Chorological differentiation of endemo-relic species Ramonda serbica Panc. and R. nathaliae Panc. & Petrov. (Gesneriaceae) on the Balkan Peninsula.

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Abstract

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Ramonda serbica and R. nathaliae, the endemo-relic species of the Balkans, are generally believed to inhabit mostly clearly separated areas; in Macedonia the dividing line between their respective areas would be the watershed between the Aegean and the Adriatic river systems. However, the recent chorological investigations challenge this view: we established the existence of two zones of sympatry in SE Serbia, as well as of several localities where R. serbica encroaches upon the Aegean region inhabited by R. nathaliae. There are also some literature data on the possibly parapatric distribution of these species in N & NW Greece. These recent investigational results are taken into account together with the literature and herbarium data and horizontal and vertical distribution of Balkan ramondas are presented.

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1. Introduction

The distribution, ecological and taxonomic differentiation of the species Ramonda serbica and R. nathaliae were first discussed in a detailed study by Košanin (1921), thereby creating the basis for further research into the phytogeographical, ecological and general biological characteristics of these undeniably interesting and important tertiary relics of the Balkan and European flora. Košanin (1921) showed that these two species are valid in taxonomic terms, which some earlier botanists either disputed or interchanged them during determination (Baldacci 1897, 1901, 1906, Velenovsky 1898, Vandas 1909, Doflein 1921). In addition to morphological differences (shape, nervature, indentation of the leaves, structure and color of floral parts, etc.), Košanin (1921) also points out differences in the ecology and distribution of the Balkan ramondas. In spite of the fact that Balkan ramondas have been investigated more than other plants of the Balkan flora, primarily due to their relic, endemic and specific ecophysiological features (poikilohydry), recent detailed investigations of their chorology, phytocoenology and ecophysiology have collected

data which enable a comprehensive perception of the biological characteristics of these plants. This work concentrates on the phytogeographical aspects and, in this regard, on certain ecological features of their differentiation on the Balkan peninsula.

2. Material and Methods

The greatest part of the data on the distribution and ecology of the Balkan ramondas was obtained from field research from 1980-1989. At that time, approximately 80% of the localities of both species were investigated, primarily in Yugoslavia. The results of this research, concerning in particular the chorology, have in part been published (STEVANOVIĆ, V. et al. 1986a, 1986b, 1987).

Important sources of data for chorological analysis included the herbaria collection of the Museum of Natural History in Belgrade and the Botanical Institute, Faculty of Biology, University of Belgrade. Numerous literature data were also used from regional floras and individual works. Due to the uncertainty in determining these species, particularly in old literature, literature data on distribution are indicated with a special sign on the presented area map (Fig. 2).

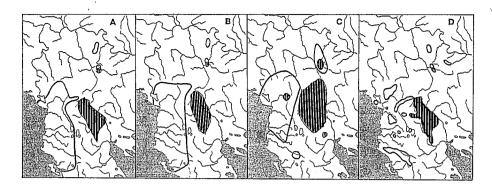
3. Results and Discussion

Special attention has been given to the distribution of the Balkan ramondas. The first area maps given by Košanin (1921, 1922), made by the contour method without designation of specific finds, were followed by the contour area map of TURRILL (1929) which provides nothing new and is in many respects less precise than Košanin's map (Fig. 1A,B). Markgraf (1932) gave a map of the distribution of the species R. serbica in Albania with designated locations, and Velchev, Jordanov and Ganchev (1968) presented in detail the distribution of the same species in Bulgaria. Forty years after Turrill, Quézel (1968) presented an area map of the Balkan ramondas with considerable imprecisions so that the map seems to be almost arbitrary (Fig. 1C). In a detailed study of the Balkan ramondas, Meyer (1970) pointed out the shortcomings of Quézel's area map and at the same time gave the most complete map of the distribution of R. serbica and R. nathaliae (Fig. 1D) which, however, is also not without certain oversights. In recent time, Voliotis (1981) gave a detailed map of the distribution of Balkan ramondas in Greece based on his own field work and literature data.

In spite of considerable attention given to the distribution of the Balkan ramondas, several unanswered questions still remain, concerning their chorological differentiation.

3.1. General distribution

At one time Košanin (1921) demonstrated, and botanists after him mostly



Ramonda serbica

Ramonda nathaliae

Fig. 1. Considerable attention was given to the distribution of Balkan ramondas. Several authors at different times gave the area maps with variable precision and care for details: A -Košanin (1921), B - Turrill (1929), C - Quézel (1968) and D - Meyer (1970).

accepted, that the boundary line between the areas of *R. serbica* and *R. nathaliae* was the watershed of the Aegean and Adriatic Seas in Macedonia, Greece and Albania. Košanin (1921) cited the region of SE Serbia in the Niš vicinity as the only place where their areas overlap. It is interesting to note that authors, who later gave area maps of the ramondas, designated this as a region where the zones bordered on each other, or as a parapatry of areas (Turrill 1929, Meyer 1970).

Our investigations in Macedonia indicated that *R. serbica* crosses the watershed of the Aegean and Adriatic in several localities, thereby encroaching on the region of *R. nathaliae* distribution (Fig. 2). The habitats of *R. serbica* in the Aegean watershed in Macedonia (the Balaban gorge in SW part of Šarplanina mountain, the Cerovačka river gorge on the northern spurs of Bistra mountain and several habitats in gorges in the upper course of the Treska, i.e. Golema River) are denoted by arrows on the presented area map (Fig. 2).

In addition to these data, VOLIOTIS (1981) also found *R. serbica* in several places relatively deep in the Aegean watershed on Voras mountain which was otherwise known as a region inhabited exclusively by *R. nathaliae*. He also cites several habitats of *R. nathaliae* in Epirus within the Adriatic watershed and deeply within the *R. serbica* area. Since he does not specify those localities for *R. nathaliae* in Epirus, it could be assumed that he used the literature data of BALDACCI (1897, 1907, 1906) which were later established to have referred to *R. serbica* (KOŠANIN 1921, MEYER 1970).

QUÉZEL (1968) also denotes a narrow region in his area map, along the Drim River in northern Albania, thus in the Adriatic watershed and deep within the *R. serbica* area, as a part of a disjunct area of *R. nathaliae* (Fig. 1C). The reliable

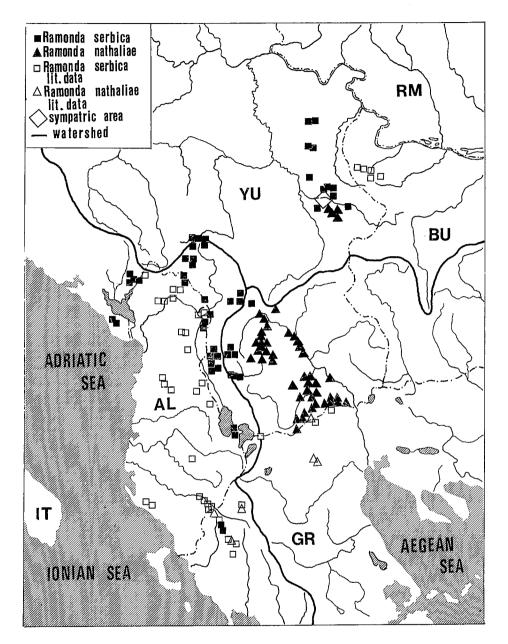


Fig. 2. Map of distribution of the species Ramonda serbica and R. nathaliae on the Balkan Peninsula (orig. Stevanović et al.).

authorities on Albanian flora, HAYEK (1917, 1923) and MARKGRAF (1932), reported only *R. serbica* in Albania. Košanin (1914, 1939), visiting the very same part of Albania which Quézel's map indicates as a distribution area of *R. nathaliae* found

only *R. serbica* and documented it with plant material. It is difficult, of course, to completely reject the possibility of finding the species *R. nathaliae* in Albania, since the flora of this Balkan country has still not been sufficiently investigated. However, all known factors regarding the chorology of the Balkan ramondas indicate little probability of presence of *R. nathaliae* in Albania, all the more so since even QUÉZEL does not report any specific habitat or source of data.

3.2. Parapatry and sympatry

All area maps produced so far of the Niš vicinity in SE Serbia indicate that it is a contact zone (parapatry) or an overlapping of areas (sympatry). Košanin (1921) considered at first this to be the only region on the Balkan peninsula where these plants' areas overlap, but withdrew later on (Košanin 1939) noting that even in this region their areas are microgeographically differentiated.

Our investigations established that while the areas in Niš vicinity remain clearly microgeographically differentiated, there exist two zones of true sympatry with mixed populations of both species: Radovanski Kamen above the village of Jelašnica and Oblik in the Sićevačka klisura gorge (STEVANOVIĆ et al. 1986) (Fig. 2).

The find of *R. serbica* inside the *R. nathaliae* area cited by Voliotis (1981) on Voras mountain in northern Greece is another region where the Balkan ramondas overlap. However, it is hard to speak of the true nature of the contact or even overlapping of areas, as Voliotis (1981) did not investigate this region from either the microgeographical or the ecological aspect, and it is impossible to get an idea of the nature of their chorological differentiation from the presented floristic data. The question remains unanswered as to whether the Balkan ramondas in this locality remain microgeographically differentiated in spite of a contact area, or whether, as in SE Serbia, there are zones of true sympatry. In this case, the questions which remain unresolved through lack of appropriate data appear similar to those encountered in Quézel's (1968) area map, where small enclaves of *R. nathaliae* were inserted within the main regions of distribution of *R. serbica* in Albania.

3.3. Different ecological patterns - the main principle of chorological differentiation

The basic chorological differentiation of the Balkan ramondas lies in fine specificities of their ecological patterns. R. serbica and R. nathaliae differ in terms of preference for microclimatic, pedological and orographic requirements. R. serbica inhabits more humid and cooler habitats, primarily sheltered by forest canopy, while R. nathaliae is found in more open, drier and warmer habitats. These ecological differences in the Balkan ramondas are, of course, expressed in their chorological differentiation, i.e. in these two species' areas of distribution - R. serbica in more western and humid parts and R. nathaliae in warmer and drier parts of the central Balkans. In addition, R. nathaliae -as a more xerophilous species- settles in more open habitats, often without the protection of surrounding forest vegetation, covering rocks from the foot all the way to the peak of some mountains, behaving like a relic

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tertiary oromediterranean plant. Contrary to this, *R. serbica* rarely leaves the forest zones and is very rarely found in zones above 1600 m. The present vertical distribution of Balkan ramondas and their differences in this regard are to a large extent the result of population migrations during the Ice Age to the main refuges in gorges and canyons of the surrounding mountains where they have remained to this day (Fig. 3).

Both species primarily inhabit crevices of limestone rocks with northern exposure, whereby *R. nathaliae* is also found in other geological rockbeds such as serpentine and some kinds of silicious rocks (STEVANOVIĆ, V. & STEVANOVIĆ, B. 1985).

The ecological differences between the Balkan ramondas are also maintained in sympatry zones in SE Serbia and in regions where their areas border on each other (the watershed of the Adriatic and Aegean seas in Macedonia). To this effect, *R. nathaliae* inhabits the open limestone cliffs in two sympatry habitats in the vicinity of Niš, while the greatest part of population of *R. serbica* is attached to the rocks in the Oriental hornbeam (Carpinus orientalis) forest. Both sympatry habitats in several places allow two species to grow side by side. In areas where their zones border on each other in Macedonia, the ecological differentiation is even more distinct. To this effect, *R. serbica* stays in region where submediterranean vegetation of the Ostryo-Carpinion type prevails with a considerable share of western Balkan floristic elements; *R. nathaliae* settles in more xerophilous regions of eastern Mediterranean alliance Ostryo-Carpinion aegeicum, in which western Balkan elements, indicators of humid climatic conditions, are absent or extremely rare.

4. Conclusion

The present distribution of the endemo-relic species Ramonda serbica and R. nathaliae is primarily the result of migration processes of both species during the Ice Age and interglacial periods. It is difficult to give a reconstruction of the Tertiary areas of Balkan ramondas due to the absence of any fossil traces. A realistic assumption is that the taxonomic and thereby chorological differentiation arose during the Tertiary or at the latest during the first glaciations. Considering the present chorological relationship between these two species, differentiation of the R. serbica and R. nathaliae areas is almost complete, except for the region of SE Serbia in the vicinity of Niš and on the Voras mountain in N Greece and, probably in Epirus in NW Greece (VOLIOTIS 1981). The existence of these overlapping zones (definitely proven only for the Niš vicinity) is probably of a secondary nature and dates from the Ice Age.

It can be said with certainty that *R. serbica* is found in Yugoslavia (SE Montenegro, SW Serbia, S Sandzak, Kosovo, E Serbia, W Macedonia), Bulgaria (NW spurs of Stara planina mountain), Greece (primarily in Epirus) and in almost the entire territory of Albania from Prokletije mountain to Epirus. The greatest number of habitats in Albania, Greece and Yugoslavia (Macedonia, Kosovo) are

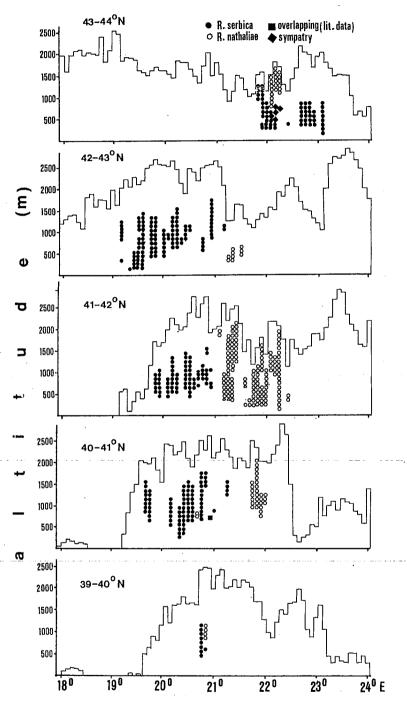


Fig. 3. Vertical distribution of the Balkan ramondas across the geographical longitude in segments at 10° of geographical latitude. The (——) line shows the highest altitude points of the relief, at 5° intervals.

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associated with the Adriatic watershed, and less so to the Aegean watershed (W Macedonia, N Greece) and the Black sea watershed (E Serbia, S Sandzak and SW Serbia along the Ibar river valley). Contrary to this, the greatest part of the R. nathaliae area is in the Aegean watershed in Yugoslavia (Macedonia) and in Greece, while small enclaves in E Serbia (around Niš) belong to the Black sea watershed.

Basically, the phytogeographic differentiation of the Balkan ramondas lies in their fine ecological differences. These are perceived through the ecological characteristics of the habitats they settle, which differ in terms of micro and mesoclimatic, pedological and orographical characteristics. Their presence today in canyons and gorges is due to the migration of their populations from mountainous regions into protected places during the Ice Age. The relatively small number of their habitats in higher mountain regions are probably the oldest, or most relic, and are perhaps the last remains of their Tertiary areas. Such is the case of *R. nathaliae* habitats in E Serbia (Suva planina mountain) and in Macedonia (Karadzica, Jakupica, Nidze, Kožuf) and of *R. serbica* in Serbia (Ošljak, on the northern spurs of Šarplanina mountain) and on some mountains in Epirus.

The decisive element in the general chorological differentiation of the Balkan ramondas, the one which greatly aided the division of their areas, are the changes in the relief of the Balkan peninsula during the Tertiary period (orogenesis, transgression of the seas, etc.). In this respect, assuming that the taxonomic differentiation, by polyploidy, arose from *R. nathaliae* as the older into the younger *R. serbica* during the Tertiary period, their areas at that time could have been separated in the course of the so-called lake phase of the Balkan peninsula by the water basins of the Aegean lakes (the Pelagonian, Eordic and Elimic lakes). Thus, they were island-type areas at that time, and only later, with the first recession of the lakes, and then during the Ice Age, was there a contraction of their already previously differentiated areas. Those phytogeographic characteristics of the two species of *Ramonda* are maintained to the present in spite of migratory changes, due to altered climatic conditions, which resulted in sporadic, contact or overlapping zones of their areas.

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