh | | | | | | | | | | 0.1 | | | 0.1 | | | | | | 2 | 11 | 0.2 | – | | |
| *Elymus europaeus* | tg | | | | | | | | | | 0.1 | | | | 0.1 | | 0.1 | | 0.1 | 4 | 22 | 0.4 | – | | |
| *Homogyne alpina* | lh | | | | | | | | | | 0.1 | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Festuca sylvestris* | tg | | | | | | | | | | 0.1 | | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Gentiana asclepiadea* | mh | | | | | | | | | | | 0.2 | 0.1 | | | | 0.1 | | | 3 | 17 | 0.4 | – | | |
| *Aruncus sylvestris* | th | | | | | | | | | | | 0.1 | | | | | 0.1 | | | 2 | 11 | 0.2 | – | | |
| *Phyteuma spicatum* | mh | | | | | | | | | | | 0.1 | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Solidago virga-aurea* | mh | | | | | | | | | | | 0.1 | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Cardamine trifolia* | lh | | | | | | | | | | | 0.7 | 0.1 | | | | | | | 2 | 11 | 0.8 | – | | |
| *Salix caprea* | ts | | | | | | | | | | | 0.1 | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Corydalis cava* | lh | | | | | | | | | | | 0.1 | | 0.1 | | 0.1 | | | | 3 | 17 | 0.3 | – | | |
| *Asplenium trichomanes* | lf | | | | | | | | | | | 0.1 | | | | | | | | 1 | 6 | 0.1 | – | | |
| *Cystopteris fragilis* | lf | | | | | | | | | | | 0.1 | | | | | | 0.1 | | 2 | 11 | 0.2 | – | | |
| *Ranunculus lanuginosus* | mh | | | | | | | | | | | | 0.1 | | | | | | 0.1 | 2 | 11 | 0.2 | – | | |
| *Carpinus betulus* (seedlings) | tse | | | | | | | | | | | | | 0.1 | | | | 0.5 | | 2 | 11 | 0.6 | – | | |
| *Stellaria holostea* | lh | | | | | | | | | | | | | 2.6 | | | | 0.2 | | 2 | 11 | 2.8 | 0.2 | 0.4 | |

| | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Carex remota* | mg | | | | | | | | | | | | | 0.1 | | | | | | 1 | 6 | 0.1 | – | |
| *Viola reichenbachiana* | lh | | | | | | | | | | | | | 16.1 | 0.1 | | | 0.1 | | 3 | 17 | 16.3 | 0.9 | 1.7 |
| *Ranunculus cassubicus* | mh | | | | | | | | | | | | | 0.1 | | | | | | 1 | 6 | 0.1 | – | |
| *Carex digitata* | lg | | | | | | | | | | | | | 0.1 | | | | | | 1 | 6 | 0.1 | – | |
| *Lysimachia nummularia* | lh | | | | | | | | | | | | | 0.1 | | | | | | 1 | 6 | 0.1 | – | |
| *Galeopsis pubescens* | mh | | | | | | | | | | | | | 0.1 | | | | | | 1 | 6 | 0.1 | – | |
| **Taraxacum officinale* | lh | | | | | | | | | | | | | 0.1 | | | | | 0.1 | 2 | 11 | 0.2 | – | |
| *Veronica officinalis* | lh | | | | | | | | | | | | | 0.1 | | | | | | 1 | 6 | 0.1 | – | |
| *Euonymus verrucosa* | ts | | | | | | | | | | | | | 0.1 | | | | | | 1 | 6 | 0.1 | – | |
| *Cornus sanguinea* | ts | | | | | | | | | | | | | 0.1 | | | | | | 1 | 6 | 0.1 | – | |
| *Bromus racemosus* | tg | | | | | | | | | | | | | | 0.1 | 0.1 | | | | 2 | 11 | 0.2 | – | |
| *Melica nutans* | mg | | | | | | | | | | | | | | | | 0.1 | | | 1 | 6 | 0.1 | – | |
| *Festuca gigantea* | tg | | | | | | | | | | | | | | | | 0.1 | | | 1 | 6 | 0.1 | – | |
| *Acer campestre* (seedlings) | tse | | | | | | | | | | | | | | | | | 0.5 | | 1 | 6 | 0.5 | – | |
| *Tilia cordata* (seedlings) | tse | | | | | | | | | | | | | | | | | 0.1 | | 1 | 6 | 0.1 | – | |
| *Quercus petraea* (seedlings) | tse | | | | | | | | | | | | | | | | | 0.2 | | 1 | 6 | 0.2 | – | |
| *Melica uniflora* | mg | | | | | | | | | | | | | | | | | 0.1 | | 1 | 6 | 0.1 | – | |
| *Ribes grossularia* | ms | | | | | | | | | | | | | | | | | 0.1 | 0.1 | 2 | 11 | 0.2 | – | |
| *Campanula rapunculoides* | mh | | | | | | | | | | | | | | | | | 0.6 | | 1 | 6 | 0.6 | – | |
| *Lathyrus vernus* | lh | | | | | | | | | | | | | | | | | 0.3 | | 1 | 6 | 0.3 | – | |
| *Fragaria vesca* | lh | | | | | | | | | | | | | | | | | 0.1 | 0.1 | 2 | 11 | 0.2 | – | |
| *Campanula persicifolia* | mh | | | | | | | | | | | | | | | | | 0.1 | 0.1 | 2 | 11 | 0.2 | – | |
| *Polygonum* sp. | lh | | | | | | | | | | | | | | | | | 0.1 | | 1 | 6 | 0.1 | – | |
| *Melittis melissophyllum* | mh | | | | | | | | | | | | | | | | | 0.1 | | 1 | 6 | 0.1 | – | |
| *Myosotis arvensis* | lh | | | | | | | | | | | | | | | | | 0.1 | | 1 | 6 | 0.1 | – | |
| *Dactylis polygama* | tg | | | | | | | | | | | | | | | | | 0.1 | | 1 | 6 | 0.1 | – | |
| *Rosa canina* | ms | | | | | | | | | | | | | | | | | 0.1 | | 1 | 6 | 0.1 | – | |
| *Heracleum sphondylium* | th | | | | | | | | | | | | | | | | | 0.1 | | 1 | 6 | 0.1 | – | |
| *Chelidonium maius* | mh | | | | | | | | | | | | | | | | | 0.1 | | 1 | 6 | 0.1 | – | |
| *Chaerophyllum hirsutum* | mh | | | | | | | | | | | | | | | | | 0.1 | 0.1 | 2 | 11 | 0.2 | – | |
| *Vicia sepium* | mh | | | | | | | | | | | | | | | | | 0.1 | | 1 | 6 | 0.1 | – | |
| *Ulmus montana* (seedlings) | tse | | | | | | | | | | | | | | | | | | 0.3 | 1 | 6 | 0.3 | – | |
| *Mulgedium alpinum* | th | | | | | | | | | | | | | | | | | | 0.1 | 1 | 6 | 0.1 | – | |
| *Lonicera xylosteum* | ts | | | | | | | | | | | | | | | | | | 0.1 | 1 | 6 | 0.1 | | |
| | | 24 | 24 | 45 | 35 | 54 | 40 | 20 | 29 | 39 | 50 | 54 | 50 | 42 | 49 | 38 | 53 | 51 | 45 | | | | | |

S – Slovakia, P – Poland, U – Ukraine

of Russia and even as near as Asia Minor or the Mediterranean region, (Kornaś 1953, 1954) to Eastern Europe. Despite this knowledge and a listing of synanthropic species reported, it is difficult to know precisely which species may have penetrated these old growth systems in the event of disturbance natural or otherwise. Added to this is the fact that natural species of disturbed situations could also invade. It is assured that **Impatiens parviflora*, **Stellaria media*, **Taraxacum officinale* and perhaps *Galeopsis tetrahit*, *G. bifida* and *G. pubescens*, the three former definite introductions, and the three latter perhaps native species of disturbed habitats, can be considered atypical and not ecological members of this forest system.

## Life form analysis

Life form of each species is designated adjacent to the name in Table 2. Seedlings of the canopy trees which contributed to the understorey of these forests are also designated and add to the total number of life form entities. The abbreviations of the life forms included are listed at the bottom of the table. The summary of the analysis is included in Table 3 in the left hand column for the European forests.

Of the 17 tree species found in the 18 stands, 88% regularly occur as mature trees in the upper canopy and 12% in the lower canopy. No trees are members which regularly are found predominantly as just saplings. Saplings (7%) and tree seedlings (8%) significantly contribute to the lower forest layers. Among the shrubs the tall shrub form is best represented (6%). Low shrubs are not present. Medium herbs have the highest representation (22%) but low herbs are also well represented (18%). Medium graminoids (5%) and medium and low ferns (3%) are best represented in these groups.

## Tree composition

Seventeen species of tree were recorded in the 18 forest stands (Table 2). *Fagus sylvatica* was of overwhelming ecological significance and not only occurred in all stands but was also the undisputed dominant in every one. In three it did not share measured importance with any other tree species. In an additional five stands it accounted for more than 80% of tree importance. In another five it contributed more than 65% of importance and in the remaining five forests it had importance between 107 and 192 (36–64%). These forests are not only strongly deciduous in nature but this life form aspect is largely contributed by a single species. *Abies alba* could be considered a secondary dominant but it has constancy (per cent presence) of only 72% and in no forest did it attain importance of 100. Importance actually varied between 1 and 95 and in more than half of the stands importance was 50 or less. Perhaps 60% of the forests could be described as deciduous-coniferous or mixed. The only other tree species of consistent occurrence (constancy 94) was *Acer pseudoplatanus*, but it had measured importance in less than 40% of stands, and was only observed as present in the others. It had highest importance contribution in those stands which had lower importance of *Fagus*, and thus augmented the dominance of deciduous species. Two species had constancy greater than 50, *Fraxinus excelsior* and *Sor-*

**Table 3.** Mesic Old Growth Deciduous Forests: Eastern Europe. Analysis of vascular life forms.

| Abbreviation | Life form | Per cent | |
|---|---|---|---|
| | | Eastern Europe | Ontario |
| utc | upper canopy tree | 8 | 9 |
| sct | sub canopy tree | 1 | 2 |
| lct | lower canopy tree | – | 1 |
| tsa | tall sapling | 7 | 6 |
| tse | tree seedling | 8 | 5 |
| wlt | woody liana tall | 1 | 1 |
| wlm | woody liana medium | 1 | 2 |
| ts | tall shrub | 6 | 6 |
| ms | medium shrub | 3 | 3 |
| ls | low shrub | – | 2 |
| th | tall herb | 7 | 7 |
| mh | medium herb | 22 | 19 |
| lh | low herb | 18 | 16 |
| lhc | low herbaceous climber | – | 1 |
| tg | tall graminoid | 3 | 1 |
| mg | medium graminoid | 5 | 10 |
| lg | low graminoid | 2 | 1 |
| tf | tall fern | 1 | 1 |
| mf | medium fern | 3 | 4 |
| lf | low fern | 3 | 2 |
| lze | low club moss | 1 | 1 |
| mxe | medium horsetail | – | 1 |
| lxe | low horsetail | – | 1 |
| mp | medium parasite | 1 | – |
| lp | low parasite | – | 1 |
| lsa | low saprophyte | 1 | 1 |

*bus aucuparia*. *Fraxinus* had measured importance in just three stands, only strongly in one, and *Sorbus* was occasionally observed as a small tree in a number of the stands but was only included in the quantitative sample as a sapling in only three (17%). In the others it was found as seedlings.

Two trees were found with constancy greater than 30, *Picea excelsa* and *Acer platanoides*. *Picea* had highest importance of 32 and in two other stands importance near 20. *Acer platanoides* had maximum importance of 27 and in two other stands 11 and 13. *Carpinus betulus*, *Tilia cordata*, *Ulmus montana* and *Prunus avium* had constancy near 20. *Carpinus* had higher values in two stands in which *Tilia* had modest importance. *Ulmus montana* had low importance of only 11 in one of these stands and *Prunus avium* which was only ever present and on just a single occasion as a tree, was also found in these stands. *Quercus petraea*, *Acer campestre* and *Ulmus carpinifolia*, all occurred in a single stand (constancy 5), and all had their highest importance in one of these same stands, the Boky Reserve, in north central Slovakia. The other trees, *Ulmus laevis* (constancy 11, highest importance 19), *Populus tremula* (5–1) and *Betula pendula* (5–7), were minor constituents of stands.

To summarize tree composition in these forests; the total number is not high for a large sample of stands extending over a considerable geographical area; most stands are strongly dominated by *Fagus sylvatica* and only *Abies alba* can be considered a secondary dominant; of all of the other species, only two attain relatively high importance (over 80) in two stands; all the others have only modest importance (over 20) in relatively few stands and this occurs mainly in communities where *Fagus* has lower importance (below 200).

These forests are composed predominantly of deciduous trees. Conifers comprise only 13% of total importance of all stands whereas 87% is contributed by deciduous tree life forms. There is no constant intermixing of these forms so these forests could not really be considered as deciduous-coniferous types.

## Dominance patterns

The order of leading dominants for each stand is provided in Table 4. This presents straightforwardly the dominance positions of all tree species in this forest complex and provides a basis for identifying the composition of each stand. *Fagus sylvatica* is the leading dominant in all stands. *Abies alba* is second dominant in 11 and a third in 1. *Acer*

**Table 4.** Mesic Old Growth Deciduous Forests: Eastern Europe. Order of tree dominance in individual stands. Numbers in superscriptes represent importance values.

| Stand | Tree dominance |
|---|---|
| 17 | *Fagus sylvatica*$^{300}$-*Acer pseudoplatanus*$^{1}$-*Abies alba*$^{1}$ |
| 19 | *Fagus sylvatica*$^{300}$-*Acer pseudoplatanus*$^{1}$-*Sorbus aucuparia*$^{1}$ |
| 9 | *Fagus sylvatica*$^{300}$-*Abies alba*$^{1}$-*Acer pseudoplatanus*$^{1}$-*Carpinus betulus*$^{1}$-*Fraxinus excelsior*$^{1}$ |
| 16 | *Fagus sylvatica*$^{287}$-*Acer platanoides*$^{13}$-*Acer pseudoplatanus*$^{1}$-*Fraxinus excelsior*$^{1}$-*Ulmus laevis*$^{1}$ |
| 5 | *Fagus sylvatica*$^{287}$-*Abies alba*$^{13}$-*Acer pseudoplatanus*$^{1}$-*Fraxinus excelsior*$^{1}$-*Sorbus aucuparia*$^{1}$ |
| 18 | *Fagus sylvatica*$^{286}$-*Acer pseudoplatanus*$^{7}$-*Acer platanoides*$^{7}$-*Fraxinus excelsior*$^{1}$-*Prunus avium*$^{1}$ |
| 24 | *Fagus sylvatica*$^{265}$-*Abies alba*$^{35}$-*Acer pseudoplatanus*$^{1}$-*Tilia cordata*$^{1}$ |
| 14 | *Fagus sylvatica*$^{249}$-*Abies alba*$^{48}$-*Ulmus montanum*$^{3}$-*Acer pseudoplatanus*$^{1}$-*Fraxinus excelsior*$^{1}$ |
| 6 | *Fagus sylvatica*$^{226}$-*Abies alba*$^{64}$-*Picea excelsa*$^{9}$-*Acer pseudoplatanus*$^{1}$-*Sorbus aucuparia*$^{1}$ |
| 3 | *Fagus sylvatica*$^{225}$-*Abies alba*$^{75}$-*Acer pseudoplatanus*$^{1}$-*Fraxinus excelsior*$^{1}$-*Picea excelsa*$^{1}$ |
| 8 | *Fagus sylvatica*$^{219}$-*Abies alba*$^{81}$-*Picea excelsa*$^{1}$ |
| 7 | *Fagus sylvatica*$^{208}$-*Abies alba*$^{63}$-*Picea excelsa*$^{20}$-*Ulmus montanum*$^{6}$-*Acer pseudoplatanus*$^{4}$ |
| 20 | *Fagus sylvatica*$^{199}$-*Carpinus betulus*$^{89}$-*Betula pendula*$^{7}$-*Tilia cordata*$^{5}$-*Acer platanoides*$^{1}$ |
| 12 | *Fagus sylvatica*$^{192}$-*Abies alba*$^{65}$-*Acer pseudoplatanus*$^{24}$-*Ulmus laevis*$^{19}$-*Fraxinus excelsior*$^{1}$ |
| 13 | *Fagus sylvatica*$^{181}$Abies alba$^{50}$-*Acer pseudoplatanus*$^{37}$-*Picea excelsa*$^{19}$-*Acer platanoides*$^{11}$ |
| 4 | *Fagus sylvatica*$^{172}$-*Abies alba*$^{95}$-*Acer pseudoplatanus*$^{33}$-*Picea excelsa*$^{1}$-*Sorbus aucuparia*$^{1}$ |
| 10 | *Fagus sylvatica*$^{140}$-*Carpinus betulus*$^{54}$-*Tilia cordata*$^{30}$-*Acer platanoides*$^{27}$-*Quercus petraea*$^{19}$ |
| 23 | *Fagus sylvatica*$^{107}$-*Fraxinus excelsior*$^{82}$-*Acer pseudoplatanus*$^{35}$-*Picea excelsa*$^{32}$-*Abies alba*$^{32}$ |

**Table 5.** Mesic Old Growth Deciduous Forests: Eastern Europe. Direct gradient analysis based on increasing latitude and longitude.

| **Latitude gradient** | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Country | S | U | U | U | U | S | S | S | S | U | S | P | P | P | P | P | P | P |
| Stand No. | 13 | 16 | 18 | 19 | 17 | 10 | 14 | 12 | 23 | 20 | 24 | 4 | 9 | 3 | 7 | 8 | 6 | 5 |
| Latitude | 48–11 | 48–12 | 48–12 | 48–13 | 48–18 | 48–35 | 48–40 | 48–40 | 48–43 | 44–10 | 49–25 | 49–27 | 49–28 | 49–28 | 49–34 | 49–35 | 49–36 | 49–46 |
| Elevation m | 900 | 760 | 620 | 550 | 700 | 400 | 750 | 875 | 875 | 350 | 800 | 875 | 550 | 900 | 900 | 850 | 1000 | 650 |
| *Tilia cordata* | – | – | – | – | – | 30 | – | – | – | 5 | – | – | 1 | – | – | – | – | – |
| *Carpinus betulus* | – | – | – | – | – | 54 | – | – | – | 89 | – | – | 1 | – | – | – | – | – |
| *Acer platanoides* | 11 | 13 | 7 | – | – | 27 | – | – | 8 | 1 | – | – | – | – | – | – | – | – |
| *Fraxinus excelsior* | 3 | 1 | 1 | – | – | 6 | 1 | 1 | 82 | – | – | – | 1 | 1 | – | – | – | 1 |
| *Fagus sylvatica* | 181 | 287 | 286 | 300 | 300 | 140 | 249 | 192 | 107 | 199 | 265 | 172 | 300 | 225 | 208 | 219 | 226 | 287 |
| *Acer pseudoplatanus* | 37 | 1 | 7 | 1 | 1 | 7 | 1 | 24 | 35 | 1 | 1 | 33 | 1 | 1 | 4 | – | 1 | 1 |
| *Picea excelsa* | 19 | – | – | – | – | – | – | – | 32 | – | – | 1 | – | 1 | 20 | 1 | 9 | – |
| *Abies alba* | 50 | – | – | – | 1 | – | 48 | 65 | 32 | – | 35 | 95 | 1 | 75 | 63 | 81 | 64 | 13 |
| *Ulmus montana* | – | – | – | – | – | 11 | 3 | – | 4 | – | – | – | – | – | 6 | – | – | – |
| **Longitude gradient** | | | | | | | | | | | | | | | | | | |
| Country | S | S | S | S | P | S | P | P | P | P | P | P | S | U | U | U | U | U |
| Stand No. | 10 | 12 | 14 | 13 | 6 | 23 | 8 | 7 | 5 | 9 | 4 | 3 | 24 | 16 | 18 | 19 | 17 | 20 |
| Longitude | 19.01 | 19.02 | 19.02 | 19.12 | 19.29 | 19.35 | 20.06 | 20.06 | 20–17 | 20–27 | 20–37 | 20–50 | 22–32 | 23–38 | 23–38 | 23–39 | 23–51 | 26–15 |
| *Ulmus montana* | 11 | – | 3 | – | – | 4 | – | 6 | – | – | – | – | – | – | – | – | – | – |
| *Tilia cordata* | 30 | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – | 5 |
| *Fraxinus excelsior* | 6 | 1 | 1 | 3 | – | 82 | – | – | 1 | 1 | – | 1 | – | – | 1 | 1 | – | – |
| *Acer platanoides* | 27 | – | – | 11 | – | 8 | – | – | – | – | – | – | – | 13 | 7 | – | – | 1 |
| *Carpinus betulus* | 54 | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – | 89 |
| *Acer pseudoplatanus* | 7 | 24 | 1 | 37 | 1 | 35 | – | 4 | 1 | 1 | 33 | 1 | 1 | 1 | 7 | 1 | 1 | 1 |
| *Fagus sylvatica* | 140 | 192 | 249 | 181 | 226 | 107 | 219 | 208 | 287 | 300 | 172 | 225 | 265 | 287 | 286 | 300 | 300 | 199 |
| *Abies alba* | – | 65 | 48 | 50 | 64 | 32 | 81 | 63 | 13 | 1 | 95 | 75 | 35 | – | – | – | 1 | – |
| *Picea excelsa* | – | – | – | 19 | 9 | 32 | 1 | 20 | – | – | 1 | 1 | – | – | – | – | – | – |

S – Slovakia, P – Poland, U – Ukraine

*pseudoplatanus* also an important tree was second dominant in three stands and third in 9. *Acer platanoides* was second dominant in one, third and fourth in 1 each and fifth in two. *Fraxinus excelsior* was fourth dominant in 4 stands, fifth in three and second dominant in 1. *Picea excelsa* was third dominant in three, fourth in three and fifth in one stand. Other tree species occupied minor positions of dominance.

In Table 5 the stands have been ordered longitudinally and latitudinally to examine possible geographical influences on tree composition. Several major trends become quite clear for more important species. Generally the stand importance of *Fagus sylvatica* increases passing eastward from Slovakia to Poland and then to Ukraine. Either in response to this geographical position or the ecological influence of increasing dominance of beech, the relative importance of other tree species also either tends to decrease or increase somewhat, and then decrease. Noteworthy are *Ulmus montana*, *Fraxinus excelsior*, *Acer pseudoplatanus*, *Abies alba* and *Picea excelsa*. Viewing the table it is clear that there is greater tree importance and biodiversity in the stands at lower longitudes in Slovakia, somewhat less in the Polish beech dominated forests, and markedly less in the Ukrainian stands at higher longitudes. Elevations are also included in the tables and if the richer stands are examined, there seem to be no straightforward effects relative to the elevations of adjacent stands.

When the stands are ordered latitudinally, there is almost a clear separation of stands of the Ukraine at lower latitudes (48–10 to 48–18), to those in Slovakia (48–35 to 49–25), to those in Poland (49–27 to 49–46). These groupings are almost clear cut with one exception. Related to this order of stands, the highest importance values of *Fagus sylvatica* occur in the Ukrainian forests. *Abies alba* with one exception is confined to the higher latitudinal forests in Slovakia and Poland. Higher importance of *Acer pseudoplatanus* occurs between latitudes 48–35 to 49–27 in Slovakia and southernmost Poland, *Fraxinus excelsior* at comparatively higher values is in the Slovakian forests. *Acer platanoides* has comparatively higher importance in the Ukranian and southern Slovakian forests and *Picea excelsa* occurs as a very modest admixture in the northern Slovakian and Polish stands. This latitudinal relationship is remarkably straightforward and appears to be stronger than the longitudinal east-west gradient. One would not have surmised that the stands were so directly disposed in considering the geography of southern Poland, eastern Slovakia and adjacent western Ukraine, due to the interposition of the Carpathians at this juncture.

## Tree size classes

In Table 6 toward the bottom of the first section on environmental factors and general compositional features, the percentages of tree size classes in each stand are provided. Minimum tree size is 77 sq. cm and the first class is from this value to 516 sq. cm and the succeeding classes are in multiples of four – 2064, 8256 and 8259+. Trees of the first size class are quite small but trees in the largest classes are very large and those over 8259 sq. cm are huge. Not all stands have these huge trees but almost all of the stands of Ukraine and Slovakia include them but less than half of the Polish forests sampled do. Most have

**Table 6.** Statistic of Mesic Old Growth Deciduous Forests: Eastern Europe.

| Tree size classes sq. cm | U | U | P | U | P | U | S | S | P | P | P | P | U | S | S | P | S | S | Average |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **17** | **19** | **9** | **16** | **5** | **18** | **24** | **14** | **6** | **3** | **8** | **7** | **20** | **12** | **13** | **4** | **10** | **23** | |
| | Tree size classes in percent | | | | | | | | | | | | | | | | | | |
| 77–516 | 27 | 28 | 24 | 21 | 4 | 11 | 37 | 39 | 17 | 20 | 24 | 30 | 13 | 41 | 57 | 25 | 36 | 5 | 26 |
| 517–2064 | 34 | 24 | 57 | 24 | 53 | 33 | 30 | 23 | 34 | 39 | 62 | 48 | 65 | 27 | 13 | 25 | 40 | 30 | 37 |
| 2065–8256 | 38 | 46 | 19 | 71 | 23 | 51 | 32 | 38 | 46 | 41 | 14 | 21 | 22 | 30 | 27 | 46 | 33 | 62 | 36 |
| 8257+ | 1 | 2 | – | 4 | – | 5 | 1 | – | 3 | – | – | 1 | – | 2 | 3 | 4 | 1 | 3 | 2 |

*Note*: Stands are indicated by numbers in boldface.

| Tree size classes sq. cm | U | S | P |
|---|---|---|---|
| | Range | | |
| 77–516 | 11–28 | 5–57 | 4–30 |
| 517–2064 | 24–65 | 13–40 | 25–62 |
| 2065–8256 | 22–71 | 23–62 | 14–46 |
| 8257+ | – – 5 | – – 3 | – – 4 |

| Tree size classes sq. cm | U | S | P | U | S | P |
|---|---|---|---|---|---|---|
| | Average | | | Unusual values | | |
| 77–516 | 20 | 36 | 24 | –2 | +1 | –1 |
| 517–2064 | 36 | 27 | 53 | +1 | –1 | –2 |
| 2065–8256 | 46 | 35 | 35 | +1 | +1 | –2 |
| 8257+ | 3 | 2 | 1 | +1 | | +1 |

S – Slovakia, P – Poland, U – Ukraine

comparatively low percentages of the smallest class, usually the percentages of the second class are below 30 and often high percentages of the third and fourth classes of trees were found.

## Canopy and tree heights

For forest sites in such nearby regions the maximum heights of the upper forest canopies would not be considered so different. In the Ukrainian forests the average for the four Carpathian foothill stands is 42 m. These forests did not contain *Abies* or *Picea* and the tall spires of these species did not complicate the measurements. In Slovakia the *Abies* did complicate determination of an upper canopy level but the average there was 41. Oddly in Poland the measurement was decidedly less at 32 with relatively little variation from stand to stand and *Abies* was also a problem there. The actual measurements are included in the initial section of Table 2.

## Understorey composition

The elements of understorey composition which may be considered with the data available are, contribution by tree seedlings which includes those which germinated in the year recorded and others of greater longevity up to 76 sq. cm basal area BH, by shrubs, and by vascular herbs. The data are included in Table 2 which includes estimated cover for all species observed in all stands, and summarized values for number of stands of occurrence, frequency (% stands of occurrence), total estimated cover, and average estimated cover.

A general feature which relates to cover of understorey elements in these forests can be noted. Cover values of five % or greater are quite significant quantitatively compared to the majority of records. If the table is divided into two halves arbitrarily, it can be determined readily that a significantly greater number, actually almost twice (48%), of values five or greater are found on the right side of the table. Since most of the stands on this side are situated in Poland and Slovakia, this is evidence that passing from east to west the productivity of understories in these mesic old growth deciduous forests tends to increase considerably. This is also true of biodiversity in the understories because the average number of species in the nine stands on the left of the table is 34, whereas that of the same number of stands on the right is 48, an increase of 41%. There seems definitely to be a trend in floristic and productive depauperization passing from west to east.

Of the 17 tree species found in all stands, tree seedlings were only observed for 14. Of these only five had average estimated cover values including *Fagus sylvatica*, *Acer pseudoplatanus*, *Fraxinus excelsior*, *Abies alba* and *Acer platanoides*. All of these had fractional values except *Acer pseudoplatanus* and *Fagus sylvatica* and only the latter can be considered to contribute significantly to understorey with values of 100 constancy and 7.7% average estimated cover. *Acer pseudoplatanus* had values of 67 and 1.0%. In respect to the contribution of tree seedlings to the understories of these forests it, can only be reported that beech is successful in the silvical environments it creates. Tree seedlings contributed 9.5% of total cover.

With respect to the contribution of shrubs to the understorey vegetation, 15 species of which 12 (80%) are tall life forms, are involved. Regardless of number and life form only five species have values for average estimated cover. These are *Rubus hirtus* (83 constancy, 5.8 average estimated cover), *R. idaeus* (72–1.3), *Vaccinium myrtillus* (11–0.3), *Sambucus nigra* (72–0.2) and *S. racemosa* (50–0.1). The only significant contributions are by *Rubus hirtus* and *R. idaeus* and the first is by far the most evident. Shrubs would thus seem to have much the same participation in the understorey vegetation as tree seedlings with the latter producing 9.5% and the former 7.7% of average estimated cover. This is about 32% of total estimated cover.

In these forest stands 109 species of various forest herbs were recorded, but of these only 16 had percentages of average estimated cover of 1 or greater. The largest contributors were *Athyrium filix-femina* and *Asperula odorata* with values of 9.6 and 9.4 respectively. *Athyrium* had constancy of 100 being present in all stands and *Asperula* 94. As expected some herbs had higher constancy and somewhat lower average estimated cover or the reverse, but it is suitable to use % total estimated cover as the basis for discussing the contributions of herbs to the understorey. Four species had higher constancies (61–89) and average cover between 4.3 and 6.4 and participated strongly in the understorey vegetation: *Impatiens noli-tangere* (6.4), *Oxalis acetosella* (5.8), *Dryopteris filix-mas* (4.7) and *Galeobdolon luteum* (4.3). Six species (constancies 17–89) had moderately high average cover: *Mercurialis perennis* (3.6), *Urtica dioica* (2.4), *Dryopteris austriaca* (1.7), *Viola reichenbachiana* (1.7), *Polystichum lobatum* (1.5), and *Dryopteris disjuncta* (1.3). Finally four additional plants which exceeded average cover of 1.0 were in constancy categories 11–67, and had modest average cover: *Geranium robertianum* (1.1), *Dentaria bulbifera* (1.1), *Impatiens parviflora* (1.1), and *Calamagrostis arundinacea* (1.1). It is notable that these 16 higher average cover species collectively contributed more than half of total cover (56.8%) in all 18 stands. Although the herbaceous life forms are generally much smaller than those of tree seedlings and shrubs, nevertheless they account for significantly more average cover (39.6%) than both of these combined (17.2).

An additional 33 herbs had average cover values less than 1. This meant that 59 (43%) herbaceous species of a total of 138 did not have average cover values indicating that their frequencies and cover values in most stands where found, were extremely low. These species may be noted as they are found throughout Table 2.

## Biodiversity

Biodiversity is essentially an indication of species richness in any location in any vegetational community. These values for vascular components for mesic old growth deciduous forests in Eastern Europe are found at the bottom of Table 2 and they vary considerably from 20 to 54, by a value of 170 per cent. The average is 41 species per stand but if the stands are averaged in local groups distinct differences are found in the three regions which indeed are not too distant from each other. In Ukraine the variation is from 24 to 42, with an average of 33. In Slovakia variation is 20–51 and average 39. In southern Poland species per stand varies from 39–54 and the average is 49.

## Tree reproduction

The DF values for all sapling species involved in the stands are presented in Table 7. The saplings growing in these mesic forest stands give some indication of what may develop in the future, whether the tree species may maintain their existing compositional position or whether they may be successionally replaced by other species.

It can be seen that of the 17 tree species occurring in the stands only 11 were found as saplings and seven of these were found in a single stand and one other occurred in just two. Actually the DF values indicate that only three species are of any reproductive consequence, *Fagus sylvatica*, *Abies alba* and *Acer pseudoplatanus*. *Fagus* is the overwhelming contributor, actually being the only sapling producer in seven stands and assuming by far the position of major sapling in an additional eight stands, thus accounting

**Table 7.** Mesic Old Growth Deciduous Forests: Eastern Europe tree reproduction. DF values for all sapling species.

| Species | Stands No. | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 17 | 19 | 9 | 16 | 5 | 18 | 24 | 14 | 6 | 3 | 8 | 7 | 20 | 12 | 13 | 4 | 10 | 23 |
| *Fagus sylvatica* | 200 | 200 | 129 | 200 | 200 | 200 | 145 | 184 | 200 | 162 | 188 | 153 | 200 | 154 | 196 | 183 | 112 | 149 |
| *Abies alba* | – | – | 71 | – | – | – | 55 | 16 | – | 38 | 12 | 43 | – | 25 | 4 | 11 | – | 42 |
| *Acer pseudoplatanus* | – | – | – | – | – | – | – | – | – | – | – | 5 | – | 15 | – | 6 | 11 | – |
| *Ulmus laevis* | – | – | – | – | – | – | – | – | – | – | – | – | – | 6 | – | – | – | – |
| *Acer platanoides* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 32 | – |
| *Carpinus betulus* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 12 | – |
| *Tilia cordata* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 23 | – |
| *Ulmus montana* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 4 | 5 |
| *Acer campestre* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 4 | – |
| *Ulmus carpinifolia* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 4 | – |
| *Picea excelsa* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 5 |

for most of the reproduction in 15 or 83% of all stands. Even in the remaining three stands it represents well over half the reproduction. *Abies alba* is sporadic in reproductive efforts and occurs only in the stands in Poland and Slovakia and tends to have higher DF in the former. DF values range form 71 to 4. *Abies* seems to be producing sufficient reproduction to maintain the species in some stands and failing to do so in others, but generally the reproductive effort of this species in terms of saplings is typically poor. These trends can be determined by comparing the DF values (to 200) in Table 6. *Acer pseudoplatanus* had measurable saplings in only four stands having lower importance of *Fagus*, two in Poland and two in Slovakia.

Another check on the overall reproductive success of species can be determined in Table 2 where data on tree density/ha and sapling density/ha is included in the upper environmental section. Trees are often large specimens particularly in old growth forests and accordingly occupy more space and there should be fewer per hectare than saplings which are much smaller and could be more numerous. If the values for tree density are carefully compared to those for sapling density in the same stands, it will be evident that in 14 (78%) there are fewer saplings per hectare and in only four (22%) are there a greater number. In three stands there are totally insufficient saplings (average of only 12), and in another three they are quite low (average 74). Even in those stands with a higher number of saplings over trees only in two are they strongly increased.

## Ordination analysis

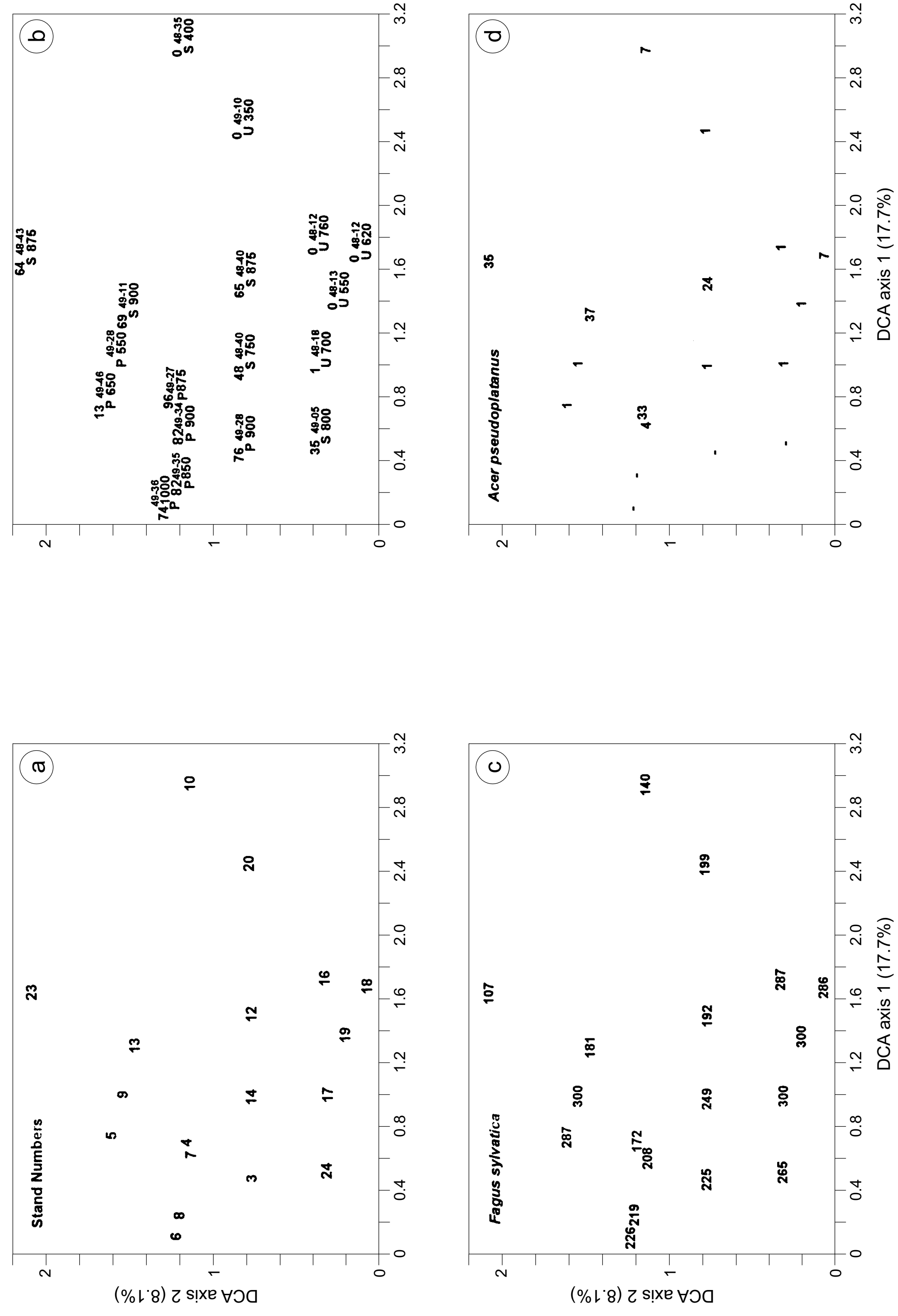
An ordination by Detrended Correspondence Analysis was undertaken but it employed the quantitative data on understorey rather than that on the tree layer. This was considered advisable because the latter is relatively simple, including just 17 tree species and with many of these contributing minimally and to relatively few stands. The tree data could subsequently be related quite independently to the ordination based on understorey.

The results of the ordination which included quantitative data for 155 species including tree seedlings, shrubs, and herbs, is presented in Fig. 1a. The first DCA axis accounts for 17.7% of stand variation and the second axis 8.1%. There is a remarkably good spread of the stands considering that they have the same site moisture and are relatively similar in composition. It is important to restate that 49 understorey species (32%) occurred on just a single occasion in any one stand and thus had little influence on the separation in the ordination.

In Fig. 1b the sum of importance of coniferous trees, essentially those of *Abies alba* (Fig. 2a) and *Picea excelsa* (Fig. 2b), is presented on the ordination. This graph also provides an indication of the ecological influences operating to give rise to the primary axis – pure deciduous forests on the extreme right and mixed deciduous-coniferous evergreen forests on the left. It is difficult to say that this is a straightforward temperature influence although in the same direction on the ordination latitude shows an increasing trend. Coincident with this trend up to a two fold increase in elevation also suggests the development of somewhat cooler conditions which may favour the coniferous evergreen habit. *Abies alba* is not, however, a boreal or upper montane species as is *Picea excelsa* but one which thrives in the lower montane zone of the Carpathians (Szafer 1966). Temperature related to increasing latitude and elevation may well be a significant influence in its occurrence in this lower montane zone.

The second axis of the ordination appears to be geographically related (Fig. 1b). At the lower end the stands sampled in the Ukraine on the eastern side of the Carpathians are grouped together closely. Centrally on this axis the stands in Slovakia are grouped together but not quite so tightly and more to the right, but then all of the stands from southern Poland are found tightly grouped together in the central and upper right of the ordination. It seems more natural to think of these three countries in a west to east direction – Slovakia–Poland–Ukraine, but at the junction of these territories there is a much more natural transition in a south-north direction from Ukraine through Slovakia and thence into southern Poland. This provides what is almost a straightforward latitudinal gradient (Fig. 1b) which, coupled with an increasing elevational gradient, may well cause distinct differences in composition. This is quite interesting because we must be reminded that the ordination, based solely on the composition of the understorey, does not include tree composition nor environmental characteristics and yet direct relationships with these phenomena do appear.

*Fagus sylvatica* is the overwhelming dominant of these mesic old growth deciduous forests and is found at quite high importance in all of them from more than a third (107) to full tree importance (300) and yet despite widespread occurrence it is worthwhile to indicate its distribution of importance on the ordination because it does have ecological significance (Fig. 1c). Stands with the highest values occur at the bottom of the second axis and are centered on the stands in the Ukraine. Centrally on the second axis this tree has intermediate importance and, with one exception, the lower values are found at the upper limits of this axis. Related to this distribution, stands with moderate values of


a
b
c
d
Stand Numbers
Fagus sylvatica
Acer pseudoplatanus
DCA axis 1 (17.7%)
DCA axis 2 (8.1%)

*Carpinus betulus* and *Fraxinus excelsior* with *Fagus* are found on the upper right (not shown), perhaps indicating site moisture on the slightly drier side of mesic. In Fig. 1d the distributional pattern of *Acer pseudoplatanus* is presented which attains optimum comparative importance in the central and upper sections of the second axis. Another species of maple, *Acer platanoides* has relatively lower importance but it is found in stands on the right half of the first axis (Fig. 2c) with little overlap with stands which have *Acer pseudoplatanus* to indicate a fairly distinct ecology for these *Acer* species.

In viewing the distributional patterns for these trees it is essential to note the continuity which characterizes many of the quantitative values which pass across or vertically on the ordination and their attainment of ecological optima in different parts of it. *Fagus sylvatica* is the species which essentially ties the system together and the other trees relate to this dominance but their relationship is not distinct and considerable overlap of their distributions occurs. This is readily apparent in the distribution patterns for *Abies alba* (Fig. 2a) and *Picea excelsa* (Fig. 2b). *Abies* is more widespread but is found in stands on the left of the first axis which are found at higher latitudes and higher elevations than those without fir at lower right. *Picea excelsa* is found in the far upper left of the ordination and only in forests in which *Abies* has higher values, so there is not only overlap in the distributions of these conifers but it is a specific overlap.

The distribution of comparative importance values for *Acer platanoides* (Fig. 2c) on the ordination are much more restricted to the right half of the ordination than those of *Acer pseudoplatanus*. It is found mostly in the stands with lower or minimal values of the latter, and yet there is overlap and some continuity. *Fraxinus excelsior* another tree species with modest importance has much the same occurrence as *Acer platanoides* and *Tilia cordata* is also similar (not graphed).

The seedlings of trees especially *Fagus sylvatica* and *Acer pseudoplatanus* and perhaps *Fraxinus excelsior* contribute significantly to the understorey vegetation (Table 2). It is instructive to determine whether the contributions are ecologically related. The pattern for *Fagus* (seedlings), the most important is presented in Fig. 2d. It attains estimated cover values as high as 20%. Most of the higher coverages are in the lowest section of the second axis, essentially in stands where *Fagus* attains its greatest importance, but these continue into the upper left where beech importance is still high. Where beech importance is lower, in the upper part of second axis, seedling coverages are quite low. Thus usually strong dominance of beech favours abundant reproduction of the species. The same pattern seems to hold true for seedlings of *Acer pseudoplatanus*, *A. platanoides* and *Fraxinus excelsior*, but not for *Abies alba* and *Picea excelsa* which have very low seedling coverages.

There are many species in the understorey vegetation and it is only possible to deter-

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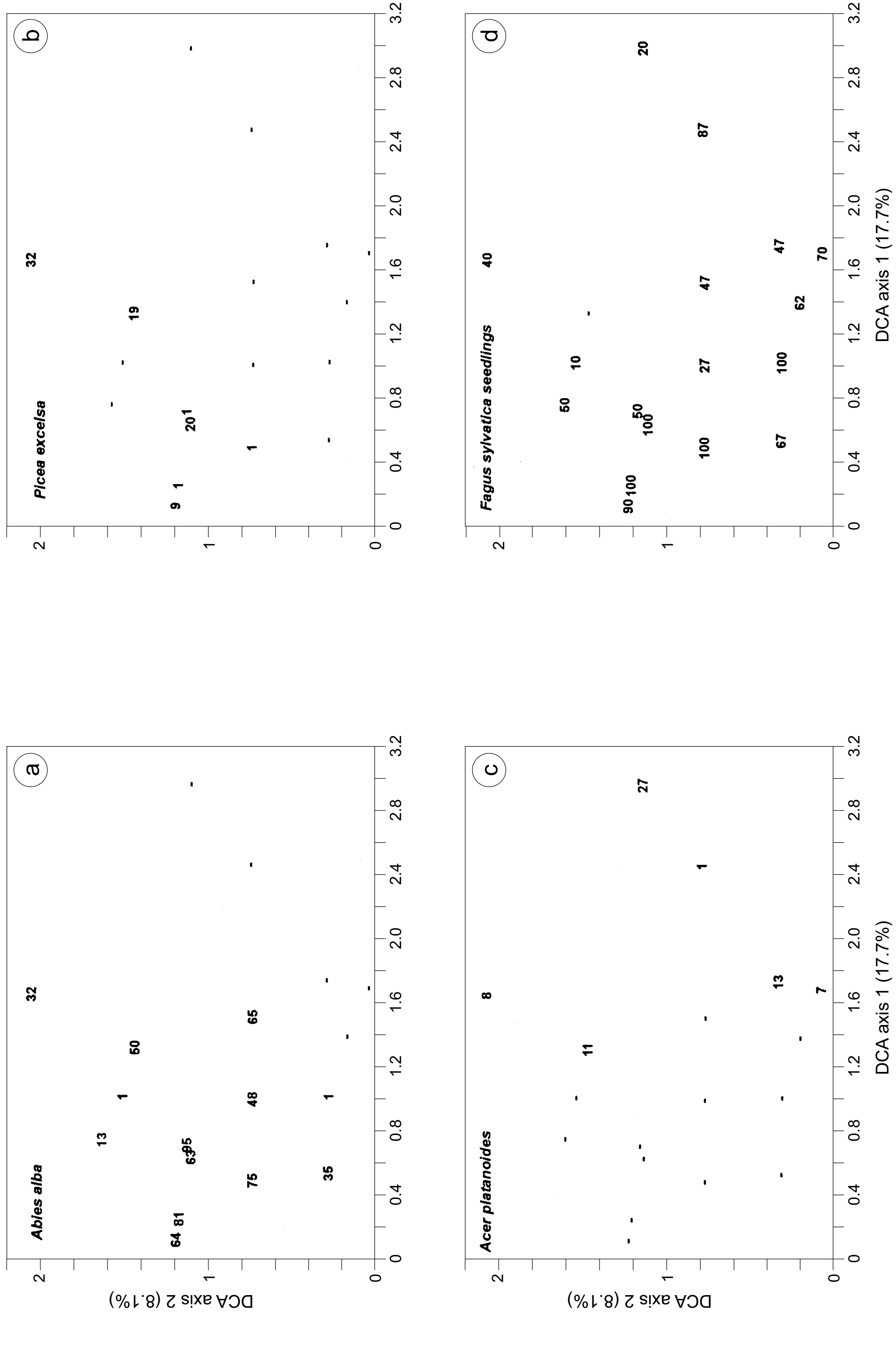
**Fig. 1.** Results of Detrended Correspondence Analysis. **a** – ordination of all stands based on understorey composition. Numbers refer to stands; **b** – stand ordination displaying sum of conifer importance (upper left value) latitudinal position (upper right), country of origin (lower left) and elevation in m (lower right); P – Poland, S – Slovakia, U – Ukraine. Distribution of stand importance values for: **c** – *Fagus sylvatica*; **d** – *Acer pseudoplatanus*.


a
Abies alba
b
Picea excelsa
c
Acer platanoides
d
Fagus sylvatica seedlings
DCA axis 1 (17.7%)
DCA axis 2 (8.1%)

mine whether specific patterns emerge and then to attempt to relate other species possibly to these patterns.

The most abundant (highest average estimated cover percentages) understorey plant was *Athyrium filix-femina* (Fig. 3a). It was found in every stand with cover values between 0.1 and 30.5 and is thus spread throughout the ordination. Despite such dispersion it clearly attains highest frequency values in the upper left sector in forests with very strong beech and highest fir importance. Similar patterns, although not to the same quantitative levels, are shown by *Oxalis acetosella*, *Rubus idaeus*, *Symphytum cordatum*, *Dryopteris austriaca*, and *Dryopteris carthusiana*. *Asperula odorata* (Fig. 3b) would seem to follow the same relationship but it has higher cover values over much of the ordination. It would seem to be straightforwardly a species associated with *Fagus* and does not attain high cover levels in beech forests with a strong admixture of conifers. It is a characteristic species of the Fagion alliance and the Fagetalia order.

The frequency values for one of the most widespread shrubs in these old growth forests-*Rubus hirtus*, is shown in Fig. 3c. It is found through most of the ordination but attains optimum occurrence in the lower left of the ordination in stands generally strong in beech with modest concentrations of fir. Species with similar patterns are *Impatiens noli-tangere*, *Prenanthes purpurea* and *Sambucus racemosa*.

*Lysimachia nemorum* (Fig. 3d) had very minor frequency values but all are strongly concentrated at the upper left hand corner of the ordination in stands dominated by *Fagus* with highest values for *Abies*. *Dryopteris phegopteris* and *Polystichum lobatum*, the latter a characteristic species of the Fagion alliance and *Fagetalia* order, show very similar patterns.

*Polygonatum verticillatum* (Fig. 4a) is almost as tightly grouped on the ordination as *Lysimachia nemorum* but shifted downward to the right and thus attaining optimum distribution in stands with highest values of *Abies*, of course with also high *Fagus*. These species in their occurrences grade very smoothly and continuously into one another on the ordination. *Polystichum braunii*, characteristic of *Fagetum carpaticum* and *Gentiana asclepiadea* have similar optima.

In Fig. 4b *Sanicula europaea* is found diagonally across the ordination from lower right to upper left. This pattern is related to intermediate levels of *Fagus* importance. Although it is characteristic of the Fagetalia order it seems to be found only in old growth systems with intermediate importance of beech, certainly not within all compositional phases. In fact it seems more associated with intermediate importance of *Fagus* and relatively high *Abies* and *Acer pseudoplatanus*. *Paris quadrifolia* has a similar distribution.

*Geranium robertianum* a species found in mesic old growth deciduous forests in Japan, China, central Europe and eastern North America as a native plant, is widespread

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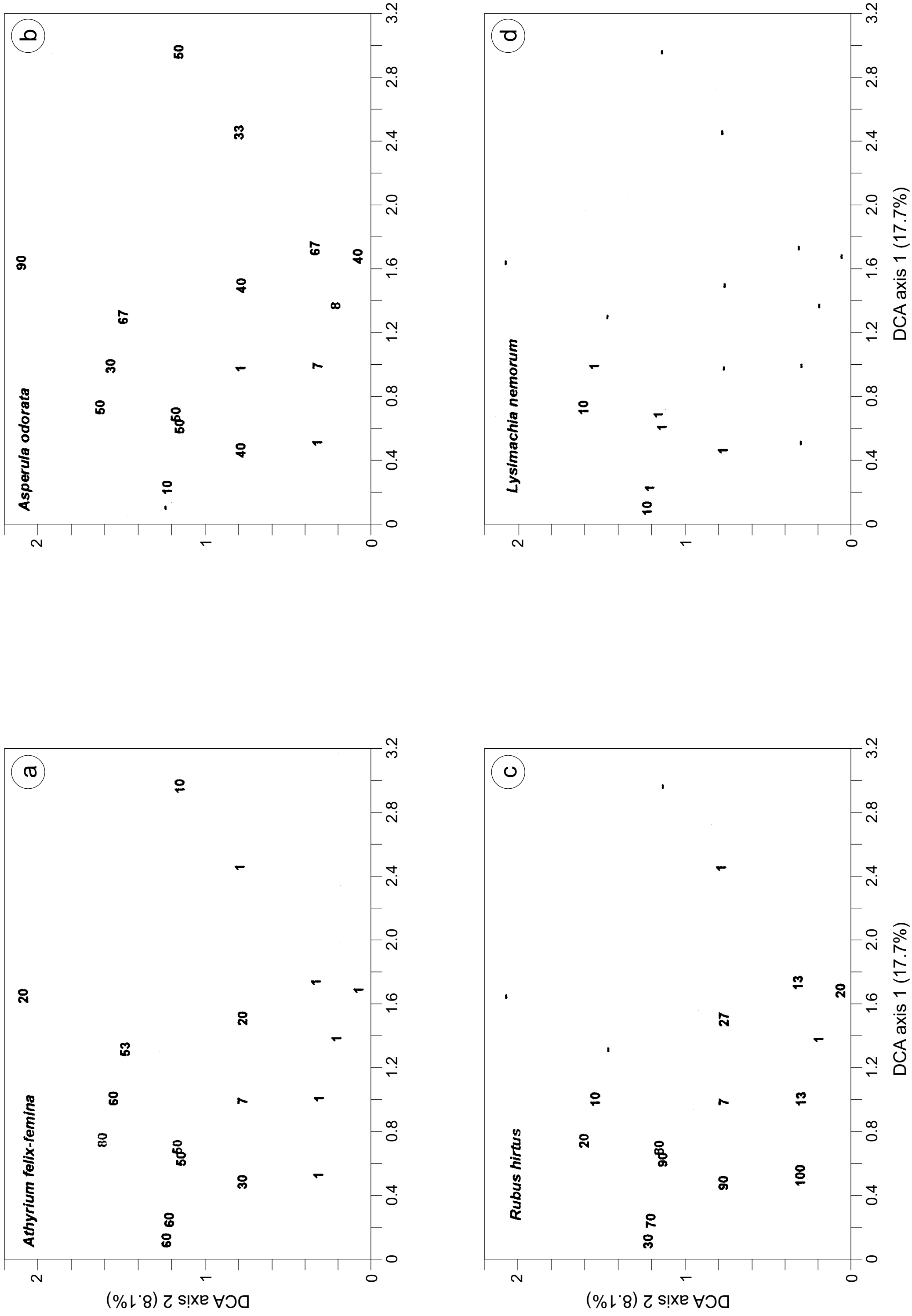
**Fig. 2.** Results of Detrended Correspondence Analysis. Distribution of stand importance values for: *Abies alba* (**a**), *Picea excelsa* (**b**) and *Acer platanoides* (**c**). Stand frequency values for *Fagus sylvatica* seedlings (**d**).


a
Athyrium felix-femina
b
Asperula odorata
c
Rubus hirtus
d
Lysimachia nemorum
DCA axis 1 (17.7%)
DCA axis 2 (8.1%)

predominantly on the upper half of the ordination indicating a strong relationship with stands of moderate *Fagus* importance and high in *Abies* (Fig. 4c).

*Mercurialis perennis* (Fig. 4d) also characteristic for Fagetalia, is found diagonally across the ordination from lower mid to upper left first axis. Nevertheless it is a graded continuous response from low values from the lower mid region to the upper left of the ordination. *Actaea spicata* and *Epilobium montanum* display quite similar distributions, related to highest *Fagus* importance to highest *Abies*-*Fagus* importance.

In the central section of the second axis *Ajuga reptans* (Fig. 5a) is limited in occurrence with relatively low values. This appears to be related to moderate importance of *Fagus* and higher importance of *Abies*.

Following down and diagonally across the ordination from center to lower right are the occurrences of *Epipactis helleborine* (Fig. 5b). This species is almost restricted to stands with maximum importance of beech. *Neottia nidus*-*avis* has an identical pattern of distribution befitting it as a characteristic species of *Fagetalia*. The absence of this parasite from so many other beech stands is difficult to understand.

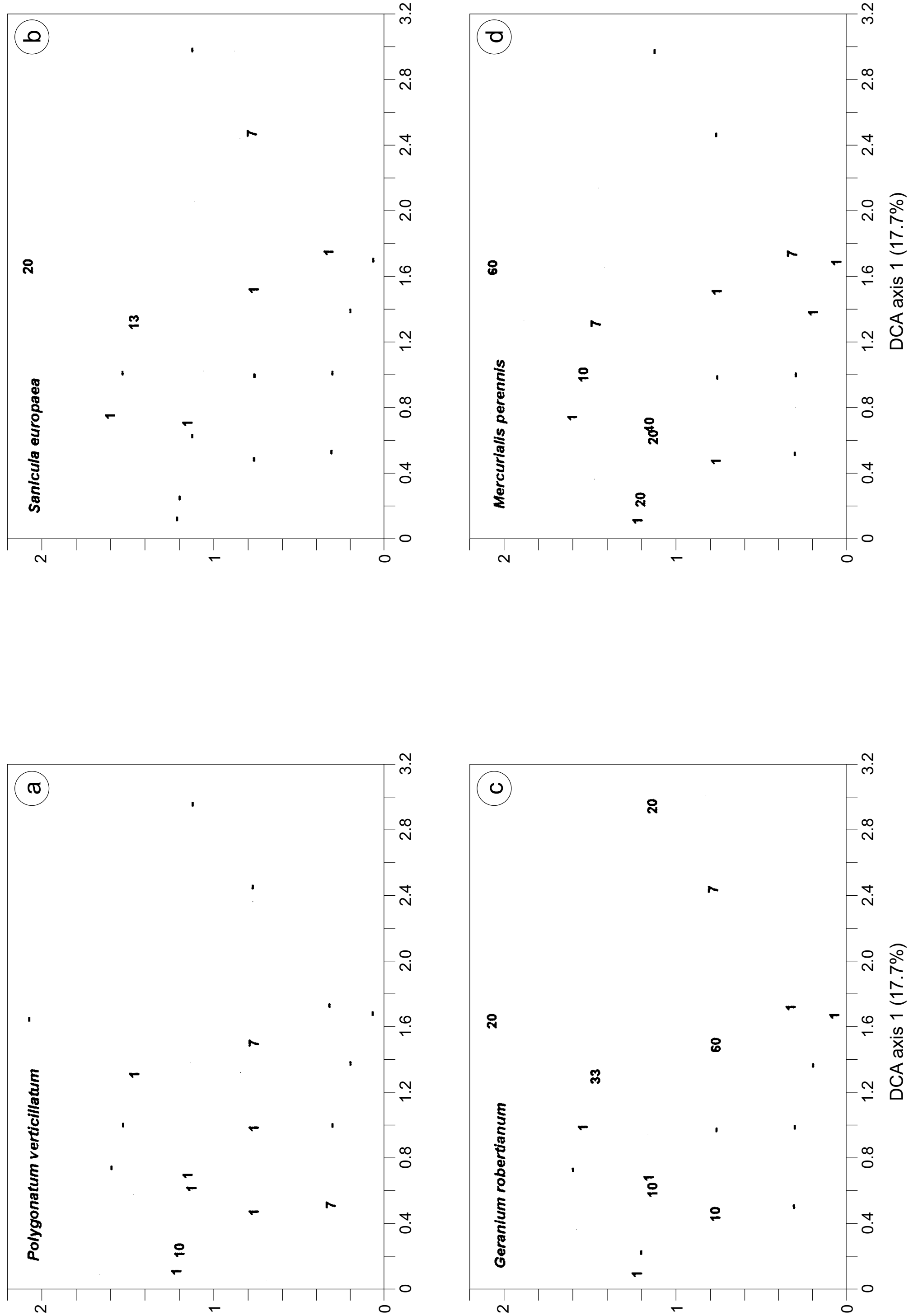
The widely distributed *Dryopteris filix*-*mas* (Fig. 5c) is a species of strong beech dominated forests with amounts of fir or *Acer pseudoplatanus*. A number of plants display similar patterns on the ordination including *Senecio fuchsii*, *Salvia glutinosa*, *Dentaria bulbifera* and *Hordelymus europaeus*.

*Hedera helix*, a woody liana, is confined to the lower right of the ordination (Fig. 5d) and is apparently restricted to deciduous stands without conifers. It is instructive to note that although this species occurred in only three of 18 stands sampled, these stands are all adjacent to one another on the ordination, indicating similar community composition. *Viola reichenbachiana* has the same relationship. Another group of plants of low constancy: *Ribes grossularia*, *Fragaria vesca*, *Campanula persicifolia* and *Chaerophyllum hirsutum* occur in adjacent stands but in the upper right section of the ordination.

## Discussion

Visually, these mesic old growth ecosystems are magnificent examples of climax deciduous forests which have evolved and developed in this Carpathian enclave of Eastern Europe. The senior author has quantitatively studied similar old growth systems in Japan, China, continental Europe, England, eastern United States and extreme Southern Canada, and those analyzed here are as impressive as any he has been fortunate to view. Although phytosociological interest in these systems has long been strong and ecological interest in old growth forest systems has greatly increased in the past decade, no comprehensive quantitative analysis has as yet been produced. The quantitative study of these remarkable

**Fig. 3.** Results of Detrended Correspondence Analysis. Stand frequency values for: **a** – *Athyrium filix-femina*; **b** – *Asperula odorata*; **c** – *Rubus hirtus* and **d** – *Lysimachia nemorum*.


a
Polygonatum verticillatum
b
Sanicula europaea
c
Geranium robertianum
d
Mercurialis perennis
DCA axis 1 (17.7%)
DCA axis 2 (8.1%)

18 stands has provided an opportunity to provide information to close this gap but also to permit a comparison with old growth systems elsewhere.

It is important to affirm at the outset that the stands chosen for intensive quantitative study were not preselected by the major investigator. He informed his collaborators, in Slovakia, Poland and Ukraine that he wished to find mesic old growth deciduous forests as found in their regions, and based on their knowledge of National Parks and Forest Nature Preserves, the known possibilities were visited. Once there, the senior investigator decided on stand selection after areas were extensively examined. This is clearly stated so it is realized that no special forest types of any particular composition or ecological relationships other than mesic deciduous were sought for. The intention was to objectively determine the quantitative composition, aspects of structure and various ecological characteristics which might influence or determine these features. In addition to understanding these mesic old growth systems, the intention was to compare them with similar systems elsewhere particularly in extreme Southern Ontario in Canada. There is so much discussion about old growth forests and plant biodiversity and yet so little comparative quantitative information using the same methodology has been published. The basis for the Ontario comparison is a sample of twelve mesic old growth deciduous forests selected from more than 200 stands the senior author has sampled over an extended period.

Floristically these forests would seem rich with 155 vascular species in 54 families but comparatively they are relatively poor in species. In only 12 similar stands in Southern Ontario there were 250 species a 161% increase. There were almost twice the number of tree species. Comparing the floras of Europe and North America such a comparison would be expected. However a richer flora should not necessarily guarantee richer plant communities, but in this case of mesic deciduous or deciduous-evergreen systems, it is apparently true.

Despite the depauperate flora and communities there is great floristic similarity in these plant systems. In Table 8, actual and possible ecological equivalents are presented. Actual taxonomic equivalents include twelve species: *Galium aparine*, *Adiantum pedatum*, *Equisetum arvense*, *E. hyemale*, *Asplenium trichomanes*, *Athyrium filix-femina*, *Dryopteris spinulosa*, *Rubus idaeus*, *Circaea alpina*, *Geranium robertianum*, *Cystopteris fragilis* and *Milium effusum*. It is of note that 7 of these 12 species are primitive more ancient and probably earlier evolved vascular plants. Another five species are introduced in Ontario but are found in identical communities: **Prunus avium*, **Epipactis helleborine*, **Solanum dulcamara*, **Chelidonium maius* and **Taraxacum officinale*. In addition there are at least an additional 40 ecological vicariads which bespeaks considerable ecological similarity in these widely separated but environmentally similar ecosystems.

An aspect of the floristics of these mesic old growth deciduous forests is related to the presence of ancient forest plant species (Hermy *et al*. 1999) which have been determined

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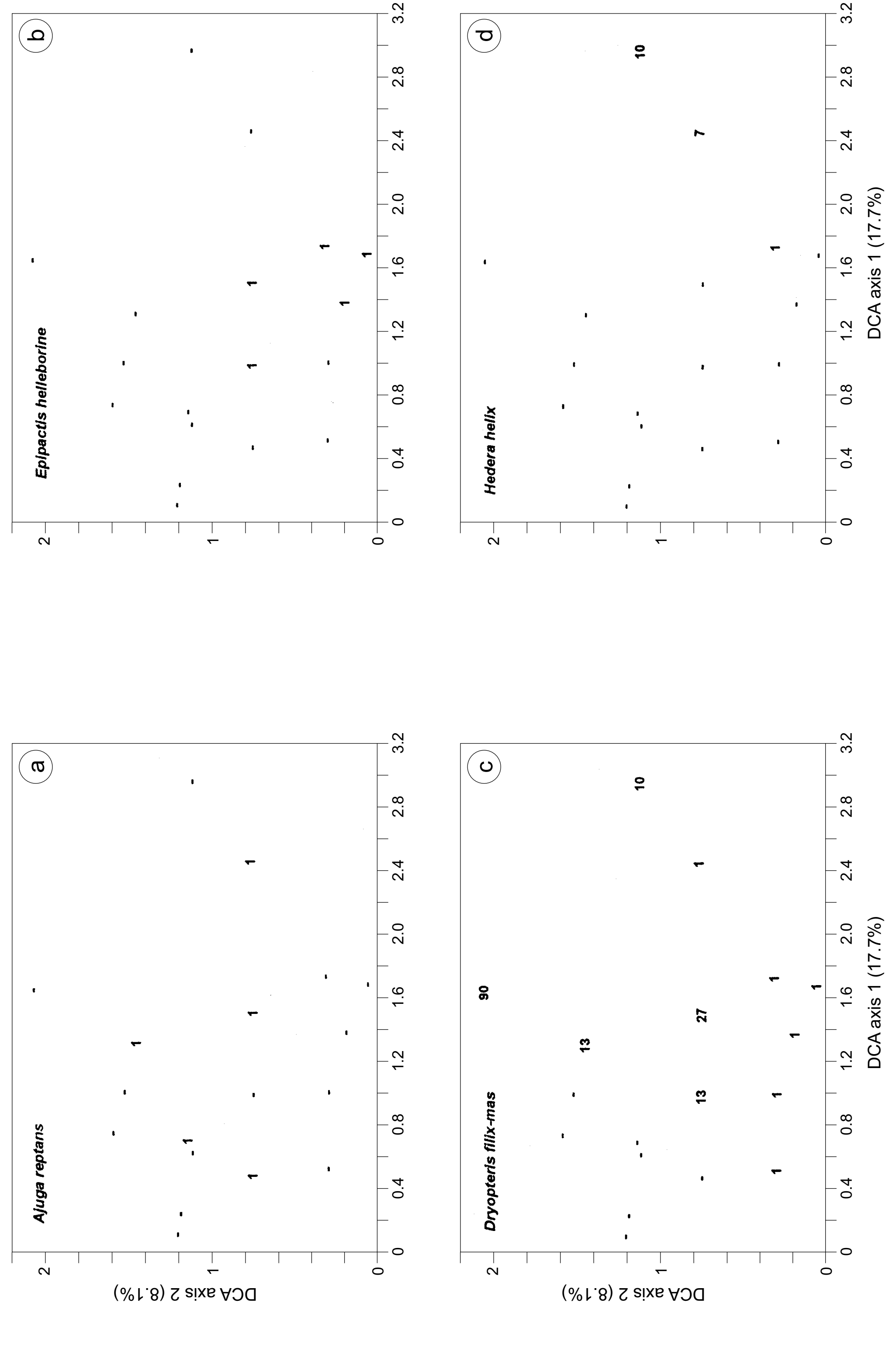
**Fig. 4**. Results of Detrended Correspondence Analysis. Distribution of stand average per cent cover values for: **a** – *Polygonatum verticillatum*; **b** – *Sanicula europaea*; **c** – *Geranium robertianum* and **d** – *Mercurialis perennis*.


a
Ajuga reptans
b
Epipactis helleborine
c
Dryopteris filix-mas
d
Hedera helix
DCA axis 1 (17.7%)
DCA axis 2 (8.1%)

for old growth forests from central northern and eastern Europe. The list was compiled from forest interiors and forest edges and only the former apply in this comparison. Only one literature source for Poland and the Czech Republic were included so the data at least for Slovakia and Ukraine represent new comparisons. Of a total of 125 species for the region from Belgium to Sweden, almost half (48%) are included, a much higher percentage for just species of the forest excluding taxa on forest fringes. This emphasizes the old growth or ancient features of these forest examples and the compositional integrity of their advanced stages.

The 18 Eastern European stands contained 17 tree species of which *Fagus sylvatica*, *Abies alba* and *Acer pseudoplatanus* were major contributors and only an additional three, *Fraxinus excelsior*, *Acer platanoides*, and *Picea excelsa*, were even modest members. In the 12 Ontario stands there were 31 species of trees. *Fagus grandifolia* and *Acer saccharum* were the major dominants, both present in all stands, but an additional four species including *Acer rubrum*, *Fraxinus americana*, *Quercus rubra*, and *Ostrya virginiana* were also significant contributors, and a further five species – *Betula lutea*, *Prunus serotina*, *Tilia americana*, *Ulmus americana* and *Liriodendron tulipifera* had an influence on composition far beyond any of the accompanying species in the European forests. It is interesting that these stands although termed deciduous also included two conifers, *Pinus strobus* and *Tsuga canadensis* although their contributions were more modest than *Abies alba* or *Picea excelsa* in the European stands. These conifers are also less nemoral in character. Without considering the number of stands compared, the Canadian forests, included by a factor of almost twice, the number of tree species.

In undertaking this research there was no intention to question the approaches which had been taken by native phytosociologists in the treatment of these systems but the quantitative approach employed permits some relevant comments. These forests are essentially monodominant *Fagus sylvatica* systems and this species comprises at least a third of total importance and in more than 75% of the stands to more than two-thirds of importance, and with many almost totally constituted by it. *Abies alba* might be considered a significant subdominant but is essentially absent from almost 40% of stands and seldom attains 20% of importance. *Acer pseudoplatanus*, *A. platanoides* and *Fraxinus excelsior* are of very low importance and the other 12 species are essentially incidentals. An analysis of tree dominance patterns which seems straightforward, emphasizes that a majority of these forests may be generally identified as *Fagus sylvatica*-*Abies alba*-*Acer pseudoplatanus* compositional types. In fact these three species account for 42 (78%) of the 54 leading major positions in characterizing leading dominants, and as well a restricted number of other tree species, actually three, account for most of the other first three positions. This is a clear statement of major tree dominance in these forests. In the Ontario forests the three most significant contributors to dominance, *Acer saccharum*, *Fagus grandifolia* and *Acer rubrum* account for 28 (77%) of the 36 leading major

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**Fig. 5**. Results of Detrended Correspondence Analysis. Distribution of stand frequency values for: **a** – *Ajuga reptans*; **b** – *Epipactis helleborine*; **c** – *Dryopteris filix-mas* and **d** – *Hedera helix*.

**Table 8.** Mesic Old Growth Deciduous Forests: Eastern Europe – Ontario. Possible ecological equivalents.

| Ontario | Europe |
|---|---|
| Fagus grandifolia | Fagus sylvatica |
| Acer saccharum | Acer platanoides |
| Acer rubrum | Acer pseudoplatanus |
| Fraxinus americana | Fraxinus excelsior |
| Quercus rubra | Quercus petraea |
| Tilia americana | Tilia cordata |
| Ulmus americana | Ulmus montana |
| *Prunus avium | Prunus avium |
| Circaea quadrisulcata | Circaea lutetiana |
| Galium aparine | [x]Galium aparine |
| Maianthemum canadense | Maianthemum bifolium |
| Carex deweyana | Carex sylvatica |
| Lonicera canadensis | Lonicera nigra |
| Polygonatum pubescens | Polygonatum multiflorum |
| Trillium grandiflorum | Paris quadrifolia |
| Adiantum pedatum | [x]Adiantum pedatum |
| Anemone quinquefolia | Anemone nemorosa |
| Galium triflorum | Asperula odorata |
| Impatiens capensis | *Impatiens noli-tangere |
| Monotropa uniflora | Monotropa hypopithys |
| Ranunculus recurvatus | Ranunculus lanuginosus |
| Sambucus pubens | Sambucus racemosa |
| Rubus hispidus | Rubus hirtus |
| Trientalis borealis | [x]Trientalis europaea |
| Vaccinium angustifolium | Vaccinium myrtillus |
| Equisetum hyemale | [x]Equisetum hyemale |
| Corylus cornuta | Corylus avellana |
| Hepatica americana | [x]Hepatica nobilis |
| Athyrium filix-femina | Athyrium filix-femina |
| Dryopteris spinulosa | Dryopteris spinulosa (D. carthusiana) |
| Rubus idaeus | Rubus idaeus |
| Prenanthes altissima | Prenanthes purpurea |
| *Epipactis helleborine | Epipactis helleborine |
| Ribes cynosbati | Ribes grossularia |
| *Solanum dulcamara | Solanum dulcamara |
| Viola conspersa | Viola riviniana |
| Asarum canadense | Asarum europaea |
| *Chelidonium maius | Chelidonium maius |
| Sanicula gregaria | Sanicula europaea |
| Dentaria laciniata | Dentaria glandulosa |
| Geranium robertianum | Geranium robertianum |
| Geum canadense | [x]Geum urbanum |
| Actaea rubra | Actaea spicata |
| Sambucus canadensis | Sambucus nigra |

**Table 8.** Continued.

| Ontario | Europe |
|---|---|
| *Solidago caesia* | *Solidago virga-aurea* |
| *Cystopteris fragilis* | *Cystopteris fragilis* |
| *Allium tricoccum* | *Allium ursinum* |
| *Circaea alpina* | *Circaea alpina* |
| *Lilium michiganense* | *Lilium martagon* |
| *Thalictrum dioicum* | *Thalictrum aquilegiifolium* |
| *Asplenium trichomanes* | [x]*Asplenium trichomanes* |
| *Equisetum arvense* | [x]*Equisetum arvense* |
| **Taraxacum officinale* | **Taraxacum officinale* |
| *Epilobium coloratum* | *Epilobium montanum* |
| *Milium effusum* | *Milium effusum* |
| *Fragaria virginiana* | *Fragaria vesca* |
| *Viburnum trilobum* | *Viburnum opulus* |
| *Euonymus atropurpureus* | *Euonymus europaea* |

* – introduced; [x] – not included in present study

positions but seven other species account for all of the other first three positions. The difference in these locations is that *Fagus sylvatica* is leading dominant in all the European stands whereas this position is shared almost equally in Ontario by *Acer saccharum* and *Fagus grandifolia*. It is not difficult to understand why many ecologists from Europe visiting North American deciduous forests, think of them foremost as beech forests.

The presence of fir and spruce as admixtures have not prevented phytosociologists from considering the association essentially a deciduous dominated one – *Fagetum carpaticum* in Poland, *Fagetea sylvaticae* in Ukraine where it is often totally deciduous and *Fagetum typicum* in Slovakia, although in the latter locality other beech associations with coniferous as well as other deciduous species, *Abieto-Fagetum*, *Fageto-Abietum*, etc. are identified. This compositional situation contrasts sharply with that prevailing in old growth forests in Southern Ontario where strong dominance is shared by *Acer saccharum* and *Fagus grandifolia* and a number of associates may have strong representation, such as *Acer rubrum*, *Fraxinus americana*, *Tilia americana*, *Quercus rubra* and *Ulmus americana* (formerly). As well there are a large number of subdominants which may also be significant contributors to composition. The differences between the Eastern European and Eastern North American ecosystems are certainly emphasized.

Floristics and composition of these forests may differ substantially from those of Ontario, but in other respects they are remarkably similar. Analysis of life form indicates remarkable similarities for a majority of the 25 classes designated. Often the values are only fractionally different and emphasize the similarities at the formational level as determined predominantly by regional climates.

An aspect of old growth forests exceedingly prevalent is the existence of large or even oversize old trees (Martin 1992; Parker 1989; Runkle 1996; Leverett 1996). No one seems to have defined this phenomenon quantitatively in the North American forests although Korpel (1989) may have done so for old growth forests in Slovakia.

In Table 6 tree size classes in each of the 18 stands are presented. In each of the categories there is considerable variation, from 4 to 57% in the class from 77 (minimum tree size) to 516 sq. cm, from 13 to 65% in the 517 to 2068 sq. cm class, from 19 to 71% in the 2068 to 8272 sq. cm class and from 0 to 5% in the huge tree class (greater than 8273 sq. cm). It is possible to calculate an average for each class but in scanning the individual values it is seen that there are values well above or below the average and this is of little help. In the first class there are four distinctly deviant values, in the second at least three and in the third at least four.

Despite these discrepancies and a considerable range of values in forests in each of the locations, the regional averages should be reasonable and it is evident they are different. In the Ukraine the third class is the highest and stands also include the highest average percentage of trees in the huge class. In Slovakia the lowest and third classes have the highest as well as comparable average values and there is strong representation in the huge class. In the Polish old growth forests the second size class is strongly represented followed by the third class and the lowest average percentage of the huge class. If the regional averages are compared to that for all stands, in the Ukraine the third class is strongly overrepresented, in Slovakia the first class is stronger and in Poland the second class is overrepresented. These patterns seem to be consistent.

Large old trees can be remnants from logging but then are of poor form and growth characteristics. The large trees in these forests are tall and straight and show normal growth patterns. It is possible that selective logging might have disrupted the normal size progressions in these stands. The highest percentages of the largest size classes clearly existing in the Ukrainian forests may be a reflection of their virgin status and the size class differences in the Slovakian and particularly the Polish stands, may be due to limited human disturbances in the distant past. The pure deciduous nature of the Ukrainian forests may also provide a more uniform environment for the long term extended growth and size increase than the conifer-disrupted canopies typical of the mixed deciduous-coniferous forests in Slovakia and Poland. One may also suggest that the size class distributions in the Ukrainian forest may be used as a common pattern for old growth stands throughout Eastern Europe.

Biodiversity is a very pertinent topic in ecology today. Much of the studies have not been quantitative and comparative. The methodology used in this study is quantitative and has been carried out in similar systems but in different world locations but within the same formations. The species totals for each stand are available at the bottom of Table 2. They vary from 20 in stand 24 at Stužica in far eastern Slovakia to 54 in stands 5 and 8 at Kostrza and Turbacz in southern Poland. The average vascular plant biodiversity in all European stands is 41, a relatively low number. As a comparison, in the twelve mesic old growth deciduous stands in Southern Ontario the values for diversity range from 55 (stand 197 – University of Western Ontario Forest, London), to 127 (stand 18 – Backus Forest, Port Rowan) and the average for all stands is 87, quite high. It should be emphasized that in all regions where the senior author has completed research in mesic old growth deciduous forests (Ontario, Japan, China, central Europe, England, eastern United States), there is great variation in the comparative species richness of stands in each region, but the overall average is quite meaningful.

Biodiversity can also vary considerably regionally as well as locally. Despite an overall average of 41, in the Ukraine, number of species per stand varied from 24 to 42, with an average of only 33. In Slovakia there are between 20 and 51 vascular species per stand with an average of only 39. These are the most variable in biodiversity and it is peculiar that the stand at Stužica is right on the borders of Slovakia with the Ukraine and Poland and it has the lowest number of species instead of at least having a transitional value between the highest and lowest. In Poland relative biodiversity is high, varying between 39 and 54 with an average of 49, well above the general average.

Another possible indication of longevity is the eventual heights attained by large old trees in these stands. The older the trees, the taller they might be although it may be possible for individuals to shunt growth into wood girth or wood height depending on different environmental conditions. The average canopy heights in the Ukrainian and Slovakian forests, excluding a lowland site in each region, are even at 42 m. This is a considerable height for deciduous forests. The Polish forests are considerably less tall and average 32 m. The writers cannot account for the difference. The regions of southern Poland and adjacent Slovakia might have been affected by industrial pollution to a greater extent than the Ukrainian slopes of the Carpathians in the past 50 years and this may have reduced canopy heights. Mean upper canopy heights in the Ontario old growth forests is somewhat less than the highest in the Slovakian and Ukrainian forests and is more variable. The terrain is flat lowland and rarely hilly but never mountainous. The average is 35 m and values between 26 and 43 have been recorded. Wilde *et al.* (1949) claimed that tree growth tends to level topography and if correct, one would anticipate taller canopies in regions of marked topography.

In the virgin forests in the Ukraine Biosphere Reserve, research workers claim (personal communication) to have measured *Fagus sylvatica* 47 m high. This is probably a world record and speaks highly for the site characteristics of that region. In the forests which have been examined by the senior author, deciduous trees tend to grow to heights on any site which are in equilibrium with the existing environmental resources. Individual trees may exceed this upper canopy height at their peril because the higher they grow beyond it, much greater is the risk of their being taken over by wind. Often it is the taller older trees which are toppled in unusual storms.

The quantitative values for species richness in each forest are reliable because the stand samples were large and at least five hours were spent in each site searching for additions to the floristic presence list before during and after the tree and sapling sampling process. Typical of these locations of the Temperate Deciduous Forest Formation is the variability in the total number of species at each stand location. In the Ontario stands, biodiversity varied from a low of 55 to a high of 127, very variable and a much richer situation. Other examples of similar variation are China, 62–147, Japan, 42–123, England, 18–50 and the southeastern United States, 59–112. Such variation is ever present and the reason for it is not straightforwardly apparent. Site moisture differences, possible soil fertility variation or visible human influences do not appear influential. The forests studied here are fine examples of old growth systems and the biodiversity values are considered to be dependable. The lower values for the Ukrainian forests may be due to the barrier of the Carpathians and the fact that beech forests and associates are on the fringe of their geographical limits in Eastern Europe. The differences between the Polish and Slovakian forests immediately adjacent to each other, are quite inexplicable. It is certain that the Ukrainian forests are virgin and the Slovakian have been long undisturbed and they can be used as prime examples for biodiversity determinations in mesic deciduous forests of Eastern Europe, for any major comparisons which may be made on a continental or world wide basis.

The effectiveness of tree reproduction in these forests can certainly be questioned. Only 11 tree species of the 17 produced saplings and of the 11, 7 did so in just a single stand and another in just two. Thus only three or four can be considered to approach successful reproduction. Considered in general, 14 of the 18 stands had fewer saplings per ha than trees and only 4 a greater number. In three stands the sapling reproduction was totally insufficient and in another three quite low. Despite these problems, the majority of reproduction was beech and since the upper canopy is predominantly beech it appears that perpetuation is insured. Regardless of what criteria are employed to judge climax, self perpetuation seems the most significant (Whittaker 1953).

Medwecka-Kornaś (1960) employing criteria based on climate and soil development characteristics, actually related to the ideas of Braun-Blanquet (1932), that development of soil and vegetation, tends to a definite end point determined by climate. Just what constitutes definite is controversial but these remarkable beech forests in the Subcarpathian piedmont and lower foothills approach as closely as any natural system to a point that can be referred to as climax. Korpel (1989) in Slovakia certainly recognized this and following intensive investigations, he claimed that in a virgin forest evolution follows a closed integrated cycle and the dynamic and cyclic development of the tree components and their structure is predominant to environmental development. He considered that in old growth beech forests the development cycle is about 250 years and that in beech-fir it is up to 400 years, because the fir is longer lived than the beech. Almost two generations of beech can occur in a single evolutionary cycle of the latter old growth forest. Duration of the development cycles depends on the life expectation of the beech or fir but the process is sustainable considering the self perpetuating cycles of these long lived species. The mesic old growth beech and beech-fir forests in these regions would seem the epitomy of the climatic climax concept.

Working in similar deciduous forests in the eastern United States Leverett (1996) reviewed structural aspects characterizing old growth forests and structural, and environmental aspects have both been presented by Runkle (1996), who related these criteria to those of Parker (1989) and Martin (1992). It is instructive to relate these features to the forests of Eastern Europe. There, despite floristic simplicity, there was a diversity of tree species involved in the forests although such was overshadowed by the strong dominance of beech. Trees were uneven-aged with significant numbers in several size classes and trees in the huge size class were often represented. There was no evidence of major catastrophic disturbances and the stands were remarkably compositionally stable. The multiple layers considered to characterize old growth systems were also present. Classically a number of trees in the upper canopy, in some locations as high as 5% of standing density, exceeding 5000 and even larger than 8000 sq. cm, must surely approach the aspects of structural diversity present in the primeval forests. The ground was sporadically uneven from windthrown tip-ups of the past but no very large recent gaps were encountered. The ground was littered with old fallen trees and large branch debris but soil profiles were intact. The absence of human logging disturbance was clearly evident. These European old growth systems have much in common structurally and environmentally with the old growth deciduous forests of eastern North America, actually constituting ecological vicariads.

These mesic old growth deciduous forests of the Circumcarpathian regions of Eastern Europe are in reality remarkable natural systems, characterized by virgin or near virgin features and they can be considered as standard benchmarks for assessing the old growth features of other similar systems throughout the North Temperate Zone. Their conservation in perpetuity is of the utmost significance.

**Acknowledgments:** As senior author, I wish to say what a pleasure and rewarding event it is for vegetation science, that so many colleagues in widely separated regions have been brought together to produce this contribution. Colleagues in ecology and taxonomy, Directors of major Institutes, foresters, rangers, villagers, have all contributed to this effort. It has been a marvelous human experience.

Director Jan Ilavský, Forestry Institute Zvolen, Slovakia provided personnel, transport and other assistance, Professor Leon Stuchlik, former Director of the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland provided personnel and encouragement, and Dr. K. Sytnik, Director of the Kholodny Institute of Botany, Kiev, Ukraine, provided personnel and use of facilities. Dr. F. Gamor, Director of the Carpathian Biosphere Reserve, Ukraine, provided access to one of the most outstanding Deciduous Forest conservation areas in the world.

Many assisted with field sampling: Jan Dokoupil, Břečlav, Czech Republic; Dr. Alexander Kagalo, Institute of Ecology of the Carpathians, National Academy of Sciences of Ukraine, Lvov, Ukraine; Mikhailo Pokoruba, Ugolka, Ukraine; Ludmila Lubinska, State Natural Park “Podilski Tovtry”, Ukraine; Dianne Fahselt, University of Western Ontario, London, Ontario and Vladimir Hruz, Zvolen, Slovakia. Their assistance is deeply appreciated. Professor Jerzy Staszkiewicz, W. Szafer Institute of Botany Polish Academy of Sciences, Kraków, Poland was very helpful locating stands for study in Southern Poland. Many offered social assistance which made much of the Research possible and enjoyable, including Dr. Vera Protopopova, Kiev, Ukraine, Ludmila Lubinska and Mykola Ryabij, Kam’ianets-Podil’skyi, Ukraine, Jan and Mrs. Dokoupil, Břečlav, Czech Republic, Professor Krystyna Grodzińska, Kraków, Poland and Dr. Małgorzata Guzikowa, Kraków, Poland. The senior author must also thank and extend exceptionally fortuitous good wishes to Professor Kazimierz Zarzycki for countless pleasant hours in the field in Poland over an extended period.

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