

## Thermophilous deciduous forests in Southeastern Europe

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### Abstract

This paper deals with the numerical elaboration of the database of 1764 relevés of thermophilous deciduous forests assigned by the authors to the order *Quercetalia pubescentis* in the northwestern part of Southeastern Europe. After elimination of relevés which were dominated by mesophilous deciduous and coniferous tree species, the stratification of relevés was carried out. The TWINSpan classification revealed eight ecologically and phytogeographically interpretable groups. Additionally the analysis of Pignatti indicator values passively projected on the PCA diagram of the eight groups, and a chorological analysis of individual groups were made. The analyses revealed that all groups in general match with the traditionally accepted alliances, such as *Quercion pubescenti-sessiliflorae*, *Aceri tatarici-Quercion*, *Quercion confertae*, *Quercion petraeae-cerris*, *Syringo-Carpinion*, *Pruno tenelle-Syrinion*, *Carpinion orientalis* and *Fraxino ornii-Ostryion*. Finally, a synsystematic classification of the elaborated group is proposed, and the nomenclature is harmonised with the International Code of Phytosociological Nomenclature. The results are also presented in a synoptic table together with calculation of the diagnostic species.

**Abbreviation:** ICPN, International Code of Phytosociological Nomenclature

**Keywords:** Chorology, ecology, fidelity, forest, Southeastern Europe, syntaxonomy, Two Way INdicator SPecies Analysis

### Introduction

The thermophilous deciduous forests of the order *Quercetalia pubescentis* spread out in the warm parts of Europe. They are climazonal in warmer parts of Europe and extrazonal in the northern, cooler regions. In some parts of Europe, this type of vegetation has already been well elaborated on a regional level, for instance in Austria (Willner & Grabherr 2007), Italy (Blasi et al. 2004), Germany (Oberdorfer 1992), the Czech Republic (Knollová & Chytrý 2004), Slovakia (Roleček 2005), Hungary (Kevey & Borhidi 2005), Bulgaria (Rousakova & Tzonev 2003) and Greece (Bergmeier & Dimopoulos 2008), but in the region under study such an overview has not yet been carried out.

We treated the order of thermophilous deciduous forests *Quercetalia pubescentis* as a part of the class *Quercio-Fagetea*, as do the studies by most authors in

the region (e.g. Horvat et al. 1974; Jovanović et al. 1986) and as also considered elsewhere (Rivas-Martínez et al. 2001, 2002). This is justified by many mesophilous plants linking the orders of the class *Quercio-Fagetea* together. Certain recent classifications (Mucina 1997; Rodwell et al. 2002) include this type of vegetation into a special class, that of *Quercetalia pubescentis*.

In Southeastern Europe, studies on the vegetation according to the central European Braun-Blanquet methodology (Braun-Blanquet 1964) has a long tradition. Horvat (1938), Tomažič (1939) and Rudski (1949) are among the pioneers who studied thermophilous deciduous forests. They were followed by numerous authors who are also among the authors of the tables drawn up and selected for this contribution. Since, due to objective circumstances, cooperation in this area has been rendered

difficult in the last few years, we were only recently able to form a group which prepared a survey of the vegetation of thermophilous deciduous forests in this area in compliance with the modern methodology.

The aim of the research was to collect material on the thermophilous deciduous forests of the *Quercetalia pubescentis* in the region, and then to establish the major vegetation types resulting from the numerical analysis, and to compare them with the major types recognised in the traditional expert-based classification. The groups are presented in a synoptic table, with calculation of diagnostic species, chorological and ecological characteristics as well as their distribution patterns.

## Methods and materials

### Geographical scope

We studied the thermophilous deciduous forests of the order *Quercetalia pubescentis* in the northwestern part of Southeastern Europe, in the territory of Slovenia, Croatia, Bosnia and Herzegovina, the former Serbia and Montenegro, and Macedonia, all states of the former Yugoslavia. The territory is a complex structure, since it comprises a part of the Pannonian basin, the coasts of the Mediterranean Sea, southern hillsides of the Alps and various mountain chains in the Balkans. The territory is classified as the Euro-Siberian region, i.e. the Apennine-Balkan and the Pannonian-Carpathian provinces, and the Mediterranean region with two provinces: the Adriatic, and the Greek/Aegean province (Rivas-Martínez et al. 2004).

### Object of the study

The objects of our research are thermophilous deciduous forests dominated by various deciduous species such as *Quercus* sp. div., *Ostrya carpinifolia*, *Carpinus orientalis*, *Fraxinus ornus*, to mention only the most important ones. In the northern part of the region, these forests occur up to a height of 600 m where they form the extrazonal vegetation, whereas in the south they appear up to 1000 m or even higher, and form the climazonal vegetation.

All relevés of communities classified by their authors in the order *Quercetalia pubescentis* were collected from the literature. We excluded the relevés whose dominant tree species (cover values 3, 4 and 5) are species of mesophilous climazonal and other forest types, above all mesophilous and coniferous ones, e.g. *Abies alba*, *Acer platanoides*, *A. pseudoplatanus*, *Carpinus betulus*, *Fagus sylvatica* subsp. *sylvatica*, *F. sylvatica* subsp. *moesiaca*, *Fraxinus excelsior*, *Picea abies*, *Pinus nigra*, *P. sylvestris*, *Quercus ilex*, *Tilia cordata*, *T. platyphyllos*,

*Ulmus glabra*. The relevés with an incomplete list of herb species indicated by the authors were also not included in the analyses.

## Methods

The 1764 relevés of forest vegetation of Southeastern Europe collected from the literature were entered into the TURBOVEG (Hennekens & Schaminée 2001) database. After exclusion of relevés dominated by the forest species mentioned above, 1715 relevés of thermophilous forests were left.

The initial data set of 1715 relevés was then stratified. Stratified resampling was made by phytosociological association as indicated by the authors. This means that up to ten relevés of one association were selected in such a way that different authors, different publications and different locations were represented (Košir et al. 2008). As the associations mostly appear in a broad phytogeographical region, a special geographical stratification is not needed. After stratification 604 relevés remained, originating from 82 associations.

As many authors did not record mosses, we excluded them from our analysis before numerical processing. For the purpose of numerical analysis and in the synoptic table we unified the system of layer division, which differs from author to author. All sublayers of the tree layer were integrated into one, whereas for woody species, the herb and scrub layers, tree saplings and seedlings, and lianas were united into a single scrub layer. Additionally, we integrated certain plant subspecies and varieties into the level of species or aggregates.

Then we carried out a classification by TWINSPAN (Hill 1979), run under the JUICE 6.5 programme (Tichý 2002). TWINSPAN pseudospecies cut levels for species abundances were set to 0–5–25 percentage scale units. Initially, six levels of division were chosen and the minimum group size for division was set to five relevés. Later on, different levels of division were accepted, resulting in eight groups of relevés interpretable in terms of ecology and phytogeography. In the group distribution map only those localities where the majority of relevés of individual groups is located are presented.

The diagnostic species of eight individual groups were determined by calculating species' fidelity (Chytrý et al. 2002; Havlová et al. 2004) and are presented in the synoptic table (Table I). As a fidelity measure we used the phi coefficient in the JUICE programme. In these calculations, each group of relevés was compared with the rest of the relevés in the data set, which were taken as a single undivided group. Each of the eight groups was virtually adjusted to 1/8 of the size of the entire data set, while holding the percentage occurrences of a species within and outside a target group the same as in the

Table I. Synoptic table of the TWINSpan classification. See also supplementary material available online at: [http://www.informaworld.com/mpp/uploads/supplementary\\_files\\_363558\\_1236759373086.zip](http://www.informaworld.com/mpp/uploads/supplementary_files_363558_1236759373086.zip)

Group number		1	2	3	4	5	6	7	8
No. of relevés		108	15	68	57	35	39	174	108
<i>Proportion of geoelements in groups (%)</i>									
Stenomediterranean		1.9	0	1.2	2.2	0	2.1	<b>6</b>	1.6
Eurimediterranean		7.6	10.2	9.4	8.9	10.3	8.2	10.5	6.7
Mediterranean–montane		1.3	0	0.6	1.7	6.6	1	3.3	<b>12.5</b>
Eurasian		66.9	65.3	61.4	58.7	55.9	58.8	50.6	52.9
SE European		5.7	6.1	7.6	6.7	<b>8.1</b>	<b>8.2</b>	<b>8.1</b>	<b>8</b>
Atlantic		1.9	2	0.6	1.1	0	0	2.1	1.3
Eurosiberian		10.2	10.2	11.7	10.6	9.6	11.3	9.3	12.5
Cosmopolite		2.5	4.1	3.5	2.2	1.5	8.2	4.2	1.9
Balkan		1.9	2	<b>4.1</b>	<b>7.8</b>	<b>8.1</b>	2.1	<b>6</b>	2.6
<i>Species diagnostic for one group</i>									
Group 1									
<i>Quercus petraea</i> agg.	t	97	.	47	58	20	8	5	23
<i>Tilia tomentosa</i>	s	49	.	13	4	.	13	1	2
<i>Festuca drymeja</i>	h	22	.	.	2	.	13	.	.
<i>Carex pilosa</i>	h	20	.	12	.	.	.	1	.
<i>Campanula persicifolia</i>	h	40	.	19	14	14	3	11	10
<i>Sorbus aucuparia</i>	s	11	.	.	.	.	.	.	3
Group 2									
<i>Quercus pedunculiflora et robur</i>	t	.	100	.	.	.	.	.	.
<i>Quercus pedunculiflora et robur</i>	s	.	93	.	.	.	.	.	.
<i>Arum maculatum</i>	h	.	100	3	2	.	3	3	.
<i>Polygonatum latifolium</i>	h	2	80	.	2	11	10	1	.
<i>Torilis japonica</i>	h	2	73	1	.	.	21	2	.
<i>Stachys germanica</i>	h	.	67	4	.	3	.	2	.
<i>Rosa corymbifera</i>	s	.	60	.	.	3	.	.	2
<i>Ulmus minor</i>	s	7	80	7	2	.	15	4	1
<i>Acer tataricum</i>	t	2	67	1	.	.	.	5	.
<i>Ulmus minor</i>	t	1	60	1	2	.	10	6	.
<i>Rosa gallica</i>	s	.	47	4	2	.	.	1	.
<i>Heracleum sphondylium</i>	h	.	47	.	2	.	.	1	3
<i>Geum urbanum</i>	h	12	93	24	44	9	44	10	6
<i>Acer tataricum</i>	s	37	87	28	12	20	8	2	1
<i>Asparagus tenuifolius</i>	h	2	73	1	5	17	3	13	17
<i>Prunus spinosa</i> agg.	s	4	73	31	7	.	21	15	10
<i>Peucedanum alsaticum</i>	h	.	27	.	.	.	.	.	.
<i>Festuca gigantea</i>	h	.	27	.	.	.	.	.	.
<i>Viola alba</i>	h	5	60	4	5	14	3	16	3
<i>Crataegus pentagyna</i>	s	.	33	.	.	3	3	5	.
<i>Malus sylvestris</i>	s	.	40	18	4	.	.	2	5
<i>Solanum nigrum</i>	h	.	20	.	.	.	.	.	.
<i>Alopecurus pratensis</i>	h	.	20	.	.	.	.	.	.
<i>Buglossoides purpureoacerulea</i>	h	17	80	25	28	6	21	37	7
<i>Poa angustifolia</i>	h	.	27	6	.	9	.	3	.
<i>Sorghum halepense</i>	h	.	13	.	.	.	.	.	.
<i>Euphorbia salicifolia</i>	h	.	13	.	.	.	.	.	.
<i>Physalis alkekengi</i>	h	.	13	.	.	.	.	.	.
<i>Calystegia sepium</i>	h	.	13	.	.	.	.	.	.
<i>Doronicum hungaricum</i>	h	.	13	.	.	.	.	.	.
<i>Tamus communis</i>	s	15	60	18	16	11	31	20	15
<i>Cornus sanguinea</i>	s	17	53	19	7	6	21	16	17
<i>Crataegus monogyna</i>	s	59	100	68	53	49	87	57	32
Group 3									
<i>Quercus frainetto</i>	t	6	47	66	35	.	.	3	.
<i>Sorbus domestica</i>	s	7	7	31	9	.	3	6	3
<i>Prunella vulgaris</i>	h	2	20	26	14	3	.	3	2
<i>Veronica officinalis</i>	h	3	.	25	21	.	.	1	4
<i>Moltkia doerfleri</i>	h	.	.	10	.	.	.	1	.
Group 4									
<i>Lathyrus laxiflorus</i>	h	1	.	7	49	.	.	1	1
<i>Luzula forsteri</i>	h	1	.	12	49	.	.	3	.

(continued)

Table I. (Continued).

Group number		1	2	3	4	5	6	7	8
<i>Trifolium pignanii</i>	h	2	.	3	46	.	.	3	2
<i>Veronica chamaedrys</i>	h	33	53	34	86	11	13	26	11
<i>Campamula sparsa</i>	h	.	.	.	19	.	.	.	.
<i>Helleborus cyclophyllus</i>	h	1	.	.	26	.	.	2	1
<i>Arenonia agrimonoides</i>	h	5	.	10	49	.	3	9	18
<i>Silene italica</i>	h	1	.	9	32	.	.	5	1
<i>Trifolium patulum</i>	h	1	.	.	19	.	.	1	.
<i>Peridium aquilinum</i>	h	1	.	15	47	.	.	11	15
<i>Potentilla micrantha</i>	h	10	.	34	54	3	5	15	9
<i>Ptilotemon strictus</i>	h	.	.	.	16	.	.	1	.
<i>Malus pumila</i>	s	.	.	1	18	.	.	1	1
<i>Lychnis coronaria</i>	h	4	.	22	33	.	5	5	.
<i>Physospermum cornubiense</i>	h	4	33	35	46	.	.	11	5
<i>Carex muricata</i>	h	.	.	.	12	.	.	1	.
<i>Asphodelus albus</i>	h	.	.	.	14	.	.	1	1
<i>Cruciata laevipes</i>	h	2	40	15	37	.	.	14	1
<i>Acer obtusatum</i>	h	1	.	4	35	.	.	11	15
<i>Fagus sylvatica</i> ssp. <i>moesiaca</i>	s	4	.	3	23	.	3	1	6
<i>Scutellaria columnae</i>	h	1	.	1	16	.	.	2	1
<i>Chamaespartium sagittale</i>	h	.	.	1	14	.	.	1	1
<i>Clinopodium vulgare</i>	h	24	40	46	67	3	13	29	22
<i>Lapsana communis</i>	h	6	13	13	25	.	5	1	1
<i>Astragalus glycyphyllos</i>	h	5	27	16	26	.	.	3	2
<i>Carex caryophyllea</i>	h	.	.	12	18	.	.	2	.
<i>Hieracium murorum</i>	h	3	.	9	26	.	.	3	12
<i>Galium pseudaristatum</i>	h	3	.	16	21	.	.	2	2
Group 5									
<i>Artemisia alba</i>	h	.	.	.	2	34	3	1	1
<i>Viola tricolor</i> s. lat.	h	.	.	1	.	31	.	1	1
<i>Melica ciliata</i>	h	.	.	.	.	34	3	6	6
<i>Rosa pimpinellifolia</i>	s	.	.	.	.	23	.	1	3
<i>Euphorbia epithymoides</i>	h	.	.	.	2	20	.	1	1
<i>Delphinium fissum</i>	h	.	.	.	.	17	.	.	1
<i>Sedum ochroleucum</i>	h	.	.	.	.	17	3	1	.
<i>Teucrium montanum</i>	h	1	.	3	.	23	.	1	7
<i>Lychnis viscaria</i>	h	.	.	.	4	14	.	.	.
<i>Alyssum murale</i>	h	.	.	.	.	11	.	.	.
<i>Alyssum montanum</i>	h	.	.	.	.	11	.	.	.
<i>Stipa pulcherrima</i>	h	.	.	.	.	11	.	.	.
<i>Seseli peucedanoides</i>	h	.	.	.	.	11	.	.	.
<i>Arabis hirsuta</i>	h	.	.	3	.	17	.	1	3
<i>Rubus idaeus</i>	s	1	.	.	4	17	.	1	1
<i>Rhamnus saxatilis</i>	s	1	.	1	.	23	8	3	5
<i>Scleranthus serpentini</i>	h	.	.	.	.	11	.	.	1
<i>Achillea clypeolata</i>	h	.	.	.	.	11	3	.	.
<i>Potentilla argentea</i>	h	.	.	6	.	17	.	2	.
<i>Juniperus oxycedrus</i>	h	.	.	1	5	31	.	17	5
<i>Dianthus petraeus</i>	h	.	.	.	.	9	.	.	.
<i>Hypericum rochelii</i>	h	.	.	.	.	9	.	.	.
<i>Echium russicum</i>	h	.	.	.	.	9	.	.	.
<i>Allium flavum</i>	h	.	.	.	.	9	.	.	.
<i>Linaria angustissima</i>	h	.	.	.	.	9	.	.	.
<i>Minuartia verna</i> ssp. <i>collina</i>	h	.	.	.	.	9	.	.	.
<i>Sesleria nitida</i>	h	.	.	.	.	9	.	.	.
<i>Thymus praecox</i>	h	.	.	.	.	9	.	.	.
<i>Cotoneaster integerrimus</i>	h	.	.	.	.	9	.	.	.
<i>Potentilla recta</i>	h	6	.	1	2	20	.	3	1
<i>Coronilla varia</i>	h	7	7	1	12	26	3	2	6
<i>Sesleria rigida</i>	h	.	.	.	.	9	.	.	1
<i>Bromus riparius</i>	h	.	.	.	.	9	.	.	1
<i>Euphrasia species</i>	h	.	.	1	.	9	.	.	.
<i>Aurinia saxatilis</i>	h	.	.	.	.	9	3	.	.

(continued)

Table I. (Continued).

Group number		1	2	3	4	5	6	7	8
Group 6									
<i>Prunus mahaleb</i>	t	.	.	.	.	.	62	1	.
<i>Parietaria officinalis</i>	h	.	.	.	.	.	44	1	.
<i>Sedum telephium</i>	h	.	.	.	.	.	36	.	.
<i>Juglans regia</i>	t	.	.	.	.	.	38	2	.
<i>Juglans regia</i>	s	.	13	.	2	.	38	1	3
<i>Clematis vitalba</i>	s	3	.	22	11	20	85	25	22
<i>Prunus mahaleb</i>	s	1	.	3	.	31	69	16	19
<i>Cornus mas</i>	t	1	.	1	.	.	38	5	.
<i>Celtis australis</i>	t	.	.	.	.	.	26	1	.
<i>Vitis vinifera</i>	s	.	.	1	.	.	31	2	1
<i>Tilia cordata</i>	s	.	.	.	.	3	31	.	5
<i>Celtis australis</i>	s	.	.	.	.	.	26	2	.
<i>Corylus avellana</i>	t	.	.	4	.	.	28	1	4
<i>Fraxinus excelsior</i>	s	.	.	.	.	3	21	.	.
<i>Asplenium ceterach</i>	h	.	.	1	.	6	54	17	19
<i>Fraxinus excelsior</i>	t	.	.	.	.	.	21	1	2
<i>Geranium robertianum</i>	h	1	.	6	2	.	36	4	12
<i>Berberis vulgaris</i>	s	.	.	1	.	6	38	5	18
<i>Tilia cordata</i>	t	4	.	1	.	.	28	.	8
<i>Acer monspessulanum</i>	s	1	.	.	5	11	49	19	19
<i>Viburnum lantana</i>	s	15	.	10	2	20	64	15	46
<i>Carpinus orientalis</i>	s	25	.	31	16	20	72	37	8
<i>Asperula purpurea</i>	h	.	.	1	.	11	36	13	6
<i>Calamintha sylvatica</i>	h	6	.	7	5	3	36	10	5
<i>Syringa vulgaris</i>	t	.	.	.	.	.	13	1	.
<i>Crataegus nigra</i>	s	.	.	.	.	.	10	.	.
<i>Ramonda serbica</i>	h	.	.	.	.	.	10	.	.
<i>Viola suavis</i>	h	1	.	.	.	.	13	1	.
<i>Acer monspessulanum</i>	t	.	.	.	4	9	38	22	6
<i>Acer pseudoplatanus</i>	t	1	.	3	.	6	26	1	19
<i>Asplenium trichomanes</i>	h	6	.	4	2	20	44	17	33
Group 7									
<i>Quercus pubescens</i>	t	25	27	12	21	.	23	83	32
<i>Clematis flammula</i>	h	.	.	.	.	.	.	10	.
<i>Paliurus spina-christi</i>	s	.	7	.	.	.	3	11	.
<i>Dioscorea balcanica</i>	h	.	.	.	2	.	.	9	.
Group 8									
<i>Ostrya carpinifolia</i>	s	1	.	6	12	9	.	9	69
<i>Amelanchier ovalis</i>	s	.	.	.	2	.	.	2	34
<i>Ostrya carpinifolia</i>	t	1	.	9	7	.	.	30	75
<i>Cyclamen purpurascens</i>	h	.	.	.	.	.	.	3	35
<i>Sorbus aria</i>	s	7	.	1	.	3	5	1	39
<i>Calamagrostis varia</i>	h	.	.	.	.	.	.	.	23
<i>Sorbus aria</i>	t	1	.	.	.	6	.	3	33
<i>Peucedanum oreoselinum</i>	h	1	.	.	.	3	.	5	35
<i>Solidago virgaurea</i>	h	1	.	3	.	3	.	1	29
<i>Erica herbacea</i>	s	.	.	.	.	3	.	.	21
<i>Cotoneaster nebrodensis</i>	s	.	.	1	2	6	8	2	28
<i>Mercurialis ovata</i>	h	.	.	1	.	.	.	7	30
<i>Buphthalmum salicifolium</i>	h	.	.	3	2	.	.	5	27
<i>Laserpitium siler</i>	h	.	.	.	.	.	.	.	15
<i>Pinus nigra</i>	t	.	.	.	2	.	.	.	16
<i>Clematis recta</i>	h	.	.	.	.	.	3	.	16
<i>Convallaria majalis</i>	h	4	7	1	2	.	3	6	31
<i>Asplenium ruta-muraria</i>	h	.	.	.	.	3	.	3	22
<i>Anthericum ramosum</i>	h	1	.	1	.	.	.	5	24
<i>Thalictrum minus</i>	h	.	.	1	.	3	3	2	20
<i>Hepatica nobilis</i>	h	1	.	.	.	.	3	2	18
<i>Campanula pyramidalis</i>	h	.	.	.	.	.	.	1	14
<i>Anemone trifolia</i>	h	.	.	.	.	.	.	.	10
<i>Sesleria tenuifolia</i>	h	.	.	.	.	.	.	1	11

(continued)

Table I. (Continued).

Group number		1	2	3	4	5	6	7	8
<i>Sorbus umbellata</i>	h	.	.	.	2	.	.	.	11
<i>Carex humilis</i>	h	.	.	1	.	26	.	6	26
<i>Frangula rupestris</i>	s	.	.	.	.	9	3	7	24
<i>Phyteuma scheuchzeri</i> ssp. <i>columnae</i>	h	.	.	.	.	.	.	.	9
<i>Lamiaeum galeobdolon</i> agg.	h	1	.	.	.	3	.	.	12
<i>Spiraea chamaedryfolia</i>	s	.	.	.	.	11	3	.	15
<i>Moehringia muscosa</i>	h	.	.	.	.	.	.	1	11
<i>Thesium bavarum</i>	h	.	.	.	.	.	.	.	8
<i>Helleborus dumetorum</i> ssp. <i>atrorubens</i>	h	.	.	.	.	.	.	.	7
<i>Rubus saxatilis</i>	s	.	.	.	.	.	.	.	7
<i>Aster amellus</i>	h	.	.	.	.	.	.	.	7
<i>Sesleria albicans</i>	h	.	.	.	.	.	.	.	7
<i>Polygala chamaebuxus</i>	h	.	.	.	.	.	.	.	7
<i>Asperula cynanchica</i>	h	.	.	1	.	.	.	3	14
<i>Polypodium vulgare</i>	h	.	.	1	2	9	3	2	17
<i>Lonicera xylosteum</i>	h	6	.	.	2	.	10	7	25
Species diagnostic for more than one cluster									
<i>Poa nemoralis</i> agg.	h	66	.	19	65	23	28	9	2
<i>Quercus petraea</i> agg.	s	54	.	29	60	6	3	1	23
<i>Tilia tomentosa</i>	t	40	.	1	.	.	41	5	.
<i>Quercus cerris</i>	s	18	100	71	74	6	21	20	6
<i>Quercus cerris</i>	t	37	100	87	91	.	18	43	17
<i>Quercus frainetto</i>	s	2	47	60	25	6	.	2	.
<i>Euonymus europaeus</i>	s	6	73	10	9	6	44	11	15
<i>Acer campestre</i>	t	16	67	28	2	6	59	14	5
<i>Brachypodium sylvaticum</i>	h	13	80	50	44	23	69	34	17
<i>Festuca heterophylla</i>	h	9	.	47	54	31	3	9	13
<i>Primula veris</i> s. lat.	h	1	.	.	30	31	.	10	8
<i>Syringa vulgaris</i>	s	2	.	3	.	100	72	7	1
<i>Cotinus coggygria</i>	s	16	.	6	.	69	54	20	37
<i>Carpinus orientalis</i>	t	26	.	12	5	.	74	49	3
<i>Sesleria autumnalis</i>	h	1	.	7	5	.	.	48	58
Other species with high frequency									
<i>Fraxinus ornus</i>	h	69	.	56	39	54	56	52	82
<i>Fraxinus ornus</i>	t	58	.	41	9	23	67	70	68
<i>Cornus mas</i>	h	47	.	46	51	14	67	57	34
<i>Acer campestre</i>	s	44	67	40	32	3	62	24	13
<i>Vincetoxicum hirundinaria</i>	h	34	40	26	5	57	13	26	51
<i>Galium mollugo</i> agg.	h	36	7	26	33	54	31	24	38
<i>Teucrium chamaedrys</i>	h	7	13	21	33	37	26	51	49
<i>Fragaria vesca</i>	h	32	27	37	39	31	15	34	21
<i>Dactylis glomerata</i>	h	40	.	51	54	26	13	33	17
<i>Rubus fruticosus</i> agg.	h	27	27	47	32	26	46	14	12
<i>Euphorbia cyparissias</i>	h	13	27	32	30	54	18	22	24
<i>Helleborus odoratus</i>	h	47	.	44	21	9	28	45	12
<i>Lathyrus niger</i>	h	36	47	51	33	.	.	20	13
<i>Pyrus pyraeaster</i>	s	18	47	32	30	11	28	11	10
<i>Corylus avellana</i>	s	5	.	22	40	20	49	17	29
<i>Sorbus torminalis</i>	h	41	.	37	44	9	5	15	21
<i>Ligustrum vulgare</i>	h	17	20	34	12	9	23	34	23
<i>Quercus pubescens</i> agg.	s	16	33	9	21	11	10	40	27
<i>Hedera helix</i>	h	30	.	13	7	3	56	34	22
<i>Rosa arvensis</i>	s	39	13	25	26	3	36	6	10
<i>Euphorbia amygdaloides</i>	h	32	.	25	40	.	33	17	10
<i>Viola reichenbachiana</i>	h	27	.	21	33	.	23	31	20
<i>Melica uniflora</i>	h	21	.	6	47	11	33	24	8
<i>Tanacetum corymbosum</i>	h	21	33	24	14	9	.	17	31
<i>Euonymus verrucosus</i>	s	20	.	4	4	20	41	28	27
<i>Chamaecytisus hirsutus</i>	h	31	.	19	12	17	10	10	39
<i>Melittis melissophyllum</i>	h	5	.	24	26	3	10	28	37
<i>Galium sylvaticum</i> agg.	h	23	.	43	11	9	5	11	29
<i>Juniperus communis</i>	h	19	.	15	28	3	.	24	33

(continued)

Table I. (Continued).

Group number		1	2	3	4	5	6	7	8
<i>Polygonatum odoratum</i>	h	20	.	6	16	14	3	22	40
<i>Hypericum perforatum</i>	h	28	13	16	5	29	13	10	6
<i>Lathyrus venetus</i>	h	25	.	28	40	.	.	18	8
<i>Viola hirta</i>	h	5	.	19	42	6	5	21	20
<i>Geranium sanguineum</i>	h	.	.	10	30	34	.	14	30
<i>Dactylis polygama</i>	h	20	40	13	26	9	.	8	2
<i>Rhamnus catharticus</i>	h	9	33	1	.	9	15	16	23
<i>Festuca valesiaca</i> agg.	h	7	13	21	11	20	28	5	.
<i>Symphytum tuberosum</i>	h	2	.	24	28	14	.	20	16
<i>Pyrus pyraster</i>	t	6	33	26	11	.	10	9	2

Species values are percentage frequencies. Diagnostic species for the groups of relevés (defined as those with  $\phi \geq 25.0$ ) are shown, ranked by decreasing value of the phi coefficient, indicated by shading: t, tree layer; s, shrub layer; h, herb layer. Groups of relevés in the table correspond to the following, traditionally accepted alliances: 1, *Quercion pubescenti-sessiliflorae*; 2, *Aceri tatarici-Quercion*; 3, *Quercion confertae*; 4, *Quercion petraeae-cerris*; 5, *Pruno tenellae-Syringion*; 6, *Syringo-Carpinion orientalis*; 7, *Carpinion orientalis*; and 8, *Fraxino ornii-Ostryion carpinifoliae*.

original data set (Tichý & Chytrý 2006). We also calculated Fischer's exact test and gave zero fidelity value to the species with significance  $P < 0.001$ . The threshold phi value for the species to be considered as diagnostic was set at 25.0. Since the diagnostic species are calculated on the basis of a matrix of thermophilous deciduous forests they are only used for the purpose of differentiating the stands within the order *Quercetalia pubescentis* (Knollová & Chytrý 2004). Species that appear in at least 50% of relevés of an individual group are treated as constant.

For further interpretation of the ecological conditions of the relevé groups, unweighted average indicator values were used (Zelnik & Čarni 2008). Average values for the eight groups were calculated using Pignatti indicator values (Pignatti et al. 2005) in the JUICE programme, were passively projected onto the Principal Components Analysis (PCA) biplot (CANOCO 4.5; ter Braak & Šmilauer 2002) in order to reveal ecological relationships among these groups and thus explain environmental gradients underlying the main ordination axes. Square-root transformed percentage frequencies were used as the input data.

We also determined a chorological spectrum of groups following Pignatti et al. (2005) and Josifović (1970–1977). The endemic Balkan species were introduced and distinguished from northern endemics, i.e. SE European species (illyric species in the broader sense). Only the species present in at least three relevés within the group were taken into consideration. The chorological spectrum of individual groups of relevés is presented as proportions (percentages) of each group of species in the entire species composition of the group, and shown at the top of Table I.

The nomenclature is according to Flora Europaea (Tutin et al. 1964–1980), except *Scleranthus serpentinii* Beck. *Fagus moesiaca* has been considered as *Fagus*

*sylvatica* subsp. *moesica* (Gömöry et al. 1999). The taxon *Quercus virgiliana* is treated as *Quercus pubescens* (Škvorc et al. 2005).

## Results

### *TWINSPAN groups of relevés and their interpretation*

The dendrogram in Figure 1 shows eight groups of relevés resulting from the TWINSPAN classification of the data set that are ecologically and phytogeographically interpretable. On the first level, there is a division of forest dominated by various oak species (*Quercus frainetto*, *Q. petraea*, *Q. cerris*) on the one hand, and those dominated by *Quercus pubescens*, *Carpinus orientalis* and *Ostrya carpinifolia* on the other. Further interpretation of individual groups is given below.

*Group 1.* Constant species in the tree layer are *Quercus petraeae* and *Fraxinus ornus*. The diagnostic species are *Quercus petraea*, *Tilia tomentosa*, *Festuca dymeia*, *Carex pilosa*, *Campanula persicifolia* and *Sorbus aucuparia*, which point out the thermophilous character of these communities that appear on deeper soils. The relevés from this group appear on the edge of the Panonian basin, in the northern part of the research area (Figure 2). The majority of relevés from this group are traditionally classified in the alliance *Quercion pubescenti-sessiliflorae*.

*Group 2.* Constant species in the tree layer are *Quercus robur*, *Quercus cerris*, *Ulmus minor* and *Acer campestre*. The diagnostic species are the most numerous in this group, from the point of view of distribution, species composition and ecological conditions. The diagnostic species are *Quercus robur*, *Arum maculatum*, *Polygonatum latifolium*, *Torylis japonica*, *Stachys germanica* and many others

showing a higher trophic status and humidity of sites. These communities can be found in the Pannonian basin (Figure 3). The relevés from this group are traditionally classified in the alliance *Aceri-Quercion*.

**Group 3.** Constant tree species in the tree layer are *Quercus cerris* and *Q. frainetto*. Among diagnostic species we can find *Q. frainetto*, *Q. cerris*, *Festuca heterophylla*, *Prunella vulgaris*, *Sorbus domestica*, and *Veronica officinalis*, which indicate warm sites with deeper soil horizons. In this, and in groups 4, 5 and 6, more Balkan species can be

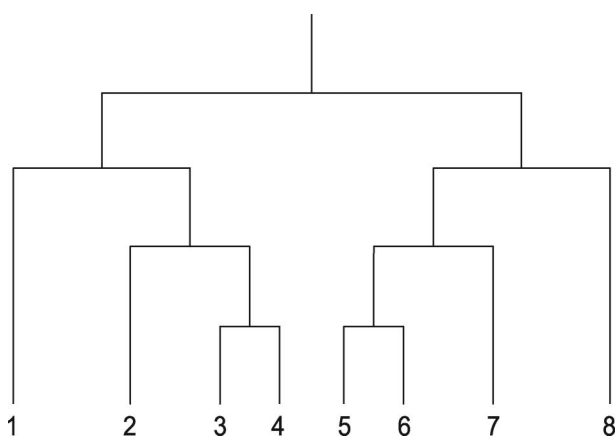


Figure 1. Dendrogram of the TWINSPAN classification of thermophilous deciduous forests in Southeastern Europe corresponding to the eight alliances.

found due to the distribution pattern of the relevés. The relevés from this group are mainly distributed in eastern Croatia, eastern Bosnia and Serbia (Figure 3). The majority of relevés from this group are traditionally classified in the alliance *Quercion confertae*.

**Group 4.** *Q. petraea* and *Q. cerris* are constant tree species in this group. The diagnostic species are numerous, indicating higher altitudes, more mesic and slightly acidic stands, including some Balkan endemics, such as *Campanula sprasa*, *Lathyrus laxiflorus*, *Trifolium pignatti*, *Veronica chamaedrys*, etc.; further diagnostic species are listed in Table I. The relevés are distributed in Macedonia, southern Serbia and Montenegro (Figure 2). The majority of relevés from this group are traditionally classified in the alliance *Quercion petraeae-cerris*.

**Group 5.** There is no constant species in the tree layer of this group, but *Syringa vulgaris*, *Cotinus coggygria* and *Fraxinus ornus* are constant in the scrub layer. Beside the physiological differences within group 6, the relevés from this group have many diagnostic species indicating open, dry habitats and the relict position of stands, such as *Artemisia alba*, *Melica ciliata*, *Rosa pimpinellifolia*, *Viola tricolor* and many others listed in Table I. The relevés from this group are distributed in the canyons of central Serbia (Figure 4). The majority of relevés from this group are traditionally classified in the alliance *Prunetenellae-Syringion*.



Figure 2. The distribution of the relevés of group 1 (*Quercion pubescenti-sessiliflorae* ●) and group 4 (*Quercion petraeae-cerris* ▲).



*Group 6.* The constant species in the tree layer are *Carpinus orientalis*, *Fraxinus ornus*, *Prunus mahaleb* and *Acer campestre*. Diagnostic species show the thermophilous character of communities and often have a Mediterranean–continental distribution pattern, they are *Juglans regia*, *Prunus mahaleb*, *Parietaria officinalis*, *Sedum telephium*, and others which are further enumerated in Table I. The relevés from this

group are found in the continental part of the Balkan Peninsula, in eastern Serbia (Figure 4). The majority of relevés from this group are traditionally classified in the alliance *Syringo-Carpinion orientalis*.

*Group 7.* The constant species in the tree layer is *Quercus pubescens*. Diagnostic species are *Quercus pubescens*, *Clematis flammula*, *Paliurus spina-christi*



Figure 3. Distribution of the relevés of group 2 (*Aceri tatarici-Quercion* ●) and group 3 (*Quercion confertae* ▲).

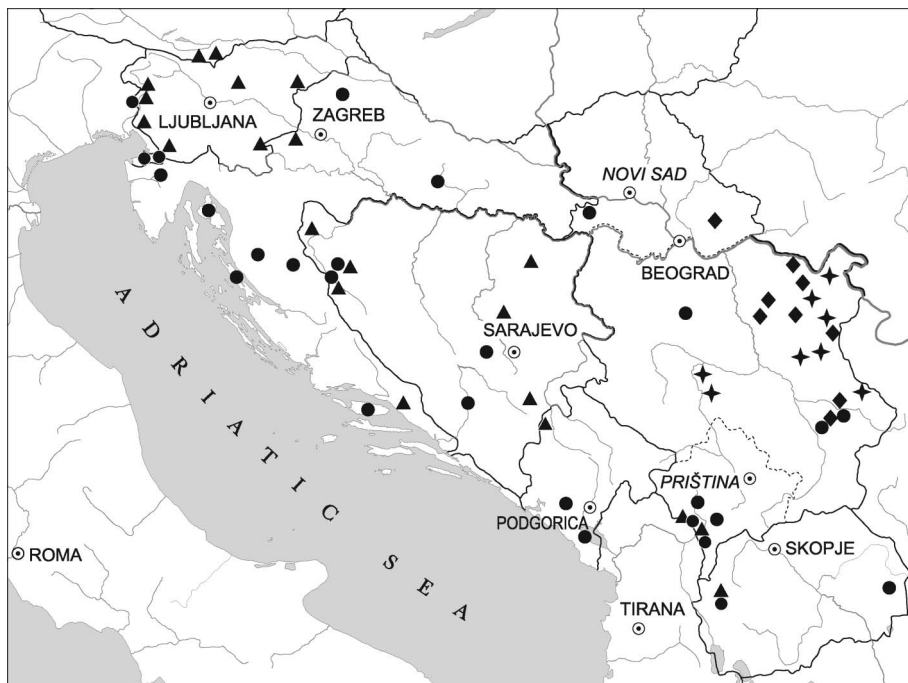


Figure 4. Distribution of the relevés from groups 5 (*Pruno tenellae-Syringion* ★), 6 (*Syringo-Carpinion orientalis* ◆), 7 (*Carpinion orientalis* ●) and 8 (*Fraxino ornī-Ostryion carpinifoliae* ▲).

and *Dioscorea balcanica* that share a (sub)Mediterranean character and grow mainly on carbonate bedrock. This group comprises more Mediterranean species. In this group, and also in groups 6 and 8, there are more species with a SE European distribution pattern. There is also a higher proportion of Balkan species due to the location of some relevés in the southern part of the region. The relevés from this group are found along the Adriatic Sea and in regions where the maritime influence extends deep into the continent, along the rivers Una, Neretva, Drim and Vardar (Figure 4). The majority of relevés from this group are traditionally classified in the alliance *Carpinion orientalis*.

**Group 8.** The constant species in the tree layer is *Ostrya carpinifolia*. Diagnostic species (e.g. such as *Ostrya carpinifolia*, *Amelanchier ovalis*, *Cyclamen purpurascens*, *Sorbus aria*) are enumerated in Table I; they belong to heliophilous, thermophilous communities that grow on shallow soil horizons over carbonate bedrock. In this group more Mediterranean–montane species can be found. They are distributed in the inner part of the mountain ranges along the Adriatic coast (Figure 4). The majority of relevés from this group are traditionally classified in the alliance *Fraxino orni–Ostryon*.

#### PCA and indicator values

The PCA of the eight groups with a passive projection of Pignatti indicator values (Figure 5) shows that the

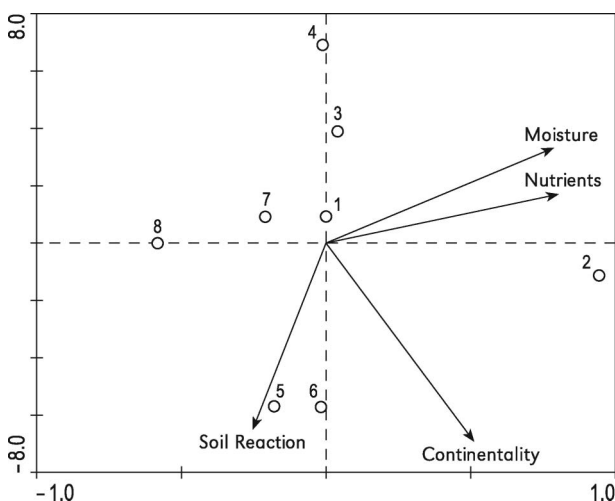


Figure 5. PCA of eight TWINSpan groups and mean Pignatti indicator values plotted as supplementary variables on the ordination diagram. Eigenvalues of first two axes are 0.279 and 0.226. The groups are numbered as in Table I. Only indicator values with the highest correlations with the first two PCA axes are shown. The highest correlations with the first axis have the indicator values for Nutrients (0.8210) and Moisture (0.7993), and with the second axis for Continentality (0.7099) and Soil reaction (0.6584).

division along the first axis is based on moisture and nutrients. Communities dominated by oak species (groups 1–4) thrive on the most propitious stands with deep soil horizons while groups dominated by *Quercus pubescens*, *Carpinus orientalis* and *Ostrya carpinifolia* (groups 5–8) occur on the shallow soils.

The second axis shows the separation on the basis of continentality and soil reaction. The most continental groups are 2, 5 and 6 found in the Pannonian plain and central part of the Balkan Peninsula, and the least continental ones are those from precipitation-rich mountain ranges bordering on the eastern Adriatic coast (groups 4 and 8). The soil reaction shows the highest pH within groups 5–8 dominated by *Quercus pubescens*, *Carpinus orientalis* and *Ostrya carpinifolia*, thriving on shallow soils over carbonate bedrock, and the lowest in *Quercus*-dominated groups 1–4, appearing in more acid sites with deeper soil horizons.

#### Discussion

After the numerical analysis, and the calculation of diagnostic species and distribution of relevés, confirmed also by the correlation with Pignatti indicator values and the chorological spectrum, it can be concluded that the groups generally correspond to the traditionally recognised alliances.

#### General view of communities

The general view of communities (Figure 1, Table I) shows that the whole data set, i.e. order *Quercetalia pubescentis*, can be divided into two parts (groups of alliances). One is dominated by various deciduous species of the genus *Quercus* (except the calciphilic *Q. pubescens*). The other is formed by communities dominated by *Carpinus orientalis*, *Ostrya carpinifolia* and *Quercus pubescens*. Such a division has already been established by Lakušič et al. (1982), who separated these two groups as orders and described a new order, *Ostryo-Carpinetalia orientalis*.

The group of oak forests (*Quercion pubescenti-sessiliflorae*, *Aceri-Quercion*, *Quercion confertae*, and *Quercion petraeae-cerris*) appears in sites with deeper, slightly acid soil horizons. *Quercus petraea* is diagnostic for alliances from the (sub)montane vegetation belt (*Quercion petraeae-sessiliflorae* and *Quercion petraeae-cerris*), *Quercus cerris* is diagnostic for Balkan and Pannonian alliances *Quercion confertae*, *Quercion petraeae-cerris* and *Aceri-Quercion*. *Quercus frainetto* is diagnostic for Balkan and Pannonian lowland alliances, i.e. *Aceri-Quercion* and *Quercion confertae*. The other group of forests dominated by *Quercus pubescens*, *Carpinus orientalis* and *Ostrya carpinifolia* is spread in the areas under the Mediterranean influence. In the coastal region, the most important

tree species is *Quercus pubescens* (*Carpinion orientalis*), that is substituted by *Ostrya carpinifolia* (*Fraxino orni-Ostryion*) in the (sub)montane vegetation belt, while *Carpinus orientalis* is characteristic for the coastal (*Carpinion orientalis*) as well as for continental communities (*Syringo-Carpinion*). The diagnostic values of constant tree species also reflect the ecological amplitude of the alliances.

In the syntaxonomic scheme the *Pruno tenellae-Syringion* is separated from the order of thermophilous deciduous forests of the *Quercetalia pubescentis* and classified in the *Fraxino orni-Cotinetalia* order of thermophilous deciduous scrub communities, based on physiognomic and floristic differences.

#### Proposed syntaxonomic scheme

*Quercion pubescenti-sessiliflorae* Br.-Bl 1932

*Aceri tatarici-Quercion* Zólyomi et Jakucs 1957

*Quercion confertae* Horvat 1954

*Quercion petraeae-cerris* (Lakušić et Jovanović 1980) all. nova

*Syringo-Carpinion orientalis* Jakucs 1959

*Carpinion orientalis* Horvat 1954

*Fraxino orni-Ostryion carpinifoliae* Tomažič 1940

*Quercetalia pubescentis* Klika 1933

*Pruno tenellae-Syringion* (Jovanović 1979) all. nova

*Fraxino orni-Cotinetalia* Jakucs 1961

*Quercio-Fagetea* Br.-Bl. et Vieger in Vlieger 1937

#### Description of the syntaxa

*Quercion pubescenti-sessiliflorae* is an alliance with a Central European distribution pattern and has the most southern irradiation in this region; *Tilia tometosa* and *Acer tataricum* can form the basis for a geographical differentiation of the alliance (Baričević & Vukelić 2006; Baričević et al. 2006). *Aceri tatarici-Quercion* is the most continental alliance and is distributed in the Pannonian plain (Jovanović 1997); *Quercion confertae* is an alliance distributed in the lowlands under the influence of the continental climate (Jovanović 1997). *Quercion petraeae-cerris* is found at higher altitudes in the eastern and southern part of the study area in contact with beech forests (Kojić et al. 1998, Em 1964); *Syringo-Carpinion orientalis* is an extrazonal Mediterranean vegetation thriving in the continental part of the central Balkans (Mišić 1981, 1997). It is confirmed based also on differences in floristic composition and physiognomy that the *Pruno tenellae-Syringion* forms a separate syntaxon thriving on sunny, steep slopes (Mišić 1981). *Carpinion*

*orientalis* is found in the waste areas under the influence of the Mediterranean climate; on more humid sites along the Adriatic coast it is classified as *Ostyo-Carpinion orientalis* and in drier sites in the southern part of the Balkans as *Syringo-Carpinion orientalis* (Horvat et al. 1974; Poldini 1988), *Fraxino orni-Ostryion* is found in the inner part of the mountain chains along the Adriatic coast at higher altitudes showing some similarities to the vegetation of the *Erico-Pinetea* (Horvat 1959; Tomažič 1940; Wallnöfer 1993).

#### Description of new syntaxa

*Quercion petraeae-cerris* (Lakušić et Jovanović 1980) all. nova hoc loco

Holotypus: *Quercetum cerris* Vukičević 1966 holotypus hoc loco

The original description is not valid according to Article 1 of the ICPN. The description of the alliance corresponds to the description of group 4; diagnostic species are indicated in Table I.

*Pruno tenellae-Syringion* (Jovanović 1979) all. nova hoc loco.

Holotypus: *Artemisio camphoratae-Amygdaletum nanae* Jovanović 1954 holotypus hoc loco

The original description is not valid according to Article 1 of the ICPN. The description of the alliance corresponds to the description of group 5; diagnostic species are indicated in Table I.

#### Conclusions

This work presents the first survey of thermophilous deciduous forests in the northwestern part of Southeastern Europe based on the numerical approach and can form the basis for further elaboration. A revision of the nomenclature of associations is needed, since the one based on geographical and ecological epithets is still widely used.

Further research is needed to analyse and to understand the ecological and phytogeographical circumstances within this type of vegetation in the context of a wider region, even on the European scale.

For the region under study connecting Central Europe and the eastern Balkans, it is important to meet the common European standards. In recent years, there have appeared some publications dealing with the forest vegetation of Southeastern Europe (e.g. Bergmeier & Dimopoulos 2001; Dring et al. 2002; Bergmeier et al. 2004; Chasapis et al. 2004; Roussakova & Dimitrov 2005; Tzonev et al. 2006) that provide a basis for further research and synthesis.

New challenges are also being faced with regard to current research projects that have revealed common features on both sides of the Adriatic Sea, on the

peninsulas of Southern Europe, i.e. the Balkans and the Apennines. They have a similar geographical position, and development of flora and vegetation. In both regions, there are beech forests of the alliance *Aremonio-Fagion* (Biondi et al. 2002; Blasi et al. 2005), and in their southern parts thermophilous beech forests of the alliance *Geranio versicoloris-Fagion* (Bergmeier & Dimopoulos 2001; Bergmeier et al. 2004; Di Pietro et al. 2004; Rosati et al. 2005). At the same time we can find the same suballiances in noble hardwood forests of the *Tilio-Acerion* (Košir et al. 2008) and *Carpinus betulus* forests of the *Erythronio-Carpinion* (Biondi et al. 2002; Marinček & Čarni 2000).

Within the order *Quercetalia pubescentis* there are suballiances of the *Carpinion orientalis* on both sides of the Adriatic Sea, and a certain degree of similarity also applies to the alliances *Quercion confertae* and *Quercion petraeae-cerris*, whereas the alliance *Quercion pubescenti-sessiliflorae* appears in the northern parts of both regions (Pignatti & Pignatti-Wikus 1987; Poldini 1988; Blasi et al. 2001, 2004; Ubaldi 2003). These studies show that a common European work on these topics is needed.

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