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Robinia pseudoacacia L. in the Western Caucasus

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Abstract—The distribution, frequency of occurrence, and tendency in change in number of *Robinia pseudoacacia* L. in the Western Caucasus and the age structure of populations and influence of this species on arboreal species diversity of riparian forests are analyzed. The results show that (1) the occurrence of *Robinia pseudoacacia* L. in different regions of the area studied is different; (2) most individuals of this species are less than 20 years old; (3) the abundance of *Robinia pseudoacacia* L. in areas of riparian forests to the greatest extent depends on the relative abundance of native dominants: the highest abundance is seen at a middle level of their dominance; and (4) replacement of native dominants by *Robinia pseudoacacia* L. does not lead to reduction in arboreal species diversity of forest stands.

Keywords: Robinia pseudoacacia, distribution, age structure, populations, dominants, species diversity, forest stands, Western Caucasus

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INTRODUCTION

Robinia pseudoacacia L. is the most common alien tree species in Europe, it is able to influence the functioning of ecosystems (Lambdon et al., 2008; Vinogradova et al., 2010) and therefore requires special attention from ecologists. However, for many regions of Russia, information about its distributions, the reasons for the unequal presence in various forest stands, the tendency for changes in abundance in recent years, and the impact on native species remains limited. The goal of this study is to make a generalization of the results of studies carried out by the authors in the period from 2007 to 2014 in order to fill this informational gap for the Western Caucasus.

MATERIALS AND METHODS

Object of Study

Robinia pseudoacacia (black locust, robinia) is a deciduous, fast-growing tree with the height of 25–30 m. The most vigorous growth in height and diameter is observed during the first 10–15 years; in particular, yearlings reach a height of 0.5–1 m. The plant is able to bear fruit from the third or fourth year; the largest number of seeds are produced between 15 and 40 years of age. The seeds remain viable for up to three years. The plant has abundant root shoots, by which it rapidly expands over the occupied territory (Shiereli, 1965; Kolesnikov, 1974).

Black locust is a macrothermophyte; it prefers a humid climate with a hot summer and warm winter—temperate and warm-temperate types of bioclimatic zones (Pilipenko, 1978). Optimal soils are fertile and not too dry; however, the species is fairly drought resistant and is generally undemanding in terms of soil conditions; it grows well in the steppe regions and can grow on poor sandy and saline soils, but it cannot stand strong salinity and excessive moisture. At the same time, the plant itself can significantly affect the environment, reducing soil moisture, but improving its structure and enriching the soil in nitrogen and calcium. Black locust is demanding in terms of light; it avoids dense forest stands unless it dominates (its open crown lets through a lot of light). However, after the first 6–8 years, this tree can withstand shade. Owing to a highly branched root system, in artificial stands, black locust strongly inhibits oak, ash, Norway maple, and related shrubs, negatively impacting their root systems (Kharitonovich, 1949; Kolesnikov, 1974; Bartha et al., 2008; Vinogradova et al., 2010).

The native range of *Robinia pseudoacacia* covers the eastern part of North America with Appalachian Mountains in the center: from Pennsylvania in the north to the north of Alabama and Georgia in the south, as well as part of Missouri, Arkansas, Oklahoma, Illinois, and Indiana. The best development of the species is in West Virginia and Kentucky. The northern border of the natural range corresponds to 41° N; it has an average January temperature of 1.7°C, average July temperature of 21°C, and average annual

Fig. 1. Study area. Roman numerals indicate the floristic regions: I—Novorossiysk; II—Sochi; III—Taman; IV—Abinsk; V—Hadyzhensk; VI—Maykop. The scheme of floristic zoning done by A.S. Zernov was used as basis (Zernov, 2006).

precipitation of 1000–1500 mm. In its native range in the Appalachian Mountains, black locust is distributed up to an elevation of 1000–1100 m a.s.l., and according to some literature, up to 1500 m. The species is naturalized up to the latitude of Quebec (46° N, average January temperature of –8°C, average July temperature of 16°C, precipitation of 1000–2000 mm) (Kolesnikov, 1974; Bartha et al., 2008; Vinogradova et al., 2010). There are indications that, in the Tertiary Period, black locust inhabited Sakhalin and Kazakhstan (Krishtofovich, 1941 by Gurskii, 1957). In the North Caucasus, the presence of genus *Robinia* was noted in upper Miocene sediments near Armavir (Galushko, 1976).

R. pseudoacacia was introduced to Europe (France) in 1601, and as a result of artificial breeding and self-propagation, it became very widespread and often forms pioneer forests in river valleys (Müller and Okuda, 1998; Bartha et al., 2008; Pyšek et al., 2009; Vinogradova et al., 2010). It grows in different habitats, but mainly at a low height.

In Russia, black locust has been cultivated since 1736. As an ornamental plant for greenery in the south of Russia, it composed up to 60–80% of the total number of trees; in the 1870s–1880s, it was widely used for steppe afforestation and the protection of railroads from snow and sand drifts (Gurskii, 1957). Currently, in the European part of Russia, invasive populations of this species have been found as far north as St. Petersburg (60° N), but mainly it is distributed south of the Gomel–Kursk–Voronezh–Saratov line (approximately 52° N) (Dudkina and Vinogradova, 2007).

Study Area

The distribution of *Robinia pseudoacacia* in the West Caucasus was studied by us within the Republic of Adygea and the Trans-Kuban part of Krasnodar krai, including the Black Sea coast and the Main Caucasian Ridge with its spurs; in the east, the region is restricted by the Laba River (43°19′–45°08′ N, 37°14′–41°30′ E) (Novorossiysk, Sochi, Taman, Abinsk, Hadyzhensk, and Maykop floristic regions (according to Zernov, 2006)) (Fig. 1).

The climatic conditions of the study area are characterized by high diversity. This area is located on the border of the temperate and subtropical zones and moderately humid European and dry Asian regions; the Main Caucasian Ridge and nonfreezing Black Sea have a significant impact on the climate. The Taman Peninsula and the Black Sea coast from Anapa to Novorossiysk are characterized by a hot and dry summer and relatively mild winter: the average temperature in January is from –1.5 to +1.0°C, the average temperature in July is 23.5°C, annual precipitation is

330–430 mm, and the area is subject to frequent dry winds. The temperature and humidity increase to the southeast. Thus, in the Tuapse region, the average annual air temperature is 13.5°C and annual precipitation is 1219 mm. In the Sochi region, the climate of coastal areas (200 m a.s.l.) is close to humid subtropical: the average temperature is 8.6°C in the coldest period and 18.5°C in the warmest period, and the annual precipitation is 1554 mm. In the mountains of the southern macroslope at the height of 600 m, the average temperature in January is –0.3°C, the average temperature in August is 19.5°C, and the annual precipitation is up to 2200 mm. The temperature decreases and the amount of precipitation increases with elevation. For example, on the Achishkho Ridge (Mzymta River basin) (1880 m a.s.l.), the average temperature in January is –5.5°C, the average temperature in August is 12.9°C, and the annual precipitation is 2617 mm. The plain and foothill territories of Ciscaucasia (northern macroslope) are influenced by continental air of the southern part of the Russian Plain: the average temperature in January is –1 to –2.8°C, and the average temperature in July is around 23°C. The area is moderately moist; the annual precipitation is 560–860 mm (*Agroklimaticheskii spravochnik*..., 1961; Rybak, 2006). In the mountainous part of the northern macroslope (Belaya River basin) within the upper limit of the forest (1800 m), the average temperature in January is –4.0 to –4.5°C, the average temperature in August is 13–14°C, and the average annual precipitation is 1780 mm (Ivanchenko et al., 1982).

The lowland part of the study area belongs to the steppe and forest-steppe zones. Most of this area is cultivated land. Along the river valleys, there are narrow strips of disturbed floodplain and riverine forests composed of *Populus nigra* L., *P. alba* L., and *Salix alba* L, with a significant presence of adventitious species (*Robinia pseudoacacia*, *Acer negundo* L., *Morus alba* L., *M. nigra* L., and others). Windbreaks consisting mainly of *Fraxinus excelsior* L., *Morus nigra*, *Gleditsia triacanthos* L., *Robinia pseudoacacia*, *Populus nigra*, *P. alba*, and others are planted along roads, fields, and vineyards. On the Taman Peninsula, small fragments of steppe areas preserved; large areas are occupied by salt marshes.

The submontane and mountainous parts of the Black Sea coast, except for the extreme northwest area are included in the forest zone. The natural vegetation of the Black Sea coast has been significantly transformed; flat areas of the submontane area of Ciscaucasia in the valleys of large rivers for a long time have been deprived of forest vegetation and mainly they are agricultural lands. However, most of the hillsides are covered with forests. The variety of forest formations is determined by the complexity of the relief, geological structure, vertical zonation, regional differences of climate, and other factors. For example, on the southern macroslope, in the northwestern part of the region, forests are represented by formations of sub-Mediterranean types. In the vegetation, hemixerophytic open forests and shibliak (*Juniperus excelsa* M. Bieb., *J. foetidissima* Willd., *J. oxycedrus* L., *Quercus pubescens* Willd., *Carpinus orientalis* Miller, *Pistacia mutica* Fischer et C.A. Meyer) are dominant; there are pine and oak-pine forests with *Pinus pallasiana* D. Don and *P. pityusa* Steven. Toward the southeast, they are gradually replaced by sessile oak forests (*Quercus petraea* L. ex Liebl.) and further by broad-leaved forests with *Castanea sativa* Miller, *Buxus colchica* Pojark., and *Taxus baccata* L. (Colchian type community). Colchian forests are most widely distributed in basins of the Psezuapse, Shahe, Sochi, Mzymta rivers. A forest strip with dominance and codominance of *Quercus robur* L., *Q. petraea*, and *Carpinus betulus* L. is located on the northern macroslope at 300–600 m a.s.l. Broad-leaved forests change to beech-fir forests (dominant and codominant species are *Abies nordmanniana* (Steven) Spach and *Fagus orientalis* Lipsky) with increasing elevation. Pure fir forests have limited distribution. *Picea orientalis* (L.) Link is found as an admixed species or forms small areas only in the basins of the Bolshaya and Malaya Laba rivers and in the upper reaches of the Mzymta River. At an elevation of 1800–2200 m a.s.l., there is a subalpine crooked forest strip (the dominant species are *Betula litwinowii* Doluch. and *Fagus orientalis*), and there are woodlands of *Acer trautvetteri* Medw. Information about the composition and structure of forest communities of the study area was presented in studies by Orlov (1951, 1953), Grudzinskaya (1953), Golgofskaya (1967a, 1967b), Grebenshchikov et al. (1990), Bebiya (2002), Frantsuzov (2006), and others.

More detailed studies of *Robinia pseudoacacia* populations were carried out by us in the riverine forests (banks, terraces and riverbed slopes) of Belaya River from the villages of Bzhedughabl to Guzeripl (70–700 m a.s.l.). The length of the profile is 102 km; the annual precipitation within it at the elevation of 70 m a.s.l. is 650 mm and at 700 m is 1150 mm; the average temperatures in July at these elevations are 22 and 18°C and the average temperatures in January are –1 and –2°C, respectively (Ivanchenko et al., 1982; Byzarov et al., 1995). According to the Shuntuk meteorological station (320 m a.s.l.), in the midstream of the Belaya River, the average annual precipitation (for the period of 1935–2009) was 830 mm, the average annual temperature was 10.5°C, the average temperature in January was –1.1°C, and the average temperature in July was 21.6°C.

In the range of elevations from 70 to 400 m a.s.l., the tree layer of riverine forests of the Belaya River is formed mainly by *Populus nigra*, *P. alba*, *Salix alba*, *Alnus incana* (L.) Moench, *Fraxinus excelsior*, and *Acer campestre* L.; then, up to an elevation of 600–660 m, the participation of *Salix alba* in stands was significantly reduced, and the participation of *Populus nigra* and *P. alba* gradually declined to zero, while the role of *Alnus glutinosa* (L.) Gaertner, *Fagus orientalis*, *Carpi-*

nus betulus, *Quercus petraea*, and *Ulmus glabra* Hudson increased. Above 660 m, riverine forests of the Belaya River are mainly represented by beech-fir communities (the dominant species were *Abies nordmanniana* and *Fagus orientalis*) with participation of *Carpinus betulus*, *Acer platanoides* L., *A. campestre*, *Alnus glutinosa*, and others in the tree layer.

Collection and Analysis of Factual Material

Information about the distribution of invasive populations of *Robinia pseudoacacia* was obtained over the course of the survey expedition to the region in 2007–2014. The whole area was covered by a network of roads and hiking trails; some areas were visited more than once. Natural and disturbed habitats of the Black Sea coast and plain, submontane, and mountainous areas of Krasnodar krai and the Republic of Adygea were investigated. The Taman Peninsula and valleys of Kuban River basin (Bolshaya and Malaya Laba, Belaya, Pshekha, Pshish, Psekups, Afips, Ubin, Ile, Hubley, Abin, Adagum, and others) and the Black Sea basin (Mzymta, Kudepsta, Hosta, Matsesta, Sochi, Shahe, Psezuapse, Ashe, Makopse, Shepsi, Tuapse, Agoi, Nebug, Psebe, Dzhubga, Vulan, Tecos, Pshada, Shebs, Aderba, Ozereyka, Sukko, and others), as well as habitats of the slopes of the mountain ranges and massifs, were studied. Considerable attention was paid to plant communities along the railways and roads and floodplain and riparian forests. Decorative plantations and self-dispersed plants in settlements were not considered.

The abundance dynamics and distribution limits of *Robinia pseudoacacia* in the Belaya River valley were estimated using the analysis of the age structure of its population at different elevations. This method is widely used to solve problems of the same type; however, native species were the object of the study (Aleksandrova, 1964; Leac amd Craber, 1974; Gorchakovskii and Shiyatov, 1985; Kullman, 1991; Hantemirov et al., 2008; Sudnik-Wójcikowska et al., 2009). It is assumed that, in the case of expansion of the altitudinal area of black locust, border populations of this species will be represented by individuals with a small age (undergrowth). If the upper border is stable, the border population should be represented by trees of different ages, including those of a significant age. If conditions of the upper border are unfavorable for the growth of species and there is a tendency of a reduction in the area, the border populations should consist mainly of individuals with a considerable age.

The trunk diameter was measured at the base. Determination of the age of the trees was done by annual growth rings on the lateral cut at the height of the root collar or by drill cores taken from the trunk at the height of about 15 cm from the soil (Korchagin, 1960). Saw cuts were taken predominantly from individuals with a trunk diameter not less than 4 cm; drill cores were taken from larger individuals. If the drill did not reach the center of the trunk, the age of the tree was determined approximately by a calculating method (Korchagin, 1960). The state of *Robinia pseudoacacia* populations was studied at twelve height levels. The trunk diameter and viability were determined for 339 trees; the age was determined for 304 trees (90%), including 124 trees determined by saw cuts and 180 trees determined by cores. For the rest of the trees, because of the poor condition of the wood or the lack of distinct annual rings, the age was determined on the basis of regression models of "diameter–age" plotted for each height level. Since the age of studied individuals could not always be determined with high precision, individuals were combined into age groups of 10 years for the analysis of population age structure.

For determination of the reasons for variation of abundance of *Robinia pseudoacacia* in different stands and the impact of this species on native tree species in floodplain forests of the Belaya River, we identified and described 131 forest plots with the area of 300 m^2, including 47 without the participation, 50 with the participation, and 34 with the dominance of this species. The following species were aboriginal dominants in these plots: *Populus nigra* (38 sites), *P. alba* (5), *Salix alba* (14), *Alnus incana* (26), *Fraxinus excelsior* (6), *Acer campestre* (5), and *Carpinus betulus* (3). For each plot, a brief description of forest communities and registration of all individual woody species with a trunk diameter of more than 6 cm at chest level were performed. A comparison of the various communities with the participation of black locust among the stands was made using the following parameters: N—the total number of trunks (species) of trees on the 300 m^2 sites (total density of the stand); N_c—the number individuals of associated species; N_m—the average density of individuals of associated species in plots; N_R—the number of black locust individuals; D—the ratio between the number of trunks of the dominant species to the total number of trunks (the dominance level, Berger-Parker index (Lebedeva and Krivolutsky, 2002)); S—the number of associated species within plots.

RESULTS AND DISCUSSION

Distribution of Robinia pseudoacacia in the Study Area

Most likely, black locust appeared in Ciscaucasia in the middle of the 19th century as the result of activities such as the creation of windbreaks and decorative plantations (Gurskii, 1957). Black locust was used especially actively in the middle of the 20th century, including the reconstruction of damaged forests (Kharitonovich, 1949; Nevzorov, 1951; Bitsin, 1961), but until the 1960s, it did not spread by itself over the territory and did not penetrate into natural and seminatural forests (Grossgeim, 1949; Kosenko, 1970). In the forests of Western Transcaucasia, wild *Robinia pseudoacacia* was found in the middle of the 20th century (Grossgeim, 1952; Kholyavko and Globa-Mikhailenko, 1976), although according to Grossgeim (1952), its blossoming in invasive populations was not noted. In recent decades, information about the species going wild and its spontaneous distribution in the Western Caucasus, including on the northern macroslope, started to appear in the literature (Zernov, 2000; Timuhin and Akatova, 2002; Bondarenko, 2003; Timuhin, 2006; Shadzhe and Akatova, 2007; Akatov et al., 2009; etc.).

According to our data, *Robinia pseudoacacia* is the most common wild introduced tree species of the region; we detected it in the majority of the studied areas in the elevation range of 11–1708 m a.s.l. However, the occurrence of this species in natural and natural-anthropogenic communities in different parts of the study area varies.

In the extreme northwestern part of the study area (Taman floristic area), invasive black locust populations were rare and were found only at a few points. In particular, seedlings and small undergrowth were detected on the coastal sand dunes on the Vityazevskaya sand spit; on the bank of Kuban River in the vicinity of the Varenikovskaya station, Robinia was part of the first layer of the floodplain forests dominated by *Salix alba* with the presence of *Populus alba*. On the Taman Peninsula, *Robinia pseudoacacia* occurs mainly in artificial plantations, both pure and together with black poplar and honey locust. In tree belt areas, there are black locust undergrowth and clumps of coppice shoots; however this species did not spread beyond these areas. It should be noted that the tree belt areas are badly affected by droughts and fires; many of the trees are dry; in some places, the undergrowth is completely burnt. Very rarely were small trees and black locust undergrowth found in open spaces and wastelands (sometimes together with *Elaeagnus angustifolia* L.) (vicinities of Taman and Temryuk), and they were detected on the bank of the river near the village of Sennaya.

Robinia pseudoacacia is widely distributed in the Novorossiysk and Sochi floristic regions. In the vicinities of Anapa and Novorossiysk, it still occurs sporadically, but it becomes a mass species to the south of the Aderbievka River. Almost everywhere, it was detected by us along the Novorossiysk–Tuapse and Dzhubga–Goryachy Klyuch highways and along the railway between the Tuapse and Goyth stations. It grows in open areas, on bare slopes (sometimes very abundantly), and on the edges in roadside forests, where it often prevails. For example, according to our calculations, in the outer line of roadside forests in the Agoysky pass–Tuapse area, including ten trees species (88 trunks), black locust accounts for 69%. Under the canopy of a deciduous forest on the slopes, this plant is quite rare (mainly undergrowth), but in some places it can penetrate up to 10 m and deeper from the forest edge. Several times, this species was detected as a part of the disturbed xerophytic oak forests (middle reaches of the Vulan River, the ridge between Nebug and Tyumensky, Cape Kadosh, and others). In particular, the density of *Robinia pseudoacacia* in a bright forest dominated by *Quercus pertaea* with the presence of *Juniperus oxycedrus* to the north of the village of Nebug was 9 large (more than 6 cm in diameter) individuals (26% of the total number of all tree trunks), 17 individuals of the large regrowth higher than 2 m (65%), and 22 individuals from 0.5 to 2 m (13%) on a 300 m^2 plot. More often, the species penetrates into floodplain and riverine forests with *Salix alba*, *Populus alba*, and *P. nigra*, where it is highly abundant and dominates in some areas. In floodplain forests, we observed both large trees up to 10–30 cm in diameter and undergrowth of different ages. Along the pebbly banks of some rivers (for example, Shebs, Pshada, Vulan, and Nebug), the presence of young growth was also detected.

The contribution of black locust to the roadside forest communities to the south of Tuapse is high close to the village of Chemitokvadzhe (between the Psezuapse and Shahe rivers); after that, its activity is somewhat reduced, but sporadically it continues to occur further along. In disturbed riverine forests and gravel banks, the species is present along almost all rivers of the Black Sea region around Sochi. In the largest of them, Shahe and Mzymta, fruit-bearing black locust trees up to 20 cm in diameter and abundant undergrowth were observed in the composition of floodplain forests dominated by alder (*Alnus barbata* C.A. Meyer) from the lower course of a river up to 200–260 m a.s.l.

In the western part of Ciscaucasia (Abinsky floristic area), invasive black locust populations are relatively rare. On edges of floodplain forests, this species was observed in the valleys of the Hable and Akhtyr rivers in the vicinity of Krymsk and the village of Sauk-Dere. Large black locust trees were detected in the composition of the riverine forest along both banks of the Kuban River near the village of Gvardeiskoe. The greatest elevation at which black locust was detected in river valleys was 165 m (Hable River above the village of Noviy). However, on the hillside of the Sober-Bash (Ubin River basin), undergrowth and young blooming trees were sporadically observed at the edge of a broad-leaved forest along a dirt road up to the elevation of 300–400 m (approximately 6 km from the settlement) and the latest finding was at the elevation of 707 m.

In the Hadyzhensk floristic region, black locust was observed in floodplain forests along the Psekups, Pshish, and Afips rivers. Both a single patch of undergrowth and groups of mature trees up to ten individuals were found; black locust undergrowth was overgrown on the sandbanks of the Afips River. This species did not grow far from the settlements; the maximum elevation of detection was 115 m a.s.l. Notably, in this region, black locust is hardly involved in the

Fig. 2. *Robinia pseudoacacia* at mountain roadside at the elevation of 1500 m a.s.l.

overgrowth of open areas and roadsides, where *Acer negundo* prevails.

Robinia pseudoacacia grows most massively on the northern macroslope in the Maykop floristic area in valleys of the Belaya and Laba rivers. In Belaya River basin, it was found up to the elevation of 1708 m a.s.l., up to the elevation of 600 m mainly in the riverine forests, higher along the newly reconstructed road from the village of Guzeripl to Yavorovaya polyana tract (Fig. 2). This species takes a significant part in the stands and often dominates up to an elevation of 200 m; above this elevation, it was found in relatively small, isolated groups of plants of seed and vegetative origin. *Robinia pseudoacacia* populations within the elevations from 300 to 600 m a.s.l. were confined mainly to the disturbed forest areas.

In the valley of Pshekha River (the largest tributary of Belaya River), *Robinia pseudoacacia* was rarely detected: its undergrowth was found on the edges of the forest behind the village of Novye Polyany (292 m a.s.l.) and before the Chernigovskaya station (320 m).

In the Laba River basin, the penetration of black locust into the riverine forest communities was detected along the entire length from the vicinity of Kurganinsk (170 m a.s.l.) to the vicinity of the Akhmetovskaya station (606 m) on the Bolshaya Laba and vicinity of the village of Psebay (640 m) on the Malaya Laba. Invasive populations of *R. pseudoacacia* were not found higher than this elevation. In the Laba River valley, black locust was often overgrown on areas along roads and railways, fallow lands, wastelands, and treeless hillsides. Very often, the undergrowth of this species was found on the slopes and roadsides along the Maikop–Labinsk route.

In general, within the studied parts of the Western Caucasus territory, *Robinia pseudoacacia* is more common in the vicinity of settlements, but along roads and along river valleys, it can be 2–4 km and less commonly up to 10 km from settlements. On the southern macroslope, this species is concentrated on the coastal and lowland areas (up to 140 m a.s.l. to the west of Dzhubga, up to 260 m south and 300 m north of Tuapse). In some cases, groups of old trees and abundant black locust undergrowth were observed in places of former settlements or apiaries, often surrounded by forest (Oblego Mountain, 450 m a.s.l.; source of the Kudepsta River, 480 m; Chvizhepse cordon in the Mzymta River basin, 411 m). On the northern macro-

Table 1. Age structure of *Robinia pseudoacacia* population at height profile

Absolute height	Number of individuals	Age classes				Maximum age
		1–10	11–20	21–30	>30	
2011						
73, 161	64	37.5*	43.8	10.9	6.3	52
190–240	104	55.8	35.6	6.7	1.9	32
307, 352	47	78.7	21.3	–	–	20
405, 465	55	38.2	45.5	7.3	9.1	43
492, 561	26	76.9	19.2	–	3.9	74
1250–1500	9	100				5
2013						
1350–1550	47	100				8
1550–1708	55	100				4

* The proportion of individuals in the age class (%).

slope, the highest elevations of *R. pseudoacacia* was detected in basins of the Belaya (1708 m) and Labe (640 m) rivers, as well as on the Sober-Bash Mountain in the Seversky district of Krasnodar krai (707 m).

On the basis of the analysis of the natural distribution of black locust in the study area, we can conclude that it prefers open habitats and riverine forest and moderately warm and moderately humid growth conditions, which confirms existing theories. Accordingly, this species occurs relatively rarely in insignificantly disturbed forests in the mid-mountain and high-mountain belts, as well as in areas with significant or, on the contrary, low amounts of precipitation. However, even in areas favorable for the growth of black locust, its distribution is also uneven, which seems to be associated with the history of expansion of this species.

Changes in Abundance and Distribution Limits of Robinia pseudoacacia in the Belaya River Basin

In order to assess the nature of changes in abundance and distribution limits of *Robinia pseudoacacia* in the Belaya River valley, the age structure of the population at different elevations was studied. Data on the age structure of populations of this species within an elevation profile area between 70 and 600 m obtained in 2011 and from 1300 to 1708 m obtained in 2011 and 2013 are shown in Table 1.

The data presented in Table 1 show that, in the elevation interval from 70 to 600 m a.s.l., the populations include one or more individuals with an age significantly higher than the age of other individuals—20–70 years (probably, some of them were planted near a river or roads). In the same elevation interval, most individuals fall into two age classes—from 1 to 10 and from 11 to 20 years (the fraction of such individuals was 85% for all studied populations), where the juveniles are often located relatively close (at a distance of 10–20 m) to trees of a considerable age. In the area of elevation profile from 1300 to 1500 m in 2011, only black locust undergrowth 2–4 years old was detected; in 2013, its abundance dramatically increased; one of the trees (at the elevation of 1396 m) reached the reproductive stage of development—flowering and fruiting; and 1- to 2-year-old undergrowth was found at an elevation of 1708 m.

Figure 3 shows that, near the upper border of the black locust distribution in the riverine forests, i.e., in the range from 70 to 600 m a.s.l., the amplitude of variation of trunk diameters remains virtually unchanged (Pearson correlation coefficient (r) between the elevation above sea level and the maximum diameter of the trunk is 0.107, $n = 339$, $P < 0.05$).

These results allow us to estimate the dynamic trend of *Robinia pseudoacacia* in the Belaya River valley.

(1) The presence of individuals of this species with a significant age (50–70 years) within 70 to 600 m a.s.l. suggests a fairly long presence of this species in the Belaya River valley. We can assume that this was the result of deliberate (planting) and unintentional (accidental introduction) human actions.

(2) A comparison of the elevation of the upper limit of black locust distribution in the Belaya River valley (1708 m) and within its natural range (1000–1500 m) probably indicates that in the last few years the plant has achieved its climatic limit. Accordingly, the upper limit of distribution of this species in the riverine forests of the Belaya River, as well as in other riverine forests (600–700 m on the northern macroslope and 300–400 m on the southern macroslope), is mainly determined by climatic rather than phytocenotic factors. *Alnus glutinosa*, *Abies nordmanniana*, and *Fagus orientalis* dominate above these limits in such forests, preventing the distribution of not only black locust but also such native species as white willow and black and

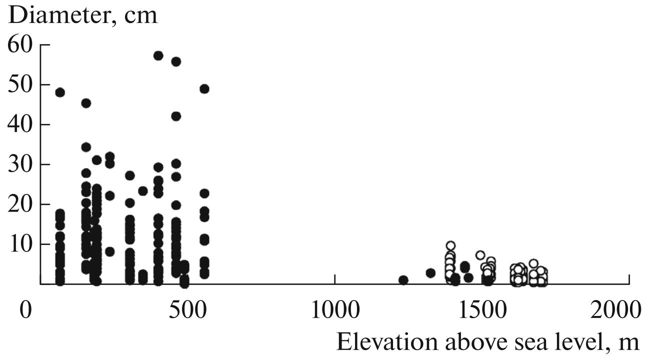

Fig. 3. Change in *Robinia pseudoacacia* trunk diameter at the elevation gradient. Black circles—data from 2011, white circles—data from 2013.

white poplar. For the riverine forests of the Belaya River, this conclusion is confirmed by the results of the analysis of height changes in the age structure of the black locust population and maximum diameter of its trunk. In this regard, it should be noted that the natural range of this species in North America, according to Gurskii (1957) is determined by biotic and not climatic factors.

(3) Despite the ability of black locust to bear fruit at the age of three to four years, its propagation (both by seeds and vegetative) and increased abundance in the majority of areas started only in the 1990s. It should be noted that this coincides with the beginning of the increase in mean annual air temperature in the study area and a number of other areas of the Western Caucasus (Panov, 2000; Ekba et al., 2007; Zhivotov, 2008), and therefore the association between these phenomena cannot be ruled out.

Interestingly, the activation of the distribution of alien species of trees in the past 20 years was detected in the neighboring region. Thus, according to Sudnik-Wójcikowska et al. (2009), in artificial plantations of *Elaeagnus angustifolia* and *Robinia pseudoacacia* created in the dry steppes of the Northern Black Sea region (Ukraine), the maximum age of the plants was 47 years, while the age of the oldest plants growing in abandoned fields and pastures, saline soils, and dry steppes did not exceed 17–22 years. The authors suggested several possible reasons for this phenomenon: (1) the crisis of agricultural production accompanied by the increased area of wastelands, fallow lands, pools, and abandoned pastures; (2) climatic changes; (3) exit from the lag phase (Sudnik-Wójcikowska et al., 2009). None of these reasons can be completely rejected in our case, e.g., for the explanation of the modern increase in abundance of *Robinia pseudoacacia* in the Western Caucasus.

Reasons for Variation of the Abundance of Robinia pseudoacacia in Riverine Forest Areas

Of the 97 riverine forest areas dominated by native tree species (*Populus nigra*, *Salix alba*, and others) that were described by us in Belaya River basin, 50 areas comprised from 1 to 20 (on average 4.2) black locust trunks with a diameter of 6 cm at chest level. Thus, its contribution to the stand was from 2 to 40% (on average 16%).

Several explanations why some plant communities are more saturated with invasive species than others were suggested recently. Among the most famous, there are hypotheses about species richness (Elton, 1958), fluctuating resources (Davis et al., 2000, 2005), and disparate species assemblage (Rabotnov, 1983; Sax and Brown, 2000; Moore et al., 2001; Davis et al., 2005; Akatov et al., 2009; etc.). In a number of publications, the species pool of communities (Moore et al., 2001; Smith and Knapp, 2001; Herben, 2005; Akatov et al., 2009) and the structure of domination, as an option—the relative abundance of dominant species (Smith et al., 2004; Mattingly et al., 2007)—were considered as invasive factor of cenoses.

It should be noted that, in most cases, the number or proportion of alien species in their composition in the communities was considered as an indicator of the degree of adventization. However, the same factors may cause variation of abundance of the number of alien species in cenoses. In this case, all of the above hypotheses complement each other well. Thus, the reduction in the density of the dominant species leads to the release of certain resources. In the case of a significant species pool, this will cause an increase in the number of species in areas of cenoses at a relatively constant average abundance. If the size of the species pool is relatively small, the released resources will be used by the already present native and alien species and the abundance of these species will increase (density compensation effect (Crowell, 1962; MacArthur et al., 1972)).

For testing these hypotheses, we selected areas of riverine forest stands with the presence of *Robinia pseudoacacia* and compared values of the following parameters: the abundance of this species, the overall density of the stand, the number of trunks of associated species, dominance level in the areas, the number of species, and their average number (Figs. 4 and 5, Table 2).

The results of analysis show the following:

(1) Stands with a low dominance level are characterized by a lower overall density of trunks but a higher total density of associated species in comparison with cenoses with relatively high dominance levels (Fig. 4a, Table 2).

(2) Reduction of the dominance level and, accordingly, increase in the density of associated species lead to an increase in species richness in cenoses (Fig. 4b, Table 2).

(3) A statistically significant correlation between the level of dominance and the average density of associated species in plots is absent (Table 2). In this case, as shown in Fig. 4b, maximum values of this parameter were observed in plots with an average level of dominance (from 0.4 to 0.7). The same figure shows that this ratio is similar to the ratio between the dominance level and abundance in *Robinia pseudoacacia* plots. Moreover, of these 13 plots, including a relatively high number of black locust (more than 5), *Populus nigra* dominated in 9 plots.

Thus, we see that *Robinia pseudoacacia is* a typical aboriginal species of riverine forests. Its relatively high density is observed in stands with a medium dominance level (0.45–0.75) and a relatively high density of other associated tree species (Fig. 5, Table 2). At the same time, it should be noted that, in riverine forests, the decreased density of the dominant species might be due to the disturbance of stands during high water periods and due to other reasons. In particular, this is due to the dying off of old plants, combined with the lack of renewal processes caused by the reduction of the areas which are generative niches (for example, moist alluvium deposits for poplars and willows) (Mirkin and Naumova, 2012).

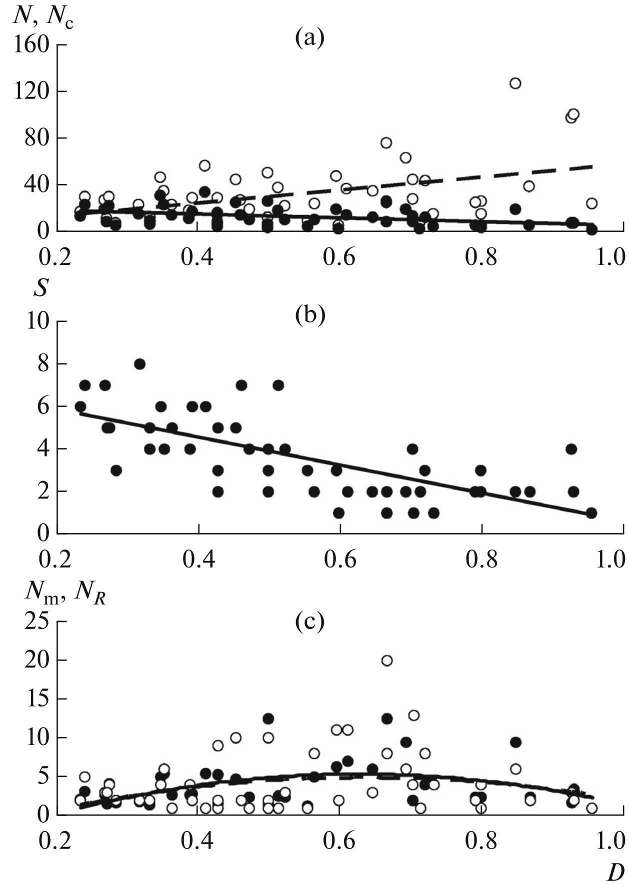

Fig. 4. The ratio between the dominance level (D), the total number of individuals of tree species (N), the number of individuals of associated species (N_c), the average density of individuals of associated species (N_m), the number of black locust individuals (N_R), and the number of associated species (S) in riverine forest areas of 300 m^2. (a) White circles, dashed regression line—N; black circles, solid line—N_c; (b) solid circles, solid line—S, (c) white circles, dashed line—N_R; black circles, solid line—N_m.

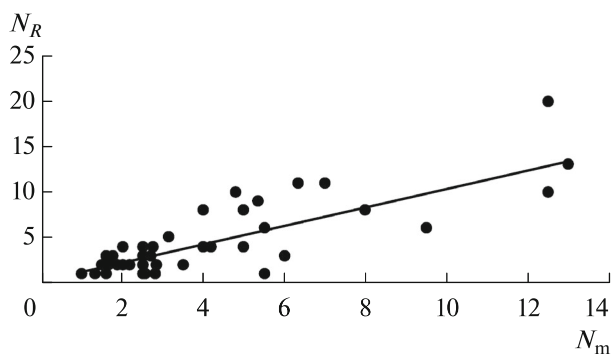

Fig. 5. The relation between the average density of individuals of associated tree species (N_m) and the number of black locust individuals (N_R) in riverine forest areas of 300 m^2.

The Effect of Robinia pseudoacacia on Species Richness of Riverine Forest Stands

There is a lot of evidence of a significant effect of alien species, pathogenic fungi, and microorganisms on the species richness and composition of natural communities (Nikolaev, 1979; Neronov and Lushchekina, 2001). However, the consequences of invasions of alien plants in natural communities are the least certain. In particular, there is an opinion that the active consolidation of alien plant species is observed mainly in unsaturated (not completed) or cenoses disturbed by man (Rabotnov, 1983; Davis et al., 2000; Akatov et al., 2009). Therefore, the majority of invasions occur without exclusion of native species (Ricklefs and Schluter, 1993; Sax and Gaines, 2003; Rejmánek et al., 2005). On the other hand, specific examples of exclusion of ecologically related species by alien plants were demonstrated (Vinogradova, 2003, 2008; Vasilyeva and Papchenkov, 2011).

Since a high abundance of *Robinia pseudoacacia* is observed in forest areas with predominantly low species richness and the number of plants of this species in stands is around the average number of plants of associated native tree species, we cannot expect a significant impact from its intrusion on the species richness of communities. However, the effects may be different in the case where this species becomes dominant. Most likely, this happens after a serious impairment of the stands or as the result of the rapid expansion of black locust in deforested areas. In this case, it is possible that *R. pseudoacacia* can be a stronger competitor in comparison with native species, which are usually dominant in such areas, and reach a higher abundance. It is known that the higher the abundance and the dominance level of the dominant

Table 2. The ratio between parameters characterizing communities of riverine forests of the Belaya River and participation of *Robinia pseudoacacia* in these communities

Parameters		n	R^2	r	P
independent	dependent				
D	N	50	0.192	0.438	<0.01
D	N_c	50	0.146	–0.382	<0.01
N_c	S	50	0.229	0.479	<0.001
D	S	50	0.478	–0.691	<0.001
D	N_m	50	0.027	0.164	
D	N_R	50	0.020	0.141	
N_m	N_R	50	0.649	0.806	<0.001

N—the total number of trunks (species) of trees on 300 m^2 plots (total density of the stand); N_c—the total number of individuals of associated species, N_m—the average density of individuals of associated species; N_R—the number of black locust individuals; D—the ratio between the numbers of trunks of the dominant species to the total number of trunks (the dominance level); S—the number of associated tree species within plots.

species, the lower the amount of resources remains for associated species; therefore, their possible abundance and species richness of communities will be lower. We also cannot exclude that the environment-forming activity of black locust (by changing the water regime and chemical properties of the soil) in communities can inhibit the growth of certain native plant species common to such types of habitats. As a result, communities with the prevalence of this species may include a lower number of species than the original communities, even at a dominance level similar to the dominance level of native species.

In order to evaluate the effect of *Robinia pseudoacacia* on native tree species, we compared the dominance level, species richness, and abundance pattern of species in the stands with the absence and the predominance of black locust. The results of analysis are presented in Figs. 6 and 7 and Table 3. The total density of the stand, the relative abundance of dominants, and the species richness of stands with a predominance of black locust and three native dominants the most common in the riverine forests of the study area are shown in Table 3. These results show that, in stands with a predominance of *Robinia pseudoacacia*, the dominance level and species richness were approximately the same as in stands with a predominance of native species. The data in Fig. 6 show that, at a certain dominance level, the species richness in the stands with the absence and the predominance of *Robinia pseudoacacia* were also about the same.

A comparison of the structure of the abundance of species in areas with the absence and the predominance of black locust was conducted by plotting "rank/logarithm of species abundance" graphs averaged for the groups of plots (rank on the x axis; logarithm of the average number of individuals of the species of ranks 1, 2, 3, ..., n for the group on the y axis) (Lebedeva and Krivolutsky, 2002). As can be seen from Fig. 7, the structure of the rank distribution of the number of species within these groups of commu-

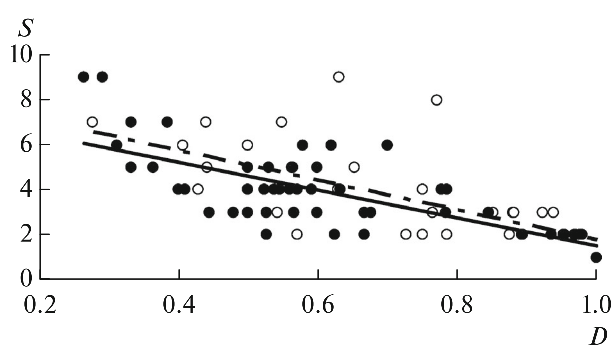

Fig. 6. The ratio between the dominance level (D) and species richness (S) in areas of stands in riverine forests. White circles, dashed regression line—with the dominance of *Robinia pseudoacacia*; black circles, solid line—with the dominance of native tree species.

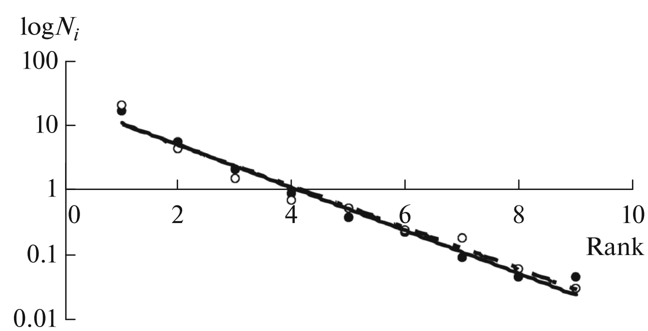

Fig. 7. Curves of species importance (rank/logarithm of species abundance) for areas of stands in riverine forests dominated by *Robinia pseudoacacia* and native tree species. White circles, dashed regression line—with the dominance of *Robinia pseudoacacia*; black circles, solid line—with the dominance of native tree species.

Table 3. Characteristics of Western Caucasus riverine forest stands with the dominance of *Robinia pseudoacacia* and native species

Dominant	*Robinia pseudoacacia*	*Populus nigra*	*Alnus incana*	*Salix alba*
Number of plots (n)	34	36	26	15
Stand density (N)	34.0 (13.5–68.3)	26.5 (4–75)	21.6 (6–80)	56.9 (6–126)
Dominance level (D)	0.71 (0.28–1)	0.61 (0.25–1)	0.59 (0.4–0.85)	0.68 (0.35–1)
The number of species per 300 m^2 (S)	3.7 (1–9)	3.6 (1–8)	3.8 (2–6)	3.9 (1–6)
Total number of species	22	19	15	10
Dominant species				
Robinia pseudoacacia	**V (19.4)**	IV (4.8)	I (0.3)	III (4.7)
Populus nigra	III (3.2)	**V (17.5)**	III (2.5)	III (6.2)
Alnus incana	I (3.2)	I (2.6)	**V (29.2)**	III (6.8)
Salix alba	I (3.1)	III (3.0)	V (11.8)	**V (45.0)**
Some associated species				
Populus alba	I (3.0)	II (2.3)	I (0.4)	I (2.5)
Salix triandra	I (1.0)	I (7.5)	III (3.8)	III (1.5)
Acer campestre	I (1.7)	I (1.3)	I (0.1)	I (1.0)
Fraxinus exelsior	I (2.0)	I (2.1)	I (0.2)	

nities was similar. This fact indicates that the replacement of native dominants by black locust did not lead to significant changes in the structure of species riches and abundance in stands of riverine forests of the Belaya River. However, we cannot rule out the impact of this process on the shrub and herbaceous layer of forest communities. A special analysis of this issue is required.

CONCLUSIONS

(1) *Robinia pseudoacacia* is the most commonly introduced running wild tree species within the studied area of the Western Caucasus, but its occurrence in natural and natural-anthropogenic communities in different parts of the region varies. For example, on the Taman Peninsula and in the western part of the Ciscaucasia (Abinsky floristic area), invasive black locust populations are rare. The plant is most widespread in the Novorossiysk, Sochi, and Maikop floristic regions. In the Maikop floristic region, it grows on a massive scale in the valleys of the White and Laba rivers. There, *Robinia pseudoacacia* was found up to an elevation of 1708 m a.s.l., including up to an elevation of 600 m mainly in riverine forests; at an elevation less than 200 m, this species takes a significant part in the stands and often dominates. In general, black locust prefers open areas and moderately warm and wet growth conditions, and, accordingly, it is relatively rare in insignificantly disturbed forests in mid-mountain and high-mountain belts and in areas with a high or, on the contrary, a low amount of precipitation.

(2) Despite the continued presence of black locust in the Western Caucasus, until the 1960s, it did not expand over the territory and did not penetrate into natural and seminatural forests. The significant growth of the majority of *Robinia pseudoacacia* populations started in the 1990s, and this species only reached the upper climatic limit of expansion (1500–1700 m) in the last few years, and only in open habitats (roadsides). The upper limit of black locust in the riverine forests of the region did not exceed 300–700 m. This limit was determined by phytocenotic rather than climatic factors. It coincided with the upper limit of the distribution of native tree species characteristic of riverine forests (white willow, black and white poplar).

(3) As a part of riverine forests, *Robinia pseudoacacia* behaves like a typical native species: its relatively high density is more often observed in stands with a relatively high density of other associated tree species. These communities often have an average dominance level (0.45–0.75). For riverine forests, a relatively low density of the dominant species may be associated both with the periodic impairment of stands and with other reasons, in particular, with the dying off of the old dominant species combined with the lack of renewal processes.

(4) The replacement of the native dominants by black locust in a number of riverine forest areas did not lead to significant changes in species richness and

population structure. However, we cannot exclude the effect of this process on the shrub and herbaceous layers of forest communities.

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