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## Phytocoenological analysis of grey alder (*Alnus incana* L.) forests in the Dinarides of Croatia and their relationship with affiliated communities

### Phytozönologische Analyse von Grau-Erlenwäldern (*Alnus incana* L.) in den kroatischen Dinariden und ihrem Verhältnis zu verwandten Pflanzengesellschaften

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#### Abstract

This paper provides a comprehensive survey of the results of phytocoenological research into *Alnus incana* forests from the alliance *Alnion incanae* in the Dinarides. Stands from the south-eastern Dinarides (*Alnetum incanae* = *Oxali-Alnetum incanae*) were analyzed and compared with those from the north-western Dinarides (*Lamio orvalae-Alnetum incanae*). The comparison reveals significant differences in the floristic composition and in the degree of differentiation – and particularly in the presence of the species of the Illyrian floristic geoelement. Focus was placed on the area of western Croatia where a geographic variant of *Helleborus dumetorum* had previously been defined within the association *Lamio orvalae-Alnetum incanae*. Two of its subtypes, *Salix alba* and *Alnus glutinosa*, were determined in our research. The former subtype thrives on occasionally flooded, moist sites, where the floristic composition is dominated by hygrophytes. The latter subtype grows on elevated and drier terraces and is richer in mesophilous species from the surrounding zonal forests. A floristic-sociological comparison of the *Lamio orvalae-Alnetum incanae* with the related syntaxa indicates the presence of about forty diagnostic species which accentuate its independence and the need to assess it at the level of an independent, regional association within the alliance *Alnion incanae*.

**Keywords:** *Alnion incanae*, *Alnus incana*, forest communities, *Lamio orvalae-Alnetum incanae*, the Dinarides

**Erweiterte deutsche Zusammenfassung am Ende des Artikels**

#### 1. Introduction

Phytocoenological research into grey alder forests in the Dinarides began in the second half of the twentieth century. In the eastern and inner Dinarides in Montenegro, Serbia and Bosnia and Herzegovina research was conducted by BLEČIĆ (1960), STEFANOVIĆ (1964), JOVANOVIĆ et al. (1983), DINIĆ & KALINIĆ (1983), and more recently by RAKONJAC (2002), BARUDANOVIĆ (2007) and RAKONJAC et al. (2009). In their published works, the authors

present 58 phytocoenological relevés which they classified into the syntaxa *Oxali-Alnetum incanae* Blečić 1960, *Alnetum incanae* Lüdi 1921 and *Alnetum glutinoso-incanae* Br.-Bl. 1915 within the alliance *Alnion incanae* Pawl. in Pawl. et al. 1928. Grey alder forests in the north-western Dinarides have been studied only recently. In Slovenia, DAKSKOBLER (2007, 2010) defined a new association *Lamio orvalae-Alnetum incanae* Dakskobler 2010, which was also confirmed in Croatia (VUKELIĆ et al. 2012). A total of 122 relevés have been presented in research to date, while this paper provides 16 new relevés. They are important because they allow new insights related to the floristic composition and variability of *Lamio orvalae-Alnetum incanae*.

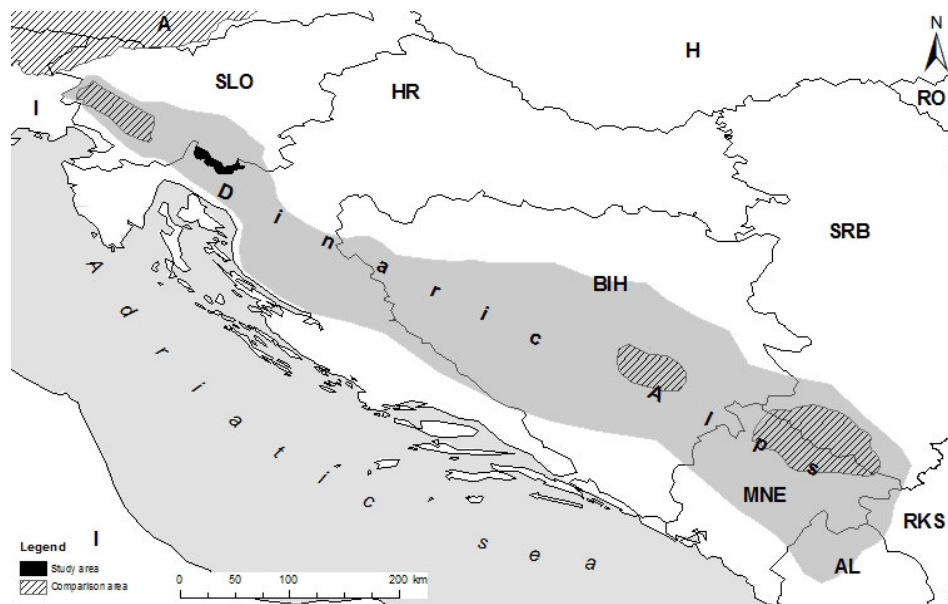
The results of the cited studies have thus far not been compared, while a comparison of the association *Lamio orvalae-Alnetum incanae* with the neighbouring areas of Austria and Italy has partially been performed (SBURLINO et al. 2012, DAKSKOBLER & ROZMAN 2013). A new concept of European floodplain forests has recently been presented (DOUDA et al. 2016), in which all the listed syntaxa are classified into the association *Alnetum incanae*. For this reason, our research sets the following goals: (1) to provide phytocoenological relevés of grey alder forests in the Dinaric part of Croatia; (2) to compare them with other Dinaric syntaxa of grey alder which belong to the alliance *Alnion incanae*; and (3) to analyse and define them in the broader European context of recent phytocoenological surveys.

## 2. Study area

Phytocoenological relevés were made in the Croatian part of the western Dinarides (Fig. 1). The Dinaric Alps in this area are composed of Mesozoic carbonates with numerous karst landforms, which create a heterogeneous landscape. The dominant soil types are swampy gleyic mineral non-carbonate soils in combination with alluvial-colluvial gleyed soil (ŠKORIĆ et al. 2003). The occurrence and growth of grey alder forests is conditioned by occasional flooding of the River Kupa and its tributaries over a length of about thirty kilometres. The average fall of the River Kupa in the research area is 2 m/km. The river partly has a canyon form and partly extends along horizontally elongated terraces, on which the forests were cut down in the past. In the last 50 years land cultivation has gradually been abandoned, giving place to natural succession. The dominant tree species in the investigated forests is *Alnus incana*, while sites with long stagnating water are dominated by *Alnus glutinosa*. Other tree species, such as *Salix eleagnos*, *S. alba*, *Fraxinus excelsior*, *Acer pseudo-platanus*, *Carpinus betulus* and *A. campestre* also occur frequently.

These stands grow at elevations from 220 to 540 m. The average annual temperature in the study area is about 11 °C, and about 17 °C in the vegetation period (April - October). The average rainfall is 2200 mm, of which 43% falls in the vegetation period. These indicators suggest the prevalence of perhumid, temperate warm climate of mountain nature.

Grey alder stands represent permanent stages. The zonal vegetation in the lower parts of the surrounding mountains is made up of oak-hornbeam forests from the alliance *Erythronio-Carpinion* (Ht. 1938) Marinček in Mucina et al. 1993, while the higher parts are inhabited by Illyrian beech forests of the alliance *Aremonio-Fagion* (Ht. 1938) Borhidi in Török et al. 1989. Plant species of these zonal forests frequently penetrate to the banks of the River Kupa and even cross over to the river islands. About 70% of the western continental part of the Croatian Dinarides is covered by forests.



**Fig. 1.** Geographical position of the study area.

**Abb. 1.** Geographische Lage des untersuchten Gebiets.

### 3. Material and Methods

#### 3.1 Methods and nomenclature

Research was conducted according to the principles of the standard Central European Phytocoenological School (BRAUN-BLANQUET 1964). Plant nomenclature was coordinated with the Flora Croatica Database (NIKOLIĆ 2004), and the mosses with ATHERTON et al. (2010). The syntaxonomic nomenclature of higher units follows the survey of DOUDA et al. (2016), and the regional syntaxa from previous studies are presented in their original form. A part of the syntaxa was described in accordance with ICPN (WEBER et al. 2000), and another part follows a multidimensional classification of vegetational units (MATUSZKIEWICZ & MATUSZKIEWICZ 1981).

The sociological species affiliation was determined according to our own understanding (VUKELIĆ 2012), but mostly follows the generally accepted and cited European phytocoenological literature (e.g., OBERDORFER 1994, AESCHIMANN et al. 2004).

#### 3.2 Data collection and analysis

Literature sources of phytocoenological relevés are given in Table 1. The 16 new relevés were made in 2016, in fully canopied stands aged from 30 to 50 years and with a tree height of about 20 m.

All the 196 relevés of grey alder forests from the Dinarides were stored in the Turboveg Database (HENNEKENS & SCHAMINÉE 2001). The cluster analysis and Simprof test were made using PRIMER v6 software (CLARKE & GORLEY 2006). The UPGMA (Unweighted Pair-Group Method Using Arithmetic Averages) agglomerative hierarchical method with the Bray-Curtis similarity index was employed. The Simprof (Similarity Profile) test was used to test the structure of the *a priori* unstructured dataset. Combined with the UPGMA analysis, it shows specific substructures in the diagram which correspond to objective (non-random) groups. The test was conducted with 999 permutations and a 5% confidence interval. JUICE 7.0 (TICHÝ 2002) was used to determine the differential species.

**Table 1.** List of literature sources and phytocoenological relevés in the analysis.**Tabelle 1.** Verzeichnis der Literaturquellen und phytozöologischen Aufnahmen in der durchgeführten Analyse.

Area, Syntaxa	No. of relevés	Average area of relevés (m <sup>2</sup> )	Source
North-western Dinarides			
Slovenia			
<i>Lamio orvalae-Alnetum incanae</i> var. geogr. <i>Anemone trifolia</i> - <i>typicum</i>	29	280	DAKSKOBLER 2007, 2010, DAKSKOBLER & ROZMAN 2013
- <i>caricetosum albae</i>	22	340	DAKSKOBLER et al. 2004, DAKSKOBLER & ROZMAN 2013
- <i>fraxinetosum excelsioris</i>	14	350	DAKSKOBLER et al. 2004
- <i>rhamnetosum fallacies</i>	35	340	DAKSKOBLER 2007, DAKSKOBLER & ROZMAN 2013
<i>Lamio orvalae-Alnetum incanae</i> var. geogr. <i>Scopolia carniolica</i>	5	200	DAKSKOBLER & ROZMAN 2013
	9	310	DAKSKOBLER 2007
Croatia			
<i>Lamio orvalae-Alnetum incanae</i> var. geogr. <i>Helleborus dumetorum</i> - <i>Alnus glutinosa</i> subtype	15	450	VUKELIĆ et al. 2012, & this article
- <i>Salix alba</i> subtype	9	390	VUKELIĆ et al., this article
South-eastern and central Dinarides			
Montenegro			
<i>Oxalido-Alnetum incanae</i> - <i>lysimachietosum nummulariae</i>	14	350	BLEČIĆ 1960
Serbia			
<i>Oxalido-Alnetum incanae</i> - <i>athyrietosum</i>	7	3800	BLEČIĆ 1960
- <i>juniperetosum communis</i>	4	140	JOVANOVIĆ et al. 1993
<i>Alnetum glutinoso-incanae</i>	4	175	JOVANOVIĆ et al. 1983
<i>Alnetum incanae</i>	8	730	RAKONJAC 2002
<i>Alnetum glutinoso-incanae</i>	10	700	RAKONJAC et al. 2009
Bosnia and Herzegovina			
<i>Alnetum incanae</i>	4	150	STEFANOVIĆ 1964
<i>Oxalido-Alnetum incanae</i>	7	100	BARUDANOVIĆ 2007
Italy			
<i>Primulo vulgaris-Alnetum incanae</i>	39		SBURLINO et al. 2012
<i>Aceri-Alnetum incanae</i>	80		SBURLINO et al. 2012
Austria			
<i>Aceri-Alnetum incanae</i>	329		WILLNER & GRABHERR 2007
Europe			
<i>Alnetum incanae</i>	232		DOUDA et al. 2016

The abundance of the species which occur in several layers was merged into one layer in Turboveg (HENNEKENS & SCHAMINÉE 2001). Particular species and subspecies were unified within the species aggregate (e.g., *Asarum europaeum* and *A. europaeum* ssp. *caucasicum*, *Campanula patula* and *C. patula* ssp. *abietina*, *Phyteuma spicatum* and *P. spicatum* ssp. *coeruleum*, *Senecio nemorensis* and *S. ovatus*, *Stellaria nemorum* and *S. nemorum* ssp. *glochidisperma* (= *S. montana*), *Aconitum lycoctonum* and *A. lycoctonum* ssp. *vulparia*, *Lamium galeobdolon* and *L. galeobdolon* ssp. *flavidum*).

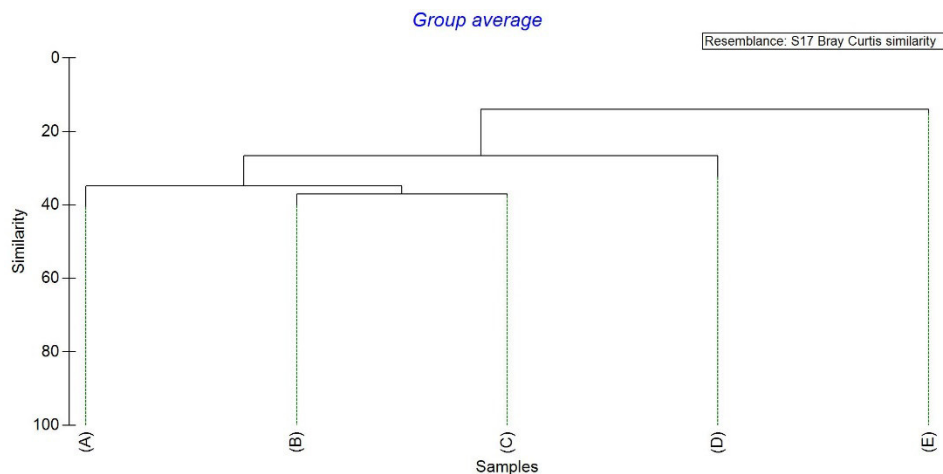
## 4. Results

A total of 615 species, of which 183 occur in only one relevé, were recorded in the 196 relevés of *Alnus incana* forests in the Dinaric Alps. There were 179 species common to the entire area.

The result of cluster analysis is presented in Figure 2. *Alnus incana* forests were classified into five groups, which largely follow its geographic distribution. Groups A–D represent all the relevés of the north-western Dinarides, while Group E contains relevés of the central and south-eastern Dinarides.

### 4.1 *Alnus incana* forests of the north-western Dinarides

According to research to date, these forests belong to the association *Lamio orvalae-Alnetum incanae*. In the ecological and sociological sense, it is characterized by two groups of species: the first group consists of species of floodplain and moist sites, which are frequent in similar vegetation types in Europe. Of these species, *Salix eleagnos*, *Rubus caesius* and *Cerastium sylvaticum* feature more frequently in relation to the affiliated *Alnus incana*



**Fig. 2.** Dendrogram of the 196 relevés of *Alnus incana* forests from the Dinaric Mountains.

A – *Lamio orvalae-Alnetum incanae* var. geogr. *Helleborus dumetorum*, subtype *Alnus glutinosa*, 15 relevés, Croatia; B, C – *Lamio orvalae-Alnetum incanae*, var. geogr. *Anemone trifolia* and var. geogr. *Scopolia carniolica*, 114 relevés, Slovenia; D – *Lamio orvalae-Alnetum incanae* var. geogr. *Helleborus dumetorum*, subtype *Salix alba*, 9 relevés, Croatia; E – *Alnetum incanae*, 58 relevés, south-eastern and central Dinarides.

**Abb. 2.** Dendrogramm der 196 Aufnahmen der *Alnus incana*-Wälder im Dinarischen Gebirge. Erläuterung s. o.

syntaxa. The second group includes mesophilous species of zonal sessile oak-hornbeam and beech forests, of which the following species of the Illyrian floristic geoelement are particularly prominent: *Lamium orvala*, *Scopolia carniolica*, *Cardamine trifolia*, *Knautia drymeia* ssp. *drymeia*, *Omphalodes verna*, *Galanthus nivalis*, *Hacquetia epipactis*, *Helleborus odorus*, *Cyclamen purpurascens*, *Cardamine enneaphyllos*, *Helleborus niger*, *Aposeris foetida* and *Primula vulgaris*. Stands from Croatia also feature *Epimedium alpinum* and *Helleborus dumetorum*, and those from Slovenia *Anemone trifolia*.

Statistical analysis indicates the chorological-floristic variability of the association *Lamio orvalae-Alnetum incanae* (Fig. 2). Groups A and D represent two types of the studied stands from western Croatia, and groups B and C represent stands from the Dinaric and south-eastern Alpine area of Slovenia. The Slovenian phytocoenologists described them in two geographic variants: var. geogr. *Anemone trifolia* Dakskobler 2010 and var. geogr. *Scopolia carniolica* Accetto 1996. The geographic variant *Anemone trifolia* is divided into the subassociations *typicum* Dakskobler, Šilc et Čušin 2004, *caricetosum albae* Dakskobler, Šilc et Čušin 2004, *fraxinetosum excelsioris* Dakskobler et Rozman 2013 and *rhamnetosum fallacis* Dakskobler et Rozman 2013. The justification for such classification was analyzed by DAKSKOBLER & ROZMAN (2013) and it is not the subject of our analysis.

We focus on stands from western Croatia, i.e., on groups A and D. In the floristic and ecological sense, they differ significantly from one another, but also from the mentioned lower syntaxa of *Alnus incana* forests in Slovenia. We compared them at the level of geographic variants and listed their differential species in Table 2. The geographic variant *Helleborus dumetorum* from western Croatia was divided into two subtypes – *Salix alba* and *Alnus glutinosa* – even though these are not ranked in the phytocoenological system. Their analytical relevés with diagnostic species are presented in Supplement S1. The differential species were determined using the JUICE programme, and the criterion used for determination was a frequency above 50% and a fidelity index above 40. Should future research show a broader distribution and a higher significance of these subtypes, it will be possible to rank them as independent subassociations within the association *Lamio orvalae-Alnetum incanae*, or its geographic variant *Helleborus dumetorum*.

#### 4.1.1 *Lamio orvalae-Alnetum incanae* var. geogr. *Helleborus dumetorum* subtype *Salix alba* (Supplement S1, columns 1–9)

Mixed stands of grey alder and white willow were recorded in a larger, temporarily flooded field and in several places along the River Kupa itself and its tributaries. Stands along the River Kupa are 1–2 m above the average water level and are periodically flooded during higher waters. Stands in karst fields and depressions are found close to the watercourses, 0.5 to 2 m above the average level. They are under the strong impact of floodwater, and the lowest depressions with high groundwater are overgrown with common reed (*Phragmites australis*). In addition, the terrain is rich in temporary watercourses, which are activated during longer rainy periods and in early spring. Floods most frequently occur in April. In extremely humid years, floods may last up to three months (MAYER & BUŠIĆ 1993). The soils are alluvial-colluvial, gleyed. Sporadic afforestation with seedlings of black alder and with clones of black poplar and pedunculate oak undertaken in 1990 was not successful in this site.

In our research, 145 species of higher plants and 19 species of mosses were recorded in nine phytocoenological plots. The distinct differential species in Supplement S1 are the best indicators of moist terraces and of the riparian belt, but are rare in the other lower syntaxa of

**Table 2.** Differential species (marked grey) for the lower syntaxa in the association *Lamio orvalae-Alnetum incanae*: Croatia - 1. var. geogr. *Helleborus dumetorum*; Slovenia - 2. var. geogr. *Anemone trifolia*, 3. var. geogr. *Scopolia carniolica*.

**Tabelle 2.** Differentialarten (grau markiert) für niedrigere Syntaxa der Assoziation *Lamio orvalae-Alnetum incanae*. Erläuterung s. o.

Group No.	1	2	3	Group No.	1	2	3
No. of relevés	24	105	9	No. of relevés	24	105	9
	frequency (%)				frequency (%)		
<b>Differential species</b>				<i>Carduus personata</i>	.	8	100
<i>Brachythecium rutabulum</i>	75	10	.	<i>Matteuccia struthiopteris</i>	4	9	100
<i>Circaea lutetiana</i>	67	6	11	<i>Scopolia carniolica</i>	29	17	100
<i>Lysimachia vulgaris</i>	58	10	.	<i>Cardamine pentaphyllos</i>	.	30	100
<i>Helleborus dumetorum</i>	58	.	.	<i>Adoxa moschatellina</i>	8	31	100
<i>Eupatorium cannabinum</i>	54	2	.	<i>Omphalodes verna</i>	21	17	89
<i>Galeopsis speciosa</i>	50	9	.	<i>Chrysosplenium alternifolium</i>	.	14	78
<i>Alnus glutinosa</i>	50	3	.	<i>Anthriscus sylvestris</i>	12	10	78
<i>Hypnum cupressiforme</i>	50	2	.	<i>Lathraea squamaria</i>	.	13	56
<i>Poa trivialis</i>	46	10	.	<i>Maianthemum bifolium</i>	.	16	56
<i>Carex brizoides</i>	42	.	.	<i>Corydalis solida</i>	.	7	56
<i>Carex remota</i>	38	2	.	<i>Myrrhis odorata</i>	.	8	56
<i>Ajuga reptans</i>	33	10	.	<i>Cardaminopsis halleri</i>	.	.	56
<i>Carex pendula</i>	33	4	11				
<i>Lycopus europaeus</i>	29	.	.	<b>Diagnostic species for more syntax</b>			
<i>Lysimachia nummularia</i>	29	1	.	<i>Ligustrum vulgare</i>	46	56	.
<i>Mentha longifolia</i>	25	.	.	<i>Knautia drymeia</i>	63	37	.
<i>Scirpus sylvaticus</i>	25	1	.	<i>Helleborus niger</i>	33	53	.
<i>Rudbeckia laciniata</i>	25	2	.	<i>Salix alba</i>	38	16	.
<i>Juncus effusus</i>	25	.	.	<i>Hacquetia epipactis</i>	16	36	.
<i>Anemone trifolia</i>	.	75	.	<i>Caltha palustris</i>	29	14	.
<i>Tilia cordata</i>	.	69	.	<i>Veratrum album</i>	21	52	100
<i>Hepatica nobilis</i>	17	61	.	<i>Oxalis acetosella</i>	21	51	100
<i>Galanthus nivalis</i>	12	54	.	<i>Anemone ranunculoides</i>	.	50	78
<i>Cyclamen purpurascens</i>	12	43	11	<i>Crocus vernus</i> agg.	4	40	78
<i>Helleborus odoratus</i>	12	49	.	<i>Aconitum lycoctonum</i>	.	68	56
<i>Carex alba</i>	16	39	.	<i>Carex digitata</i>	21	56	56
<i>Veratrum nigrum</i>	.	39	.	<i>Gagea lutea</i>	.	20	56
<i>Tilia platyphyllos</i>	4	37	11	<i>Fagus sylvatica</i>	29	69	67
<i>Ostrya carpinifolia</i>	.	35	.	<i>Lonicera xylosteum</i>	12	52	44
<i>Isophyrum thalictroides</i>	4	25	.	<i>Myosotis sylvatica</i>	.	33	44
<i>Malus sylvestris</i>	.	23	.	<i>Dactylorhiza fuchsii</i>	.	20	11

this association. These are *Salix alba*, *Mentha longifolia*, *Scirpus sylvaticus*, *Stachys sylvatica* and *Lysimachia vulgaris*. Locally, *Impatiens noli tangere*, *Eupatorium cannabinum*, *Galeopsis speciosa*, *Urtica dioica*, *Petasites hybridus*, *Lamium maculatum* and *Glechoma hederacea* can also be singled out in relation to the subtype *Alnus glutinosa*.

Mixed grey alder and white willow stands have also been described in other European regions (e.g., OBERDORFER 1992, DAKSKOBLER et al. 2004, WILLNER & GRABHERR 2007, DAKSKOBLER 2016). However, they are primarily communities of the type *Salicetum albae* s.l. and are classified within the alliance *Salicion albae* Soó 1930. The presence of different species in these stands also reflects different biogeographic characteristics. Therefore, POLDINI et al. (2011) point out that these stands belong to the Central European vegetation type with different geographic variability.

#### **4.1.2 *Lamio orvalae-Alnetum incanae* var. geogr. *Helleborus dumetorum*, subtype *Alnus glutinosa* (Supplement S1, columns 10–24)**

This subtype is frequent in the study area, always occurring at higher positions than those of the previous. It inhabits a drier riparian part, on elongated terraces along the course of the River Kupa and its tributaries which are generally 2 to 6 m above the average water level. It sporadically rises for some fifteen metres above the river bed along wet slopes. The distance of the stands from the river course is generally up to 200 m. In the years with less rainfall this subtype is not flooded, but the soil is moist due to the runoff of water from the surrounding slopes. The soils are alluvial carbonate, gleyic and non-gleyed with inclusions of pseudogley, and are partially anthropogenic.

The tree layer is relatively heterogeneously composed, with grey alder frequently accompanied by black alder, common hornbeam and European ash, while the presence of other species is linked to the geomorphological features of the microsite, the distances from the water courses, anthropogenic impacts and the like. In relation to the other lower syntaxa within the association *Lamio orvalae-Alnetum incanae* the differential species are *Alnus glutinosa* and *Poa trivialis*. Locally, *Acer campestre*, *Carpinus betulus*, *Ligustrum vulgare*, *Crataegus monogyna*, *Primula vulgaris*, *Allium ursinum*, *Anemone nemorosa*, *Hedera helix*, *Knautia drymeia* and *Cirsium oleraceum* can also be singled out in relation to the subtype *Salix alba*.

#### **4.1.3 Syndynamics**

Syndynamic processes which lead to the formation of the association *Lamio orvalae-Alnetum incanae* were explained in detail by DAKSKOBLER (2010) along the course of the River Idrijca in western Slovenia. They are identical along the course of the River Kupa in Croatia as well. In simple terms, the development of vegetation starts from bare pebbly banks over different weedy, ruderal and other communities (most frequently the stage with the species *Petasites hybridus*) towards smaller shrubby groups of grey willow and purple osier (*Salicetum eleagno-purpureae petasitetosum hybridi* (Šilc et Čušin 2000) Oriolo et Poldini 2002). With a rise in the terrain, decreased wetness and the development of the humus-accumulative soil horizon, willows assume tree-like forms and the stands are penetrated by the more mesophilous elements of the surrounding zonal forests. This is how the association *Lamio orvalae-Salicetum eleagni* Dakskobler, Šilc et Čušin ex Dakskobler 2007 is formed, and it follows similar processes to develop into the community *Lamio orvalae-Alnetum incanae*, in which *Acer pseudoplatanus*, *Fraxinus excelsior*, *Alnus glutinosa* and



*Carpinus betulus* have a high degree of presence. Sometimes the tree layer also features *Fagus sylvatica* and *Picea abies*, but their vitality is significantly reduced. Stands developed in such a way remain as permanent stages, and their further development generally ends in the form of zonal communities of common hornbeam or beech.

One part of grey alder stands in western Croatia is characterized by a considerable presence of black alder, which is not typical of the association *Lamio orvalae-Alnetum incanae* in the rest of its distribution range. The higher presence of black alder is favoured by the longer retention and slower runoff of water on flat terraces and the formation of swampy gleyic soils.

#### 4.2 *Alnus incana* forests of the south-eastern and central Dinarides

Grey alder forests in the central and south-western part of the Dinarides were investigated in the south-west of Serbia, in Montenegro along the rivers Tara and Lim, and in Central Bosnia in the mountains of Trebević and Vranica. Their distribution range is larger, but their composition is very similar. The stands extend from 900 to 1100 m and grow on mountain dystric pseudogley (with the presence of acidophilic species *Festuca heterophylla*, *Potentilla erecta*, *Deschampsia flexuosa*) with short periods of wet phases, because the water on the slopes with an inclination from 5 to 20° exhibits faster lateral drainage. The average annual temperature is about 7 °C, and rainfall is 670 mm in the eastern part (SW Serbia), and about 1100 mm in the inner part (Central Bosnia and Herzegovina).

The floristic composition of grey alder forests in this area features a very small number and low frequency of its diagnostic species in relation to other syntaxa. In the Supplement S2, nine (9) diagnostic species were recorded whose frequency is generally below 40 %. The classification of these forests in the association *Alnetum incanae* is justified (cf. columns 1 and 6 in Supplement S2). They display more floristic differences in relation to the north-western Dinarides than to the affiliated *Alnus incana* forests of the Romanian Carpathians (SANDA & MIHAILESCU 2003, COLDEA & URSU 2016) or Central Europe (e.g., DOUDA 2008, CHYTRÝ 2013, SLEZÁK et al. 2014, PIELECH 2015).

### 5. Discussion and conclusions

In the synthetic table (Supplement S2), the association *Lamio orvalae-Alnetum incanae* was compared with neighbouring and related communities which were classified into the alliance *Alnion incanae*. There are 290 species of higher plants in the Table, but those represented in only one column below 15% were left out. Only those diagnostic species which relate to the association *Lamio orvalae-Alnetum incanae* were listed. They were determined subjectively, i.e., those represented only in this association or only those whose presence in the association is at least 30% higher than in other communities were considered. Species which are more frequently present in all the compared syntaxa have been omitted.

According to the comparison, with regard to the presence of basic species of temporarily flooded and moist sites (a total of about 100 species of the alliance *Alnion incanae* and classes *Alnetea glutinosae* Malcuit 1929, *Salicetea purpureae* Moor 1958, *Galio-Urticetea* Passarge ex Kopecký 1969, *Molinio-Arrhenetheretea* R. Tüxen 1937 em. R. Tüxen 1970, *Phragmiti-Caricetea elatae* Klika in Klika et Novak 1941), the studied communities show relatively few differences and a small number of diagnostic species.

As for other species, primarily those from the surrounding zonal forests, there are very significant differences. In this sense, the grey alder forests investigated in the north-western Dinarides are particularly distinct. Of the syntaxa compared in Supplement S2, they are floristically richest and show the highest degree of differentiation. Supplement S2 contains 39 species which differentiate them from other syntaxa.

The large number of diagnostic species of the association *Lamio orvalae-Alnetum incanae* is due to several factors. The presence of the species of the Illyrian distribution, as well as of some more thermophilous elements, is mainly the consequence of the biogeographic position and floristic-genetic development of the western Dinarides – one of the floristically richest forest areas in Europe. A higher number of species of the alliance *Tilio-Acerion* Klika 1955 is the consequence of deeper river canyons, a perhumid climate and high air humidity over the year. Mesophilous species from zonal oak-hornbeam and beech forests inhabit narrower slopes and belts along river courses where water is not retained for longer periods. These species penetrate from the surrounding slopes and mix with hygrophytes. Part of the year without much moisture in the soil is conducive to their growth. The geomorphology of the terrain is also important. In areas in which the stands along the watercourses in the Dinaric karst fields are spatially more distant from the slopes with zonal forests, the number of mesophilous species from these communities is much smaller. However, these localities are predominantly covered with forests dominated by black alder. Another important factor is also the anthropogenic factor, whose impact is reflected in the presence of anthropophytes.

The distinct diagnostic species and chorological characteristics are the main reason for which DAKSKOBLER (2010) placed stands of this type into an independent association, despite the fact that in 2007, during research along the River Soča, he had originally included them into the association *Alnetum incanae* and into syntaxonomic schemes that comprised several different biogeographic regions (e.g., MÜLLER & GÖRS 1958, SCHWABE 1985, partly WILLNER & GRABHERR 2007). DAKSKOBLER (2010, p. 12) concludes "that riparian grey alder forests and other broadleaf forests along mid-mountain and mountain water courses in the northern part of the Illyrian floristic province should be classified into the association *Lamio orvalae-Alnetum incanae*. Its diagnostic species are *Lamium orvala* and *Scopolia carniolica*, and indirectly some other diagnostic species of the alliances *Aremonio-Fagion* and *Erythronio-Carpinion*".

The association *Lamio-orvalae-Alnetum incanae* also displays the majority of its floristic-diagnostic properties towards the community *Alnetum incanae* (sensu DOUDA et al. 2016) and does not fit in its Cocktail formula in several parameters. This example illustrates the following: defining one syntaxon over a large area may cause a number of problems, such as the loss of the biogeographic identity, biodiversity and evolutionary characteristics of regional forests, the levelling of ecologically diverse regions, and so on. This relates particularly to refugial areas such as the Dinarides, which are characterized by an unequal presence of species of the Illyrian floristic geoelement, and by rich but heterogeneous floristic compositions. DOUDA et al. (2016) point out: "Although many associations were not retained by our approach, some of them may still be kept in the national and regional vegetation surveys as they probably include region-specific species combinations that are not transferable to the European scale. Yet, they may remain meaningful within some regions".

On the other hand, we should be aware that syntaxa which are defined too narrowly and locally are frequently needlessly described. The basic prerequisite for an objective solution of these problems is the systematic study of forests documented with a relevant number of phytocoenological relevés. This is not the case with the Dinarides and south-eastern Europe, to which DOUDA et al. (2016) draw attention.

Based on the performed analysis, we conclude that *Alnus incana* forests of the south-eastern Dinarides can be included in the association *Alnetum incanae*, whereas in the north-western part of the Dinarides they belong to the regional association *Lamio orvalae-Alnetum incanae*. This regional association differs from the stands which were described in the associations *Primulo vulgaris-Alnetum incanae* Sbrulino, Poldini, Andreis, Giovagnoli et Tasinazzo 2012, *Equiseto-Alnetum incanae* Moor 1958 and *Aceri-Alnetum incanae* Beger 1922 in the neighbouring areas of northern Italy and Austria (cf. DAKSKOBLER & ROZMAN 2013).

In the syntaxonomic sense, the analyzed associations *Alnetum incanae* and *Lamio orvalae-Alnetum incanae* are classified in the suballiance *Alnenion glutinoso-incanae* Oberd. 1953, the alliance *Alnion incanae* Pawl. in Pawl. et al. 1928, of the order *Fagetalia sylvaticae* Pawl. in Pawl. et al. 1928 and class *Quercu-Fagetea* Br.-Bl. et Vlieger 1937.

In the new synsystematic classification of vegetation of Europe (MUCINA et al. 2016), the alliance *Alnion incanae* was classified in the order *Alno-Fraxinetalia excelsioris* Passarge 1968 and class *Alno glutinosae-Populetea albae* P. Fukarek et Fabijanić 1968. Future analyses will show the justification of such an approach.

## Erweiterte deutsche Zusammenfassung

**Einleitung** – Im Artikel werden phytozoologische Untersuchungen der Syntaxa der Grau-Erle aus dem Verband *Alnion incanae* Pawl. in Pawl. et al. 1928 in den Dinariden (Abb. 1) vorgestellt. Der nordwestliche Teil umfasst das Dinaridengebiet Sloweniens und Kroatiens, wo auf der kollin-submontanen Höhenstufe (200 bis 700 m) das *Lamio orvalae-Alnetum incanae* Dakskobler 2010 vorkommt. In den mittleren Dinariden in Bosnien und Herzegowina und den südöstlichen Dinariden im Südwesten Serbiens und in Montenegro dominiert das *Oxali-Alnetum incanae* Blečić 1960. Diese Syntaxa wurden bislang nicht miteinander verglichen, und in der Übersicht der Überschwemmungs- und Feuchtwälder in Europa (DOUDA et al. 2016) wurden sie als *Alnetum incanae* Lüdi 1921 aufgefasst. Das Ziel dieser Arbeit war daher, die Grau-Erlenwälder im dinarischen Gebiet Kroatiens phytozoologisch zu analysieren (1), und sie mit verwandten Wäldern in anderen dinaridischen und benachbarten Gebieten zu vergleichen (2).

**Materialien und Methoden** – Die Forschungen wurden nach den Prinzipien der standardisierten phytozoologischen Schule (BRAUN-BLANQUET 1964) durchgeführt. Von den 196 Vegetationsaufnahmen (Tab. 1) stammten 138 aus dem nordwestlichen (Tab. 2) und 58 aus dem südöstlichen Teil der Dinariden. Von den Vegetationsaufnahmen der nordwestlichen Dinariden sind 16 bisher noch nicht publiziert worden (Beilage S1).

Alle Vegetationsaufnahmen wurden in der Turboveg-Datenbank (HENNEKENS & SCHAMINÉE 2001) gespeichert. Die Cluster-Analyse, sowie der Simprof-Test wurden im PRIMER v6 (CLARKE & GORLEY 2006) durchgeführt. Als Clustering-Methode wurde die UPGMA (Unweighted Pair-Group Method Using Arithmetic Averages) angewendet, sowie der Bray-Curtis-Ähnlichkeitsindex. Die Differentialarten wurden mit dem Programm JUICE 7.0 (TICHÝ 2002) ermittelt.

**Ergebnisse und Diskussion** – Das Ergebnis der statistischen Analyse sind fünf getrennte Gruppen von Vegetationsaufnahmen (Abb. 2). Diese stimmen in hohem Maße mit der geographischen Verbreitung der dinaridischen Grau-Erlenwälder überein.

Die Gruppen A bis D präsentieren die Assoziation *Lamio orvalae-Alnetum incanae* in den nordwestlichen Dinariden. Die Gruppen A und D aus Westkroatien können als zwei neue Subtypen aufgefasst werden: Der Subtyp von *Salix alba* und der Subtyp von *Alnus glutinosa*. Der erste Subtyp umfasst 9 Aufnahmen aus sehr feuchten, zeitweilig überschwemmten und tiefer liegenden Standorten um das Ufer des Flusses Kupa und seinen Nebenflüssen (Spalten 1–9 in Beilage S1). Der zweite Subtyp umfasst Bestände auf höheren Flussterrassen, trockeneren Standorten und daher mit einer höheren Anzahl mesophiler Arten der umliegenden zonalen Wäldern (Spalten 10–24 in Beilage S1). Die Gruppen B und C stellen Grau-Erlenwälder Nordwestsloweniens dar, die in früheren Untersuchungen (DAKSKOBLER, 2007, 2010, DAKSKOBLER & ROZMAN 2013) in zwei geographische Varianten und vier Subassoziationen gegliedert wurden. Zur Gruppe E gehören Wälder der zentralen und südöstlichen Dinariden. In deren Artenzusammensetzung treten Hygrophyten hervor, und die Gesamtzahl sowie die Frequenz der Differenzialarten sind sehr niedrig, sodass sie der Assoziation *Alnetum incanae* (vgl. Beilage S2, Spalten 1 und 6) angeschlossen werden können.

Die Ergebnisse unserer Untersuchung deuten auf eine Vielfalt der Grau-Erlenwälder in den Dinariden hin, auf eine reichhaltige und heterogene Artenzusammensetzung und eine ungleichmäßige Präsenz des illyrischen Florenelements. Die Sonderstellung der Assoziation *Lamio orvalae-Alnetum incanae* (Beilage S2, Spalte 2) innerhalb der untersuchten Syntaxa kann als das Ergebnis der biogeographischen Lage an der nordwestlichen Grenze der Dinariden, der unterschiedlichen vegetationsgeschichtlichen Entwicklung, der vielfältigen Umweltbedingungen und, in einem geringeren Maße, der anthropogenen Einflüsse verstanden werden.

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### Supplements

**Supplement S1.** *Lamio orvalae-Alnetum incanae* var. geogr. *Helleborus dumetorum* in the Croatian Dinarides.

**Beilage S1.** *Lamio orvalae-Alnetum incanae* var. geogr. *Helleborus dumetorum* in den kroatischen Dinariden.

**Supplement S2.** Comparison of the association *Lamio orvalae-Alnetum incanae* with affiliated communities of the Dinarides and neighbouring areas.

**Beilage S2.** Vergleich der Assoziation *Lamio orvalae-Alnetum incanae* mit verwandten Gesellschaften der Dinariden und benachbarter Gebiete.

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