Genesis of the floras in the arid Intermountain basins of the North Caucasus

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Abstract. The aim of the study was to explore history of flora formation in arid basins of the North Caucasus, and to identify the correlation between this flora and those of arid regions of neighboring areas. We applied generally accepted methods of flora study and analysis. The arid intermountain basins of the North Caucasus are an original and poorly studied formation. Surrounded by forest and alpine vegetation, they have preserved in their composition a xerothermic flora that differs from the flora of the steppe of the Ciscaucasia and takes in the features of the flora of the Southwest Asia and the Mediterranean region. The first large array of arid vegetation is located in the upper reaches of the Kuban River in the Jurassic depression, which runs between the Main Caucasian and Side ridges. Further to the East, arid basins are founding in the basins of all major tributaries of the Terek River. After the Argun and Sharoargun rivers in the Republic of Dagestan, the xerothermic vegetation of the arid basins are replaced by a belt of upland xerophytes of mountain dry and desert steppes, which stretches to the south and connects with the arid regions of the Eastern Transcaucasia. Our studies show a genetic relationship between the flora of the arid basins of the North Caucasus and the areas of xerothermic vegetation on the one hand in Azerbaijan and Iran, on the other-in the Mediterranean, from where its formation began in the territory under consideration. The xerothermic period of the late Miocene is the driest in the history of the Caucasian flora and contributed to the deep penetration of the Southwestasian arid flora into the territory of the North Caucasus after the connection of the Caucasian Isthmus with the southern mainland.

1. Introduction
The flora of the North Caucasus is one of the richest and most original in the territory of the Russian Federation. It includes about 6,000 taxa, while the flora inventory is not yet complete. The nature of the relief, the presence of various ecological niches for the growth of plants and the peculiarities of the history of the formation of flora influenced the high biological diversity of this territory. Despite more than 200 years of studies of the North Caucasian’s flora and vegetation, many issues remain unresolved. The study of the processes of florogenesis and the formation of modern types of vegetation and local floras are fundamental issues of the formation of modern vegetation cover.

The arid basins of the North Caucasus are forming in intermountain depressions located between the Skalisty, Lateral and Main Caucasian ridges. They are surrounded by forested and alpine
landscapes of mountain ranges and watersheds. The flora of the basins differs sharply from the flora of the adjacent territories, being distinguished by the predominance of xerophytes, unique life forms (for example, thorny cushion plants), the complex structure of the vegetation cover, the composition of the dominants of plant communities, etc.

The formation of the flora of the arid basins of the North Caucasus is poorly covered in the literature and purposeful studies on this problem have not been carried out. A.A. Grossheim [1–2], A.I. Galushko [3–4] paid the most attention to this issue. The flora of the basins is fundamentally different from that of the steppe and desert-steppe areas of the Ciscaucasia, despite their geographic proximity. The flora of the arid basins shows a connection with the arid regions of Eastern Transcaucasia and Western Asia, the leading dominant species of plant communities, the general composition of the flora and the presence of isolated relict populations of some plant species bring these floras closer.

The aim of the research was to study the history of the formation of the flora of the arid basins of the North Caucasus, as well as to identify the relationship of this flora with the flora of the arid regions of neighboring territories.

2. Materials and Methods
The research was carried out in intermountain basins in the territory of Karachay-Cherkessia, Kabardino-Balkaria, North Ossetia, the Chechen Republic and the Republic of Dagestan from 2005 to 2019. The studies cover areas of distribution of arid vegetation in the basins of the rivers Kuban, Malka, Baksa, Chegem, Cherek Balkarsky, Cherek Bezengiysky, Urukh, Ardon, Fiagdon, Terek, Argun, Sharorgun, as well as extensive areas of distribution of arid vegetation in Avar and Kazikumukh Koisu.

The area of distribution of arid vegetation covers the North Jurassic depression located between the Skalisty and Bokovy ridges, and, in part, the Central Jurassic depression, which lies between the Main Caucasian and Side ridges [5]. The intermountain basins of the North Jurassic depression are 5 to 30 km wide and are located at absolute heights from 1300 to 1700 m. They represent graben-synclinal depressions, the bottom of which is composed of rocks of the Middle and Lower Jurassic. The basins of the Central Jurassic depression are 6 to 15 km wide, with absolute elevations ranging from 1800 to 3200 m. They are composed of Middle Jurassic schists and metamorphic rocks.

The lower boundary of the distribution of arid vegetation runs at an altitude of 800–1200 m, to the north it is limited by the rocks of the Rocky Range and river canyons. On the slopes of the southern exposure, the zone of distribution of xerophilous communities rises to 1700 m, on the slopes of the northern exposure it is limited to heights of 1200-1300 m. Usually, inversion of vegetation belts is observed when xerophytes are present on the southern slope, and meadow and forest mesophilic communities are distributed on the northern slopes.

As a result of many years of research, more than 5,000 herbarium sheets have been collected. As a result of many years of research, more than 5,000 herbarium sheets of vascular plants have been collected. The selection of plants was carried out at random in different types of habitats and at different heights. To accurately determine the location, geographic coordinates and altitude were recorded using GPS. In cameral conditions, the herbarium material was dried and marked. All herbarium specimens are available for general use in the herbarium collections of the Perkalsky Arboretum (PALE) and the Komarov Botanical Institute of the Russian Academy of Sciences (LE).

The nomenclature of species is given according to the Internet resource The Plant List [6]. Life forms of plants were classified according to the Ch. Raunkiaer division [7]. The chorology of taxa was determined using data on distribution in the lists of flora, systematic summaries and in the "Caucasian flora conspectus" [8-11].

In the geographical analysis of the flora, the technique and scheme for identifying the geographical elements of the flora of the Caucasus, developed by N.N. Portenier [12, 13], were used. According to this scheme, N.N. Portenier, identifies 29 geographical elements, combined into 4 large groups: widespread species, boreal, ancient Mediterranean, and binders. Widespread species include
pluriregional, that is, species distributed in different regions of the globe, and Holarctic, distributed throughout the Holarctic (including the Palaearctic). Highlighted by N.N. Portenier, the group of binders species, according to the author himself, is subjective. Criteria that make it possible to objectively distinguish between these groups of geographic elements can be obtained by analyzing the behavior of species on the territory of specific floristic provinces.

3. Results and Discussion
Arid basins are represented in the North Caucasus from the Kuban River basin, where xerophilic vegetation is common in the vicinity of the Uchkulan village. Further, large massifs of arid flora are presented in Kabardino-Balkaria in the Bylymskaya, Verkhnechechegemskaya, Bezengi and Verkhnebalkarskaya depressions. In North Ossetia, xerophilic vegetation is developed along all large tributaries of the Terek River: the Urukh, Ardon, Fiagdon, Karmadon, Daryal rivers. In Ingushetia these are the Dzheyrakhskaya and Targimskaya depressions in the Terek and Assy basins. In the Chechen Republic, xerophilic vegetation is widespread in the Chanty-Argun river basins in the vicinity of the Itumkale village and in the Armkhi tract. On the territory of the North Caucasian republics, the arid flora reached its greatest distribution in Dagestan, from the Andiyskoe Koisu River to the middle reaches of the Samur River.

The distribution scheme of arid vegetation in the depressions of the North Caucasus is shown in figure 1.

Figure 1. Distribution of arid basins in the North Caucasus.
1. Verkhnekubanskaya, 2. Bylymskaya, 3. Verkhnechechegemskaya, 4. Bezengi, 5. Verkhnebalkarskaya, 6. Urukhskaya, 7. Zaramagskaya, 8. Mizurskaya, 9. Unalskaya, 10. Verkhnefiagdonskaya, 11. Gizeldonskaya, 12. Karmadonskaya, 13. Dzheyrakhskaya, 14. Targimskaya, 15. Itumkaliskaya, 16. Sharoyskaya, 17. Botlikhskaya, 18. Hindakhskaya, 19–20. Samurskaya.

N. I. Kuznetsov combined most of these types of vegetation into a single type of upland xerophytes [14]. 1342 species of vascular plants are found in the upland xerophyte belt of the North Caucasus. Data on the floristic diversity of arid basins in the republics of the North Caucasus is presented in table 1.
Table 1. The number of taxa in the flora of arid basins in the republics of the North Caucasus.

| Republic                                | Number of taxa |
|-----------------------------------------|----------------|
|                                         | species        | genera | families |
| Karachay-Cherkessia                     | 543            | 183    | 54       |
| Kabardino-Balkaria                      | 648            | 192    | 43       |
| North Ossetia                           | 884            | 263    | 80       |
| Chechnya and Ingushetia                 | 1035           | 374    | 82       |
| Dagestan                                | 1245           | 385    | 87       |

From the data in the table, it can be seen that as we move eastward, the number of taxa of the flora of arid basins increases. This is due to the wide variety of environmental conditions in the eastern regions of the North Caucasus. In the Western part of the North Caucasus basins take up less space. Their flora includes species typical of the subalpine and alpine belts. In the Eastern Caucasus, especially in Dagestan, the arid flora occupies much larger areas of terrain, and at the same time, it is enriched by species of other ecological groups. Mainly, the flora of the East Caucasian arid regions increases by species of Transcaucasian and Southwest-Asian origin.

It is necessary to distinguish three main aspects in the analysis of the florogenetic relations of the flora and vegetation of the arid basins of the North Caucasus with the steppes of the Mediterranean, the Ciscaucasia and the arid regions of the Transcaucasia and Western Asia:
1. identification of local isolated populations of rare plant species;
2. characteristics of the main types of plant communities with the identification of the main dominant species that are important in the composition of plant communities;
3. study of the complex of species common to the flora of individual arid basins.

To date, the flora of the Upper Balkar basin [15], the Jeyrakh, Targim and Itumkalinsky basins [16] are the most studied.

Phryganoid vegetation of shrub communities and thorny cushion plant formations, arid open woodlands, communities of mountain dry and desert steppes form the vegetation cover of arid basins of the North Caucasus.

The distribution of phryganoid vegetation is common to the arid regions of the Eastern Caucasus and Southwest Asia. "Phrygana" is a formation of low-growing xeromorphic semi-shrubs and shrubs. In the North Caucasus, this type of vegetation is formed by shrubby representatives of the genera *Astragalus* and *Onobrychis*, forming "thorny cushion plants". From the Kuban River basin to the basins of the Chechen Republic, only two species are dominant in this type of vegetation: *Astragalus aureus* Willd. and *A. denudatus* Steven (figure 2). In Dagestan, such species as *Astragalus denudatus* Steven are found in tragankanth formations. The main distribution area of all these species is located in the Eastern and Southern Transcaucasian region, and Southwest Asia. On the territory of Azerbaijan and Armenia, the number species of *Astragalus* of tragankanth formations increases even more. For example, in the arid regions of the Republic of Nakhichevan, communities consist of such species as: *Astragalus compactus* Willd., *A. lagurus* Willd., *A. persicus* Fisch. & C.A. Mey., *A. pycnophyllus* Steven, *A. strictifolius* Boiss.et al. [17].

From the Baksan river basin and further to the east, *Onobrychis cornuta* L. begins to occur in the composition of phryganoid vegetation; it is most widespread in Dagestan (figure 3), in Azerbaijan and in Armenia, where this species often forms a separate type of cushion sainfoin communities. The distribution of *Onobrychis cornuta* L. is directly related to the arid regions of Southwest and Central Asia.

Such species of communities of the phryganoid type as *Berberis vulgaris* L., *Ephedra procera* Fisch. & C.A. Mey., *Juniperus oblonga* M. Bieb., *Rhamnus pallasii* Fisch. & C.A. Mey., *Spiraea hypericifolia* L. and others bring the flora of the arid basins of the North Caucasus closer to the arid regions of the Caucasus and Asia Minor. Even more species common with the flora of Transcaucasian
region are found in the flora of Dagestan. *Atraphaxis daghestanica* (Lovelius) Lovelius, *Caragana grandiflora* (M. Bieb.) DC., *Cerasus incana* (Pall.) Spach, *Cotoneaster morulus* Pojark., *Juniperus polycarpos* K. Koch, *Lonicera iberica* M. Bieb., *Paliurus spina-christii* Mill., *Prangos ferulacea* (L.) Lindl., *Rhus cariaaria* L. are present here in the composition of phryganoid vegetation.

![Figure 2](image2.png)

**Figure 2.** Communities of *Astragalus aureus* and *A. denudatus* (Fiagdon River, North Ossetia).

![Figure 3](image3.png)

**Figure 3.** Arid communities of *Onobrychis cornuta* (settlement Gunib, Dagestan).

A distinctive feature of the phryganoid plant communities of Transcaucasus is the significant participation in their composition of representatives of the genus *Acantholimon*, which are rare in the arid regions of the North Caucasus. The only known local populations *Acantholimon schemachense* Grossh. are given for Southern Dagestan [18]. The isolated population of *Acantholimon glumaceum* (Jaub. & Spach) Boiss. is located in the Cherek Balkarsky River basin in Kabardino-Balkaria [19]. The main area of this element of flora is confined to the Eastern and Southern Transcaucasus, and Iran.

Significant areas of the slopes of the arid basins are occupied by grass communities of mountain dry and desert steppes, consisting mainly of hemicryptophytes, with minor participation of therophytes, cryptophytes and semi-shrubs. Communities of upland xerophytes dominated by *Achnatherum caragana* (Trin.) Nevski, *Festuca sclerophylla* Boiss. ex Bisch., *Salvia canescens* C.A. Mey., as well as the dominant communities of *Artemisia austriaca* Jacq., *A. lerheana* Weber ex Stechm., *A. marschalliana* Spreng., *A. salsoioides* Willd., *A. scoparia* Waldst. & Kit. are typical for the grassy slopes of the arid basins of the North Caucasus. As a rule, grass communities without shrubs or their insignificant participation are formed in conditions of increased grazing.

The species *Salvia canescens* (incl. *S. daghestanica* Sosn.) is endemic to the North Caucasus. It belongs to the Caucasian-Asian section of the *Stenarrhena* (Don) Briq. and shows kinship relations with the Southwestasian species *S. aethiopis*, *S. syriaca* L., *S. verbascifolia*, *S. candidissima* Vahl [20]. The number of species of Southwestasian origin is not large in the Central Caucasus. In the basins of the Kuban, Baksan and Cherek rivers, such species include *Botryochloa caucasica* (Trin.) C.E. Holubb., *Hyssopus angustifolius* M. Bieb., *Teucrium orientale* L. and some others. Their number increases significantly in the Eastern Caucasus and reaches a maximum in Dagestan. Here are such Southwestasian species as *Lallemantia peltata* (L.) Fisch. & C.A. Mey., *Peucedanum paucifolium* Ledeb., *Sedum corymbosum* Grossh., *S. sempervivoides* Fisch. & M. Bieb., *Stachys fruticulosa* M. Bieb., *Thymus transcaucasicus* Ronn., *Ziziphora serpillacea* M. Bieb.et al. they are confined to communities with the dominance of sage graying.

The geographical spectrum of the flora of the arid regions of the republics of the North Caucasus is presented in table 2.
Table 2. The spectrum of the geographical elements of the flora of the arid regions of the republics of the North Caucasus.

| Geographical element        | Karachay-Cherkessia | Kabardino-Balkaria | North Ossetia | Chechnya and Ingushetia | Dagestan |
|-----------------------------|---------------------|--------------------|---------------|------------------------|---------|
| Plurinacional               | 4                   | 3                  | 5             | 15                     | 17      |
| General Antarctic           | 134                 | 112                | 128           | 224                    | 198     |
| Boreal                      | 312                 | 247                | 425           | 519                    | 426     |
| Ancient Mediterranean       | 137                 | 187                | 231           | 153                    | 348     |
| Binders                     | 75                  | 82                 | 73            | 121                    | 213     |
| Total                       | 533                 | 631                | 862           | 1032                   | 1202    |

According to the data in table 2, the flora of the arid basins can be characterized as Boreal-ancient Mediterranean. The number of ancient Mediterranean species increases as we move east. Most of the species of this group are characteristic of petrophytic and xerophytic habitats, so their number will increase in the east and decrease in the west of the North Caucasus. The western part of the North Caucasus is characterized by an increase in the area occupied by forest and meadow communities. It should be attributed to the species that connect the flora with the steppe regions of the Ciscaucasia, 

Artemisia marschalliana, A. pontica L., Berberis vulgaris, Dianthus capitatus Balb. ex DC., D. lanceolatus Steven ex Rchb., Goniothalamus tataricum (L.) Boiss., Kohlrauschia prolifera (L.) Kunth, Stipa pennata L., S. paludicola K. Koch et al. There are much more species whose range covers the entire ancient Mediterranean region. This group of species has an ancient origin. Most of them appeared in the Caucasus in the Tertiary period, when the arid flora was just beginning to form. Such elements of the flora of arid basins include: Capparis herbaea L., Cheilanthes pteridioides (Reichard) C. Chr., Juniperus sabina L., J. oblonga M. Bieb., J. oxycedrus L. (Dagestan), Notholaena marantae (L.) Desv., Quercus petraea L. ex Liebl.

The participation of the species of the Mediterranean and Pontic floristic provinces in the composition of the flora and vegetation cover of the arid basins is no less important. It is particularly interesting to find conditional relicts in a particular area, i.e. populations of species isolated from their main distribution area.

Astragalus calycinus M. Bieb. is a characteristic species of the steppes of the CisCaucasia. The main range of the species covers South-West Asia, Eastern and Southern Transcaucasia, Eastern Caucasus and the Ciscaucasia. The species is found in the arid vegetation of North Ossetia and Dagestan. In North Ossetia and Kabardino-Balkaria, the species could have entered the arid basins from the north from the Ciscaucasia territory. Its distribution in Dagestan must have come from the Eastern Transcaucasia.

The distribution area of Clausia aprica (Stephan) Korn. - Trotzky is located in Eastern Europe, Southern Siberia and Central Asia. In the North Caucasus, the species is known from the vicinity of the city of Kislovodsk. In the herbarium of LE there are collections of N. N. Portinier from the vicinity of the village of Bezengi [20].

Crambe gibberosa Rupr. is found in the vicinity of the village of Bezengi [21], as well as in Central Dagestan in the vicinity of the villages of Gimry, Ashilta and Tlokh [17]. The species is confined to the steppe and phryganoid communities. The main distribution area of the species covers the CisCaucasus, Eastern Caucasus and Eastern Transcaucasia. Due to the absence of this species in other arid basins, its penetration into the Cherek Bezengiysky River basin must have occurred from the north, from the territory of the Ciscaucasia.

Ononis pusilla L. is extended in the Black Sea region, Transcaucasia, the Eastern Caucasus and South-West Asia. Several isolated populations are found in the upland xerophyte belt of North Ossetia and Dagestan. A small population was found in Karachay-Cherkessia [22]. The species entered the North Caucasus from the Transcaucasia, probably from both the west and the east.

The only one population of Onosma sericea Willd in the North Caucasus is found in Dagestan in the basin of the Sulak and Karakoysu rivers on open xerophytic slopes. The main range of the species
is located in the Southern Transcaucasia region and South-West Asia [23]. The origin of the population of *Onosma sericea* in Dagestan is not quite clear yet. Most likely, the distribution of the species must have originated from the Eastern Transcaucasia.

Presence of *Polygala sibirica* L. in the North Caucasus is of interest. The Caucasian population of this species was distinguished as an independent species *Polygala sosnowskyi* Kem.-Nath., but morphologically poorly separated from *P. sibirica*. The main distribution area of this species covers Eastern Europe and Southern Siberia. In the North Caucasus, *Polygala sibirica* is found in the foothills. The species is present in Transcaucasian region and its appearance in the arid basins of the Central and Eastern Caucasus could occur only from the north from the foothills. Isolated populations of *Ziziphora clinopodioides* Lam. (incl. *Z. borzhomica* Juz.) are located in the upper reaches of the Ardon River and in the vicinity of the village of Burkikhian in Southern Dagestan. The distribution area of the species covers Transcaucasus, Southwestern and Central Asia, and southern Siberia.

Several factors have influenced on the origin of the arid basin flora. The main of these factors is the periods of aridization of the climate of the Caucasus region in the past geological epochs. Common ancient Mediterranean species are the most ancient representatives of the flora. Their appearance should probably be attributed to the end of the Miocene. By this time, evergreen forests of the Pontic type already dominated the Caucasus. By the end of the Miocene, the Alpine belt began to form in mountainous areas and minor glaciers formed [24]. The uplift of the Rocky Ridge and due to this the formation of the North Jurassic Depression affected the strengthening of the continental climate in the mountainous areas.

Pliocene tectonic and climatic conditions had a global impact on the formation of arid basins in the highlands of the North Caucasus. One should fully agree with the opinion of O.E. Agakhanyants [25], A.A. Teimurova, Z.S. Abdulkhadzhieva, M.A. Dzhamaldinov [26] that the formation of an arid climate and the formation of xerophilous flora occurred after the Late Pliocene formation of the Forefront Ridges, which separated the plains of Dagestan and the Ciscaucasia from the intermountain regions. Broad-leaved forests give way to vegetation of open spaces due to the increased dryness of the climate. Further orogeny of the Rocky Ridge was of great importance. The redistribution of air mass flows associated with this process led to a decrease in the amount of jiggling in the intermountain basins. Moist air masses lingered on the northern slopes of the Rocky Range. This process made it possible to preserve the broadleaved beech and hornbeam forests of the Colchis type with the participation of *Hedera pastuchovii* Woronow, *Ilex colchica* Pojark., *Ostrya carpinifolia* Scop., *Taxus baccata* L., *Vaccinium arctostaphylos* L. on the northern slopes. Formation of steppe and phryganoid vegetation occurs in the intermountain basins of the North Caucasus.

In the Pliocene, the dispersal of species during the formation of the flora and vegetation of arid basins proceeded along three main directions.

The first group of species, typical for the western Mediterranean and the Black Sea region, settled along the foothills and depressions from the west, expanding their range to the Central Caucasus. The formation of the Caucasian species *Salvia canescens*, which inhabited the open arid slopes of intermountain basins, should be attributed to this time.

Species of arid regions of Southwestasian origin penetrate from the east from Western Asia (Iran, Turkey) through the Southern and Eastern Transcaucasia, first to the Eastern Caucasus (Dagestan), and then to the Central Caucasus. It is important that the formation of modern thorns cushion plant communities and the phryganoid type of vegetation should be attributed to Pliocene. The dispersal of thorny cushion plant species of the genus *Astragalus*, which later began to act as dominants, was the most active. The emergence of the *Onosma sericea* population in Dagestan should be attributed to this period. The flora of the arid regions of Dagestan has many similarities with corresponding regions of Azerbaijan, Armenia, and Iran. However, it also has many differential features. In particular, communities with representatives of the genera *Acantholimon* and *Onosma* were not widespread in the North Caucasus. The preservation during the period of maximum climate aridization of significant territories occupied by the Hyrcanian forests in the Samur river basin and the Kuban region of Azerbaijan could contribute to this. The penetration of xerophytes took place along the middle
mountains of these regions. We attribute to Pliocene the formation of not only the main core of xerothermal vegetation in the Central and Western Caucasus, but also the penetration of a number of mesophilic species here, in particular, the emergence of isolated populations of Papaver orientale L., Gypsophyla glandulosa (Boiss.) Walp., Tulipa humilis Herb. and etc. [27].

4. Conclusion

The flora of the arid basins of the North Caucasus is unique. The beginning of the formation of its individual species should be attributed to the end of the Miocene. Fundamental fractures in the flora and vegetation cover of the Caucasus occurred in the middle of the Pliocene in connection with the processes of orogenesis, the formation of advanced ridges, and, as a consequence, a change in the climatic situation and the redistribution of the movement of air masses in mountainous regions. Owing to this, the flora of the arid basins of the North Caucasus was formed on the basis of the Mediterranean and Southwestasian flora. The xerophytic flora of inland Dagestan should be considered the most ancient, it received the main core of xerophytes first, and in conditions of long isolation, a large number of endemic species and forms formed in it.

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