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Relative Competitiveness of Adventive Plant Species in Herbaceous Communities of the Western Caucasus

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Abstract—The relative competitiveness of adventive plants in herbaceous communities of the Western Caucasus is analyzed using a simple mathematical model, $S_a = N_a(S/N)$, where N and S are the numbers of vascular plant species on 15-m^2 and 0.5-m^2 plots, respectively, and N_a and S_a are the numbers of adventive plant species on 15-m^2 and 0.5-m^2 plots, respectively. The model is based on two assumptions: (1) stochastic character of the processes of species immigration and extinction occurring on the area of plant communities, and (2) ecological equivalence of indigenous and adventive species. If adventive species of a herbaceous community are characterized by a higher or lower competitiveness as compared with indigenous species, then one should expect the actual number of these species on 0.5-m^2 plots to be higher or lower as compared with the number calculated using this model. The communities of low-mountain and mid-mountain near-riverbed shoals, forest glades, steppe meadows, annual crop fields, fallow lands, and the herbaceous layer of low-mountain forest communities are chosen as the objects of this study. The results show different competitiveness of adventive plants in different herbaceous communities of the Western Caucasus.

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INTRODUCTION

In recent years, many hypotheses were offered to explain why some plant communities are less resistant to the invasions of foreign species than others. The best known hypotheses are the hypotheses of species richness (Elton, 1958), fluctuating resources (Davis et al., 2000, 2005), and species incompleteness of phytocenoses (Rabotnov, 1983; Sax and Brown, 2000; Davis et al., 2005; Akatov et al., 2009; etc.). Testing these and other hypotheses, scientists usually assume that indigenous and adventive plant species have equal abilities to disseminate and survive in the studied cenoses. Of course, this assumption is simplified, but the level of such simplification is rather unclear. On one hand, many studies take note of the fact that the active dissemination of adventive species is provided by their competitive advantages over indigenous species (Vinogradova, 2003, 2008; Ovcharenko and Zolotukhin, 2003; Vasilyeva and Papchenkov, 2011; etc.). These advantages can include a higher seed productivity, higher rates of germination and growth, better ecological plasticity and resource consumption efficiency, and the absence of dangerous phytophages and parasites in a new environment (Mirkin and Naumova, 2002; Vinogradova, 2003, 2008). On the other hand, owing to a greater possibility of a transcontinental seed transfer, the leading positions in the adventization of many regions are occupied by eutherophytes, the majority of which represent species typical of the initial stages of restorative successions on their homeland. In the case of acceptor regions, such species usually grow in often disturbed cenoses (Réjmánek et al., 2005). Therefore, the lower degree of adventization of other (closed) communities can be caused by a higher competitiveness of dominating indigenous perennial plants as compared with foreign eutherophytes, rather than by a general resistance of these communities to invasions. Finally, according to the concept of neutralism in the organization of plant communities, the expansion and long-term presence of any species (including adventive ones) in plant communities do not necessarily indicate their competitive success as compared with other species; these effects can be determined by the ecological similarity (Gilyarov, 2010).

Thus, the question of the relative competitiveness of adventive plant species in various types of plant communities most likely does not have a simple answer. In this study, we tried to perform a quantitative analysis of this problem by the example of herbaceous phytocenoses of the Western Caucasus.

MATERIALS AND METHODS

Objects of Study

The objects of our study were herbaceous communities and the herbaceous layer of forest phytocenoses of the Western Caucasus. The material was collected in 2005–2009 in the basins of the following rivers: Malaya Laba, Belaya, Kisha, Pshish, Psekups (northern macroslope), Shepsi, Psezuapse, Western Dagomys, Sochi, Khosta, Matsesta, and Mzymta (southern macroslope). We described open plant communities (groups) of low-mountain and mid-mountain near-riverbed shoals of the southern and northern macroslopes; communities of mid-mountain glades and low-mountain steppe meadows, used for haymaking or pasture; communities of annual crops fields (wheat, maize, sunflower, and soybean) and fallow lands; and the herbaceous layer of piedmont and low-mountain floodplain forests, located along the riverbeds of the northern and southern macroslopes.

Phytogroups of low-mountain near-riverbed shoals were described along the Shepsi, Belaya, Psezuapse, and Western Dagomys rivers at a height of 70–200 m above sea level. For all areas of these habitats, the total projective cover did not exceed 25%. Among the constant species, we observed *Polygonum persicaria* L., *Setaria pumila* (Poiret) Schult. [= *S. glauca* P. Beauv.], *S. viridis* (L.) P. Beauv., *Medicago lupulina* L., *Ambrosia artemisiifolia*, etc. The number of species on 15-m^2 plots varied from 7 to 33. Phytogroups of mid-mountain near-riverbed shoals, located at a height of 450–900 m above sea level, were described along the Belaya and Malaya Laba rivers; their total projective cover did not exceed 25%. The following species were constant and most abundant for this habitat type: *Calamagrostis pseudophragmites* (Hall. Fil.) Koel., *Leontodon hispidus* L., *Pyrethrum parthenifolium* Willd., *Epilobium montanum* L., *Prunella vulgaris* L., and the undergrowth of *Salix alba* L. and *S. purpurea* L. (0.1–0.5 m). The number of species on 15-m^2 plots varied from 14 to 31.

The descriptions of steppe meadow communities were made in the basin of the Belaya River at an elevation of about 200 m above sea level. These communities were characterized by the domination of two indigenous species, *Botriochloa ischaemum* (L.) Keng and *Festuca valesiaca* Gaudin, and a high constancy of both indigenous (*Agrimonia eupatoria* L., *Achillea millefolium* L., *Plantago lanceolata* L., *Trifolium arvense* L., *Convolvulus arvensis* L., *Centaurea micrantha* S.G. Gmelin, *Chondrilla juncea* L., etc.) and some adventive (*Erigeron annuus*) species. The projective cover of these communities varied from 50 to 100%. Glade communities located in broad-leaved and mixed forests at an elevation of 600–680 m above sea level did not contain any marked dominants. A relatively high constancy was observed for *Agrostis stolonifera* L., *Prunella vulgaris* L., *Potentilla erecta* L., *Salvia verticillata* L., *Phleum pratense* L., *Dactylis glomerata* L., and *Erigeron annuus*. The total projective cover reached 98–100%. The species richness of steppe meadow and forest glade communities was 19–46 species on a 15-m^2 plot.

The segetal communities of annual crop fields (wheat, maize, sunflower, and soybean) were described in the basin of the Belaya River (200 m above sea level). The average species richness of these groups was 20.2 species on a 15-m^2 plot, which was close to that for near-riverbed shoals; on the contrary, the number of species on 0.5-m^2 plots located on fields (7.9) was higher than that on the shoals (4.4–4.9). Constant indigenous species were represented by *Convolvulus arvensis*, *Cynodon dactylon* (L.) Pers., *Elytrigia repens* (L.) Nevski, *Chenopodium polyspermum* L., and *Polygonum minus* Hudson. The communities of fallow lands were also described in the basin of the Belaya River; the plots were located at the same elevation above sea level as the plots for segetal communities. The species richness of these communities was similar to those of the forest glade and steppe meadow communities and exceeded those of the shoal and segetal communities. There were almost no obvious dominants among the indigenous species; the constant species included *Agrimonia eupatoria* L., *Cichorium intybus* L., *Cirsium arvense* (L.) Scop., *Daucus carota* L., and *Elytrigia repens*.

The herbaceous layer of floodplain forests of the northern macroslope was described in the basins of the Belaya, Pshish, and Psekups rivers at an elevation of 100–300 m above sea level. The studied phytocenoses included willow–poplar communities with the domination of *Salix alba* L., *Populus nigra* L., and *P. alba* L.; alder communities with the domination of *Alnus glutinosa* (L.) Gaertner and/or *Alnus incana* (L.) Moench and participation of some adventive tree species (*Morus alba*, *Acer negundo*, and *Robinia pseudoacacia*); oak–ash communities with the domination of *Quercus robur* L. and *Fraxinus excelsior* L.; and maple–ash communities with the domination of *Acer campestre* L. and *Fraxinus excelsior*. The tree layer density and the projective cover of the herbaceous layer varied from 0.2 to 0.8 and from 5 to 90%, respectively. There were no obvious dominants on the sample plots; a high abundance was observed for *Rubus caesius* L. High frequencies were observed for *Brachypodium sylvaticum* (Hudson) P. Beauv., *Viola hirta* L., *Geum urbanum* L., *Clematis vitalba* L., and also for several adventive species, such as *Amorpha fruticosa*, *Erigeron annuus*, *Solidago canadensis*, *Bidens frondosa*, and *Parthenocissus quinquefolia*. The total number of species on sample plots varied from 5 to 45.

The herbaceous layer of floodplain forests of the southern macroslope was described along the Mzymta, Khosta, Matsesta, and Sochi rivers at an elevation of 50–300 m above sea level. We observed the domination of *Carpinus betulus* L., *Fraxinus exvcelsior*, and *Acer campestre* and a significant participation of *Buxus colchica* Pojark.; the domination of *Alnus glutinosa*, *Populus alba*, *Pterocarya pterocarpa* (Michaux) Kunth ex Dippels, and *Ailanthus altissima* was also observed. The tree layer density and the projective cover of the herbaceous layer near the sample plots varied from 0.4 to 0.8 and from 5 to 95%, respectively. There were no obvious dominants. The constant species were represented by *Oplismenus undulatifolius* (Ard.) P. Beauv., *Aegopodium podagraria* L., *Galeobdolon luteum* Hudson, *Circaea lutetiana* L., *Glechoma hederacea* L., and *Hedera colchica* C. Koch. The total number of vascular plant species on sample plots varied from 19 to 48; the number of adventive species varied from 1 to 7.

Methods Used to Collect the Actual Material

The descriptions were performed using 15-m^2 plots, each containing 20 small plots (0.5 m^2) formed by a regular method. For both large and small plots, we registered the observed plant species (herbaceous plants and the undergrowth, whose height did not exceed 25 cm) and visually evaluated the total projective cover (in fractions, approximated to 0.05, 0.10, 0.15, 0.20, etc.) and the projective cover of particular species using a scoring scale (1 point means the species is represented by 1–3 individuals; 2, 3, 4, 5, 6, and 7 points mean that the cover is 1–5, 6–15, 16–25, 26–50, 51–75, and 76–100%, respectively). The descriptions were made only for the plots on which adventive plant species were observed. The total number of descriptions was 187, including 38 for low-mountain near-riverbed shoals, 26 for mid-mountain near-riverbed shoals, 16 for glades and steppe meadows, 25 for annual crop fields, 35 for fallow lands, and, finally, 28 and 19 for the herbaceous layer of floodplain forests of the northern and southern macroslopes, respectively.

On the basis of the obtained descriptions, the values of the following indices were determined: S, the average number of all plant species on 0.5-m^2 plots; S_a and S_n, the average number of adventive and indigenous plant species on these small plots, respectively; N, N_a, and N_n, the total number of all, adventive, and indigenous plant species on 15-m^2 plots; and P_a, the total number of adventive plant species, found on all described plots within the certain habitat type.

Methods of Analysis

If we suppose that the species richness on small plots of plant communities results from the stochastic processes of the species immigration and extinction and that indigenous and adventive species have equal abilities to disseminate and survive (i.e., they are ecologically equivalent), then the ratio between the number of species of these groups on small plots and in their species pools should be the same (Fridley et al., 2004). According to this assumption, the percentage of adventive species in the total number of species in the species pools of communities (or on large areas of communities) should be equal to their percentage on small plots. In this case, the number of adventive species on these small plots can be calculated using the following formula: $S_a = N_a(S/N)$, where N and N_a are the numbers of all and adventive plant species in the species pool (or the large area of the community), respectively, whereas S and S_a are the numbers of all and adventive plant species on a small plot of the community, respectively.

If the average local competitiveness of indigenous and adventive species is about the same, then the expected number of adventive species on plots (ES_a) calculated using the above-mentioned model should correspond to their actual number (FS_a) or at least, taking into account the influence of stochastic processes, the number of cases where ES_a values exceed FS_a values should be about equal to the number of cases with the inverse correlation of these parameters. On the contrary, if adventive species are characterized by a higher or lower competitiveness as compared with indigenous species, then one should mainly expect either higher or lower actual number of adventive species on the plots as compared with the calculated value. To test the relevancy of the hypothesis about the ecological equivalence of indigenous and adventive species, we used a chi-square method. The level of the relative local competitiveness of adventive species was evaluated via the FS_a/ES_a value.

The relative competitiveness was evaluated for all adventive plant species included in the descriptions and also for their groups distinguished according to the way of their transfer and the life form of plants. These groups included (1) herbaceous xenophytes, represented mainly by unintentionally introduced weeds; (2) herbaceous ergasiophytes (herbaceous plants escaping cultivation and ones being introduced); and (3) woody ergasiophytes, including woody plants escaping cultivation and ones being introduced (Mirkin and Naumova, 1998). The characteristics of the studied communities and the values of indices reflecting the relative competitiveness of adventive plant species of different origin and life forms are shown in Tables 1–3.

The relative role of the factors N_a, S, and N in the variation of the number of adventive species on 0.5-m^2 plots (S_a) was determined by a multiple regression analysis (Eliseeva and Yuzbashev, 1996). The contribution of each of these factors to the forecast of the dependent variable was evaluated on the basis of the coefficient of separate determination (d^2, equal to the product of the paired correlation coefficient of a certain factor and its *Beta* coefficient), whereas the total contribution was evaluated on the basis of the multiple determination coefficient (R^2). All calculations were carried out using Microsoft Excel and Statistica 6.0.

RESULTS AND DISCUSSION

The total number of described adventive species was 37, including 15 xenophytes, 11 herbaceous ergasiophytes, and 11 woody ergasiophytes (Table 1). The majority of unintentionally introduced plants originated from North America (67%); three species originated from Tropical and South America; finally, Southeast Asia and the Mediterranean region were represented by one species each. The majority of herbaceous plants becoming wild were also represented by species originating from North America (seven species, or 64%), two species originated from Southeast Asia, and two more species originated from the Mediterranean and Asia Minor regions. Among the described woody ergasiophytes, five species (45%) are from North America, four species (36%) originated from Japan and China, and two species (18%) originated from Western Asia. The relative competitiveness of adventive plant species of different origin was considered separately for each community type.

Table 1. General characteristics of the analyzed herbaceous communities of the Western Caucasus

Communities	1	2	3	4	5	6	7
Number of descriptions	16	38	26	25	23	28	19
Elevation above sea level (m)	200–680	70–200	440–900	180–220	180–220	100–300	50–300
Projective cover (average and limiting values, %)	91 (50–100)	9 (5–15)	12 (5–25)	80 (40–100)	90 (70–100)	47.5 (5–90)	50 (5–95)
Number of adventive species	5	9	5	16	18	14	13
Xenophytes (herbaceous species) (1)							
Ambrosia artemisiifolia L.	II (22)	V (29)	II (37)	V (88)	V (48)	I (5)	I (1)
Erigeron annuus (L.) Pers.	V (59)	I (18)	IV (13)	III (48)	V (73)	V (12)	II (5)
Erigeron canadensis L.	I (22)	III (22)	V (63)	II (23)	II (44)	I (6)	
Oxalis stricta L.	III (46)			I (19)	III (33)		II (8)
Bidens frondosa L.		II (25)	I (5)	I (5)	I (50)	III (10)	II (2)
Xanthium californicum Greene		II(12)		I (15)	I (20)		
Amaranthus retroflexus L.		I (8)		I (15)	I (100)		
Euphorbia nutans Lagasca		II (11)					
Scrophularia peregrina L.		I (9)					
Oenothera biennis L.			II (41)			II (3)	
Galinsoga parviflora Cav.				I (5)			
Acalypha australis L.				I (38)			II (10)
Matricaria matricarioides (Less.) Porter				III (34)	I (50)		
Amaranthus albus L.					I (37)		
Paspalum thunbergii Kunth ex Steudel					I (10)		
Ergasiophytes (herbaceous species) (2)							
Asclepias syriaca L.	I (3)			I (43)	II (57)		
Helianthus annuus L.				III (35)			
Helianthus tuberosus L.				I (10)	I (100)	I (9)	
Sorghum halepense (L.) Pers.				I (10)	I (30)		
Solidago canadensis L.				I (5)	II (80)	III (7)	
Abutilon theophrasti Medikus					I (38)		
Silphium perfoliatum L.					I (100)		
Secale cereale L.					I (5)		
Echinocystis lobata (Michaux) Torrey et Gray						I (1)	
Duchesnea indica (Andr.) Focke							V (15)
Phytolacca americana L.							II (4)
Ergasiophytes (woody species) (3)							
Robinia pseudoacacia L		I (6)		I (25)			
Amorpha fruticosa L.						II (13)	
Morus nigra L.					I (30)	I (6)	
Acer negundo L.						II (13)	
Parthenocissus quinquefolia (L.) Planch.						I (2)	
Gleditsia triacanthos L.						I (9)	I (1)
Morus alba L.						I (1)	II (5)
Ailanthus altissima (Miller) Swingle							I (5)
Ficus carica L.							I (2)
Hydrangea macrophylla (Thunb. ex Murr.) Ser.							I (I)
Trachycarpus fortunei H. Wendl.							I (3)

Note: Community description: 1—steppe meadow and mid-mountain forest glades; 2—low-mountain near-riverbed shoals; 3—mid-mountain near-riverbed shoals; 4—annual crop fields; 5—fallow lands; 6—herbaceous layer of floodplain forests of the northern macroslope; and 7—herbaceous layer of floodplain forests of the southern macroslope.

The Roman numerals in the table fields indicate the species constancy on 15-m^2 plots; the Arabic numerals in parentheses indicate the species frequency (%) on 0.5-m^2 plots, formed within 15-m^2 plots.

Table 2. Values of parameters characterizing the studied communities

Communities	1	2	3	4	5	6	7
Number of descriptions	16	38	26	25	35	28	19
N	29.9	18.1	20.9	20.2	27.7	27.6	29.7
N_n	27.9	14.9	18.7	16.4	23.8	23.9	26.6
N_a	2.0	3.2	2.2	4.2	3.9	3.7	3.2
N_{a1}	–	–	–	3.0	3.0	1.9	1.0
N_{a2}	–	–	–	1.2	0.9	0.75	1.4
N_{a3}	–	–	–	–	–	1.0	0.8
S	12.8	4.4	4.9	7.9	11.7	6.4	9.2
S_n	11.9	3.8	4.0	6.0	9.6	4.9	8.1
S_a	0.9	0.6	0.9	2.0	2.1	1.5	1.1
S_{a1}	–	–	–	1.7	1.5	0.8	0.3
S_{a2}	–	–	–	0.3	0.6	0.3	0.7
S_{a3}	–	–	–	–	–	0.5	0.1

Note: Communities: 1—steppe meadow and mid-mountain forest glades; 2—low-mountain near-riverbed shoals; 3—mid-mountain near-riverbed shoals; 4—annual crop fields; 5—fallow lands; 6—herbaceous layer of floodplain forests of the northern macroslope; and 7—herbaceous layer of floodplain forests of the southern macroslope.

Parameters: S and N represent the average number of all plant species on 0.5-m^2 and 15-m^2 plots, respectively; S_n and N_n represent the average number of indigenous plant species on 0.5-m^2 and 15-m^2 plots, respectively; S_a, S_{a1}, S_{a2}, S_{a3} and N_a, N_{a1}, N_{a2}, N_{a3} represent the average number of adventive plant species on these plots (a, all adventive species; a_1, herbaceous xenophytes; a_2, herbaceous ergasiophytes; a_3, woody ergasiophytes).

Steppe meadow and forest glade communities. The total number of adventive species revealed in these communities was five: *Ambrosia artemisiifolia*, *Erigeron annuus*, *Erigeron canadensis*, *Oxalis stricta*, and *Asclepias syriaca*; all except the last one belong to the xenophyte group. The average number of such species on 0.5-m^2 and 15-m^2 plots was very small (Table 2). According to Table 2, the expected number of adventive species on the small plots of the forest glade and steppe meadow communities does not differ significantly from their actual number; this fact may indicate a similar average competitiveness of adventive and indigenous species in these habitats. At the same time, the number of cases where $FS_a/ES_a < 1$ exceeded the number of cases where $FS_a/ES_a > 1$, which does not argue in favor of adventive species.

Phytogroups of low-mountain near-riverbed shoals. The total number of adventive species described in these communities was nine; the majority of them were xenophytes. A relatively high frequency was observed for *Ambrosia artemisiifolia*, *Erigeron canadensis*, and *Bidens frondosa*. The average number of adventive species on 0.5-m^2 plots was even lower than in the case of meadow phytocenoses (Table 2). On average, indigenous plant species growing on low-mountain shoals are better adapted to these habitats than adventive ones (Table 3).

Phytogroups of mid-mountain near-riverbed shoals. In these communities, we observed only five adventive species (*Ambrosia artemisiifolia*, *Erigeron canadensis*, *Erigeron annuus*, *Bidens frondosa*, and *Oenothera biennis*), all belonging to xenophytes. The most frequent adventive species were *Erigeron canadensis* and *E. annuus*. In contrast to low-mountain shoals, the FS_a value obtained for this habitat type significantly exceeded the ES_a value (Table 3). This fact may indicate an altitude-dependent increase in the average competitiveness of adventive plants, though the number of such species decreases as the altitude increases.

To clarify the reasons for this phenomenon, we compared the ecological structure of the pools of indigenous plants in phytogroups located at different altitudes. The results showed that, as the altitude increases, the fraction of species typical of open habitats, such as disturbed areas, agricultural lands, and shoals (*Polygonum persicaria*, *Setaria pumila*, *S. viridis*, *Convolvulus arvensis*, *Crepis setosa* Hall. Fil., *Verbena officinalis* L., etc.), decreases, whereas the fraction of species transferred to the shoals from the neighboring closed forest, meadow, and other communities (*Galega officinalis* L., *Leontodon hispidus*, *Alchemilla oxysepala* Juz., etc.) increases. For example, phytogroups growing on the southern macroslope at an elevation which does not exceed 60 m above sea level included more than 60% of species typical of open habitats; at elevations of 60–125 and 200 m above sea level, the fraction of such species was 45–53% and 36%, respectively (Akatov and Akatova, 2006, 2010). In the case of shoals located on the northern macroslope, the fraction of species originating from open habitats was 63, 46, and 20% for the elevation of 200, 400, and 800–900 m, respectively. This fact is probably connected with a different level of disturbance of shore phytocenoses. This result allowed us to suppose that, in the case of shoals, indigenous spe-

Table 3. Results of the examination of a hypothesis about the ecological equivalency of indigenous and adventive species of herbaceous plants

Communities	Groups of adventive species	n	FS_a/ES_a	Variants		χ^2
				$FS_a > ES_a$	$FS_a < ES_a$	
Forest glades and steppe meadows	$a(a_1)$	20	1.0	7	13	0.90
Low-mountain shoals	$a(a_1)$	38	0.7	6	32	8.90 (<0.01)
Mid-mountain shoals	$a(a_1)$	26	1.9	20	6	3.77 (<0.05)
Annual crop fields	a	25	1.3	17	8	3.24 (<0.1)
	a_1	25	1.6	21	4	11.56 (<0.001)
	a_2	17	0.7	5	12	2.88 (<0.1)
Fallow lands	a	35	1.3	34	1	31.11 (<0.001)
	a_1	35	1.2	24	11	4.83 (<0.05)
	a_2	23	1.8	18	5	7.35 (<0.01)
Herbaceous layer of forests (northern macroslope)	a	28	2.1	25	3	17.29 (<0.001)
	a_1	24	1.9	17	7	4.17 (<0.05)
	a_2	18	1.4	11	7	0.89
	a_3	15	2.5	13	2	8.07 (<0.01)
Herbaceous layer of forests (southern macroslope)	a	19	1.2	12	7	1.32
	a_1	10	0.7	3	7	1.6
	a_2	19	2.0	15	4	6.37 (<0.02)
	a_3	14	0.4	1	11	10.29 (<0.01)

Note: Designations: n, number of descriptions; S_a, average actual number of adventive species on 0.5-m^2 plots; ES_a, average expected number of adventive species on 0.5-m^2 plots; figures in parentheses indicate the confidence level for the chi-square criterion; groups of adventive species: a_1, unintentionally introduced herbaceous species; a_2, herbaceous plants escaping cultivation; a_3, woody plants escaping cultivation; a, all species.

cies from open habitats take up stronger positions compared to foreign species than the species from forest or meadow communities; this fact substantially determines a relatively high average competitiveness of a few foreign species in the phytogroups of mid-mountain shoals.

Segetal communities of annual crop fields. The total number of adventive species revealed in this type of communities was 16, which is significantly higher than in all examined communities. Among these 16 species, ten were xenophytes and six were ergasiophytes. The most frequent adventive species of the xenophyte group were *Ambrosia artemisiifolia*, *Erigeron annuus*, and *Matricaria matricarioides*; in the case of ergasiophytes, the most frequent species was *Helianthus annuus*. According to Table 3, the relative competitiveness of adventive plants differs depending on the groups to which they belong. The average competitiveness of xenophytes (group 1) is significantly higher than that of indigenous species; at the same time, the average competitiveness of ergasiophytes (group 2) is reliably lower than that of indigenous plants, though this difference is not as large as in the case of group 1. *Ambrosia artemisiifolia*, a xenophytic species, was the most abundant species on the majority of plots located on the territory of segetal coenoses.

Fallow land communities. In these communities, adventive species, including both xenophytes and ergasiophytes, dominated on the majority of plots. The most frequent species was *Erigeron annuus*; frequent species also included *Solidago canadensis*, *Ambrosia artemisiifolia*, and *Asclepias syriaca*. Other species were described only for one or two plots (*Helianthus tuberosus*, *Abutilon theophrasti*, and *Silphium perfoliatum*). The maximum average abundance was registered for *Solidago canadensis*. The total number of adventive species revealed in this community type was 18, which exceeded the corresponding values obtained for other studied communities. Among these species, 17 represented two groups, xenophytes (10) and herbaceous ergasiophytes (7). One more species, *Morus nigra*, belonged to woody ergasiophytes. The maximum constancy was observed for *Ambrosia artemisiifolia*, *Erigeron annuus*, and *Oxalis stricta* (group 1) and *Asclepias syriaca* and *Solidago canadensis* (group 2). *Morus nigra* was observed only as single individuals. On the majority of plots located on fallow lands, the actual number of adventive species exceeded the expected one, which may indicate that their competitiveness in such cenoses significantly exceeds that of indigenous species. Such a conclusion can be made for both groups of adventive species; however, it is important that the relative competitiveness of ergasiophytes on the plots on which they were observed exceeded that of xenophytes (Table 3). A high competitiveness of nonnative species on fallow lands was also confirmed by their domination on the majority of plots.

Herbaceous layer of floodplain forests of the northern macroslope. The total number of observed adventive species was 14, including five xenophytes, three herbaceous ergasiophytes, and six woody ergasiophytes. The number of adventive species observed on the described 15-m^2 plots varies from one to nine. The data obtained for this habitat type (see Table 3) showed that both total and the individual relative competitiveness of the groups of adventive plant species were considerably higher than that of indigenous species. At the same time, the competitiveness of different groups of adventive plants differed from each other. The highest competitiveness was observed for the undergrowth of adventive woody plants, followed by herbaceous xenophytes. The worst relative competitiveness among adventive plant species was observed for herbaceous ergasiophytes, though its level still remained higher than that of indigenous plants.

Herbaceous layer of floodplain forests of the southern macroslope. The total number of observed adventive species was 13 with the domination of herbaceous xenophytes (five species) and the undergrowth of woody plants (six species). However, the maximum frequency and abundance (up to the predominance) were observed for a herbaceous ergasiophyte, *Duchesnea indica*. The composition of xenophytes observed in the herbaceous layer of floodplain forests of both macroslopes is similar (Table 1); however, the competitive positions of this group of adventive plants are significantly lower in the case of the southern macroslope as opposed to the northern macroslope (Table 3). The relative competitiveness of the undergrowth of adventive woody species observed in this habitat type of the southern macroslope is even lower; at the same time, it is considerably higher in the case of herbaceous ergasiophytes, whose species composition (*Duchesnea indica* and *Phytolacca americana*) differs from that of the forests of the northern macroslope.

Apparently, these results do not confirm a supposition that adventive plant species are unambiguously more competitive than indigenous ones; the level of competitiveness depends on the type of plant community, bioecological features of adventive and indigenous species, and particular circumstances. For example, in the case of herbaceous communities of the Western Caucasus, the most frequent invaders are xenophytes. Adventive plants from this group are characterized by a significantly higher competitiveness as compared with indigenous plant species in the communities of fallow lands and annual crop fields, in phytogroups of mid-mountain near-riverbed shoals, and in the herbaceous layer of low-mountain forests of the northern microslope. However, in the communities of forest glades and steppe meadows, the advantages of one of these plant groups are feebly expressed. As to the communities of the low-mountain shoals and the herbaceous layer of floodplain forests of the southern macroslope, our data show that indigenous species forming these communities are more competitive than xenophytes.

The most advantageous position of herbaceous ergasiophytes was observed in the fallow land communities and in the herbaceous layer of floodplain forests of the southern macroslope, where they often dominate. In the case of the herbaceous layer of floodplain forests of the northern macroslope, their competitive advantage over indigenous plant species is less obvious. In the case of annual crop fields, this group of plants obviously loses to local weeds, and they hardly invade into the communities of forest glades, steppe meadows, and near-riverbed shoals. The undergrowth of woody ergasiophytes was observed mainly under the canopy of floodplain forests. In the forests of the northern macroslope, the species from this group were more competitive as compared with indigenous ones (both herbaceous species and the undergrowth of woody plants), whereas in the case of the forests of the southern macroslope, the situation was quite the opposite. The reason for this phenomenon is hardly determined, since the herbaceous and shrub layers of the forests located on different macroslopes are characterized by a significantly differing composition of both indigenous and adventive plants. To solve this problem, some additional population studies are required.

In conclusion, we would like to discuss the results with respect to the problem of the invasibility of plant communities. The above-described model can serve as a good basis for such a discussion, since it allows us to formalize the majority of the known ideas about this property of plant communities. First, it shows that the number of adventive species on small plots (S_a) can be determined by the number of these species in the region (or on larger plots) which are able to grow under particular conditions and provide diaspores for the small plots (N_a) (Usher et al., 1988; Lonsdale, 1999; Meekins and McCarthy, 2001; Hierro et al., 2005; Richardson and Pysek, 2006). According to this supposition, a higher content of adventive species in some communities does not necessarily indicate their higher internal invasibility (Richardson and Pysek, 2006). Second, the number of adventive species on small plots can be determined by the features of their cenotic structure, such as their local species richness S (it assumes that environmental factors which determine a high species richness of plant communities are often also favorable for invasive species (Sax and Brown, 2000; Brown and Peet, 2003; Gilbert and Lechowicz, 2005; Richardson and Pysek, 2006; Davies et al., 2007)), the size of species pools N (Herben hypothesis) (Herben, 2005), and the S/N ratio (Akatov et al., 2009; Akatov and Akatova, 2010). Finally, the number of adventive species on small plots of cenoses can be determined by the competitiveness of plant species forming these cenoses toward adventive species.

Using this model and the method of multiple regression analysis, it is possible to estimate the role of the listed factors in the determination of the level of saturation of the plots of plant communities with adventive species in the Western Caucasus. Our calculations showed that the contribution of N_a to the variation of S_a was 43% ($d^2 = 0.426$) and the combined contribution of S and N was 17%; therefore, the combined contribution of all three factors reached 60% ($R^2 = 0.592, n = 187, P < 0.001$). In this case, the role of the relative competitiveness of indigenous and adventive species in plant communities in combination with seemingly stochastic processes determines the level of adventization of these communities by about 40%. In the case of merely herbaceous communities (i.e., without the herbaceous layer of forest phytocenoses), the relative contributions of N_a, N, and S in the determination of S_a will be 24% (N_a) and 38% (S/N ratio); however, the role of competitive relations will remain the same (about 38%).

Thus, the results of our analysis indicate a different relative competitiveness of adventive species toward indigenous species in different herbaceous phytocenoses of the Western Caucasus. This fact plays a significant role in the level of resistance of plant communities to the invasions of such species, which is at least comparable with the role of their cenotic structures.

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