

Composition and Species Richness of Fallow Plant Communities with Predominance of Adventive Species (Belaya River Basin, Western Caucasus)

T. G. Eskina^a, V. V. Akatov^b, and T. V. Akatova^a

^a Caucasian State Nature Biosphere Reserve, Maykop, 385000 Republic of Adygea, Russia

^b Maykop State Technological University, Maykop, 385000 Republic of Adygea, Russia

e-mail: akatovmgti@mail.ru

Received June 16, 2011

Abstract—The effect of adventive dominants (*Erigeron annuus*, *Solidago canadensis*, *Ambrosia artemisiifolia*, *Asclepias syriaca*, etc.) on the composition and species richness of fallow plant communities (Belaya River basin, Western Caucasus) are analyzed. The results show that (1) adventive dominants have light effects on the composition of fallow communities; (2) communities with more abundant adventive dominants are characterized by lower community species richness on the plots of 0.5 and 15 m² as a whole, and a lesser number of native species and higher number of adventive ones; and (3) communities with more abundant adventive dominants are characterized by a lower average frequency of native and adventive species on the plots of 0.5 m². However, the relations between all these characteristics are poor.

DOI: 10.1134/S2075111712030022

Keywords: adventive species, fallow lands, dominants, species composition, species richness, frequency, Western Caucasus

INTRODUCTION

The process of adventization of the vegetation cover often results in replacement of native dominants by adventive (alien) ones. There are at least two reasons that can lead to the decrease in the species richness of plant communities. First, alien species of plants can be stronger competitors as compared to native species dominating in such habitats and reach a higher abundance and higher level of dominance (Meiners et al., 2001; Silliman and Bertness, 2004; Hejda et al., 2009). The higher the level of dominance, the less resources are available for accompanying species and the lower their possible abundance and species richness of the community (Whittaker, 1980; Mirkin and Naumova, 1998; McKane et al., 2002; Kunte, 2008). Secondly, the role of some alien species in the ecosystem formation (by selective use of mineral resources, changing of the light regime, physical and chemical properties of soils, allelopathy, etc.) can hinder the growth of certain aboriginal species in the cenoses that are common for such habitats (Callaway and Ridenour, 2004; Reinhart et al., 2005; Hulme and Bremner, 2006). As a result, the communities with the predominance of alien plants can contain a fewer number of species than the initial ones even if the abundance of native dominants in the initial communities was high as well.

It should be noted that publications on this issue contain examples both of a significant effect of alien

dominants on the species richness and the composition of cenoses (Meiners et al., 2001; Silliman and Bertness, 2004; Reinhart et al., 2005; Hejda et al., 2009) and of its absence (Houlahan and Findlay, 2004; Sagoff, 2005; Hulme and Bremner, 2006). And this applies even in the cases where invasions of the same species are considered but in different sites of the communities (Hejda and Pyšek, 2006; Mills et al., 2009).

In the Western Caucasus, the alien species of plants often become dominant in communities of fallow lands which usually have no well-expressed dominants in their natural state. So it is interesting to know how adventive dominants affect the composition and species richness of cenoses in fallow lands. The following questions are considered in the paper: (1) whether adventive dominants have a specific effect on the composition of fallow communities; (2) what relations exist between the abundance of adventive dominants and the species richness of aboriginal and adventive plants in parts of fallow lands of different area; (3) what relations exist between the abundance of adventive dominants and average frequency of aboriginal and adventive species.

MATERIALS AND METHODS

Communities of fallow lands were described in 2008 and 2009 in the basin of the Belaya River at the height of 200 m above sea level (coordinates of the

central part of the region under studies: 44°37.249'N, 40°00.059'E). Descriptions were made in sites of phytocenoses of 15 m²; within each of the sites, 20 plots 0.5 m² in size were arranged. In small plots, the species of plants (herbaceous and shrubs) were documented, and the total projective cover was evaluated visually (in portions, rounding off to 0.05, 0.10, 0.15, 0.20, etc.) as well as the projective cover of certain species using the point scale (1 point means the cover is less than 1%; 2 points, the cover is 1–5%; 3 points, 6–15%; 4 points, 16–25%; 5 points, 26–50%; 6 points, 51–75%; 7 points, 76–100%). A total of 35 sites of fallow lands of 15 m² each were described. In all sites, adventive species were recorded and one of them was dominant; i.e., the species had higher abundance, which was evaluated as the average point value of the cover in plots of 0.5 m², as compared to other plants, both adventive and aboriginal.

On the basis of the descriptions in addition to the average point value of the cover, the values of the following characteristics were determined: S is the average number of plant species in plots of 0.5 m² (within the site of 15 m²); S_n and S_a are the average number of aboriginal and accompanying (i.e., except the dominant) adventive species of plants in the plots; N , N_n , and N_a are the total number of plant species and the number of aboriginal and accompanying adventive species in sites of 15 m², respectively; F , F_n , and F_a are the average frequency of accompanying plant species including aboriginal and adventive ones in plots of 0.5 m² (within 15 m²). The data were processed by the methods of correlation and factor analysis. The calculations were performed using Microsoft Excel 2003 and Statistica 6.0.

RESULTS AND DISCUSSION

A common description of communities in fallow lands with the predominance of different adventive species of plants is presented in Tables 1 and 2. As is seen from Table 1, they contain a significant number of general (constant) species which are common in such habitats (*Elytrigia repens*, *Convolvulus arvensis*, *Taraxacum officinale*, *Plantago major*, etc.). No distinct dominants were recorded among aboriginal species in the sites under study. The total number of adventive species of plants in this type of communities was 18 (10% of the total number of described species), which is more than in the majority of other types of habitats in the studied region (steppe meadows, forest clearings, shoals, etc.). This can be explained not only by the high invisibility of fallow phytocenoses but also by the bioecological properties of most of the adventive species of plants which were introduced into the region under study (Akatov et al., 2010). It should be noted that in this paper we do not consider archeophytes as adventive species, but we analyze only alien plants that have been recently introduced into the

region (since 18th century), so-called neophytes. Most of them (72%) originated from North America; the other species were introduced from Asia. By way of transfer, 50% of the considered adventive species are ergasiophytes (wild and introduced species); the second half are xenophytes (unintentionally introduced weeds) (Mirkin and Naumova, 1998). Annual and biennial plants prevail among xenophytes and most of the perennial adventive plants are “escapees from cultivation.” Of seven adventive species which dominate in the communities of fallow lands, five are wild.

As is seen from Table 1, *Erigeron annuus* is the most frequent dominant in fallow lands; *Solidago canadensis*, *Ambrosia artemisiifolia*, and *Asclepias syriaca* dominated less frequently; and the other species dominated in single cases. In some sites, *Solidago canadensis* reached the highest abundance (the average point value of the cover was 7.0); *Ambrosia artemisiifolia* (5.9), *Erigeron annuus* (5.9), and *Silphium perfoliatum* (5.9) had lower abundance; and *Asclepias syriaca* (4.7), *Helianthus tuberosus* (4.1), and *Abutilon theophrasti* (4.1) had the lowest abundance. The characteristic of the average abundance of these species for the groups of sites is presented in Table 1. The highest average abundance was recorded for *Solidago canadensis*, and the lowest was recorded for *Erigeron annuus*. In addition, it should be noted that, in one of eight plots with the predominance of *Solidago canadensis*, this species had an average point value of the cover of less than 4 (i.e., the cover was no more than 15%). For plots with a relatively high abundance of *Ambrosia artemisiifolia*, such a situation occurred in one plot of four; for *Erigeron annuus*, in 15 of 16 plots; and for *Asclepias syriaca*, in three plots of four. Thus, in 20 of 35 described plots, adventive species prevailed quantitatively, but their abundance was not high.

In order to determine the presence or absence of the specific effect of concrete adventive dominants on the species composition of the communities in fallow lands, an attempt was made to distinguish the groups of aboriginal species which had relatively high or relatively low average frequency in communities with the predominance of one particular species. As is seen from Table 1, only eight species had a relatively high average frequency. Five of them were mainly recorded in phytocenoses with the prevalence of *Ambrosia artemisiifolia* and three were recorded in phytocenoses with the prevalence of *Erigeron annuus*. In communities with other adventive dominants, the species which were typical of them were not found. In addition, we recorded three species which were not found in communities with the prevalence of *Ambrosia artemisiifolia*, but had relatively high frequency in other plots under discussion (*Agrimonia eupatoria*, *Equisetum arvense*, and *Rubus caesius*). These species were not found in communities with the dominance of other adventive species.

Thus, the results indicate a relatively weak specific effect of concrete adventive dominant species on the

Table 1. General characteristic of described plots of fallow lands

No. of species	Groups of descriptions *	1	2	3	4	5
	Number of plots of 15 m ² (0.5 m ²)	8 (160)	4 (80)	16 (320)	4 (80)	3 (60)
	Cover	100	100	100	100	100
	Height of grass stand, cm	127.5	80	98.8	120	133.3
Average point value of cover in 15 m ² and frequency in 0.5 m ² (in parentheses, %) of adventive dominants						
1	<i>Solidago canadensis</i> L.	6.2 (100)		0.1 (5.3)		
2	<i>Ambrosia artemisiifolia</i> L.	0.3 (24.4)	4.8 (100)	0.4 (39.1)	0.1 (7.5)	1.0 (33.0)
3	<i>Erigeron annuus</i> (L.) Pers.	0.5 (36.9)	0.2 (18.8)	2.2 (100)	0.9 (87.5)	1.5 (68.0)
4	<i>Asclepias syriaca</i> L.	0.2 (23.8)		0.1 (10.3)	2.9 (100)	
5	<i>Helianthus tuberosus</i> L.					1.4 (33.0)
6	<i>Abutilon theophrasti</i> Medikus	0.1 (1.3)	0.1 (1.3)			1.4 (33.0)
7	<i>Silphium perfoliatum</i> L.					2.0 (33.0)
Frequency of adventive species in 0.5 m ² , %						
8	<i>Oxalis stricta</i> L.	6.9		13.1	23.8	1.7
9	<i>Erigeron canadensis</i> L.	11.9	2.5	12.2		31.7
10	<i>Xanthium strumarium</i> L.		5.0	2.2		8.3
11	<i>Sorghum halepense</i> (L.) Pers.	0.6		4.4		5.0
12	<i>Bidens frondosa</i> L.			9.4		1.7
13	<i>Amaranthus albus</i> L.	0.6	25.0			
14	<i>Paspalum thunbergii</i> Kunth ex Steudel		7.5			3.3
15	<i>Morus nigra</i> L.	3.7				
16	<i>Amaranthus retroflexus</i> L.		50.0			
17	<i>Secale cereale</i> L.			0.3		
18	<i>Matricaria matricarioides</i> (Less.) Porter					33.3
Frequency of the most common aboriginal species in 0.5 m ² , %						
19	<i>Elytrigia repens</i> (L.) Nevski	66.3	63.8	81.6	100	86.7
20	<i>Festuca pratensis</i> Hudson	67.5	22.5	76.3	95.0	20.0
21	<i>Convolvulus arvensis</i> L.	32.5	33.8	48.1	16.3	38.3
22	<i>Setaria pumila</i> (Poir.) Schult.	12.5	70.0	2.2	1.3	38.3
23	<i>Trifolium repens</i> L.	35	26.3	30.6	33.8	20.0
24	<i>Trifolium medium</i> L.	3.1	1.3	26.9	3.8	55.0
25	<i>Cichorium intybus</i> L.	7.5	26.3	39.4	36.3	10.0
26	<i>Cirsium arvense</i> L. (Scop.)	6.3	17.5	16.6	40.0	11.7
27	<i>Daucus carota</i> L.	13.1	16.3	47.8	35.0	15.0
28	<i>Potentilla reptans</i> L.	23.1	10.0	13.1	18.8	28.3
30	<i>Plantago major</i> L.	1.3	16.3	18.1	1.3	31.7
Frequency of species which are typical for communities with certain dominants in 0.5 m ² , %						
31	<i>Atriplex patula</i> L.		43.8			
32	<i>Chenopodium album</i> L.		61.3	0.9		
33	<i>Echinochloa crus-galli</i> (L.) P. Beauv.		33.8			2.0
34	<i>Polygonum minus</i> Hudson	1.3	47.5	0.3		
35	<i>Portulaca oleracea</i> L.		48.8			2.0
36	<i>Avena fatua</i> L.	3.8		22.5		
37	<i>Plantago lanceolata</i> L.	1.3	3.8	30.6	14.0	2.0
38	<i>Sonchus arvensis</i> L.		6.3	25.6		
Frequency of species which were not recorded in communities with a certain dominant in 0.5 m ² , %						
39	<i>Agrimonia eupatoria</i> L.	15.6		31.3	45.0	10.0
40	<i>Equisetum arvense</i> L.	26.3		15.6	5.0	33.3
41	<i>Rubus caesius</i> L.	13.9		8.8	35.0	41.7

* Groups of descriptions of fallow plots with the predominance of certain species of adventive plants: 1. *Solidago canadensis*; 2. *Ambrosia artemisiifolia*; 3. *Erigeron annuus*; 4. *Asclepias syriaca*; 5. *Helianthus tuberosus*, *Abutilon theophrasti*, *Silphium perfoliatum*.

Table 2. Values of parameters which characterize plots of fallow lands with dominance or co-dominance of certain adventive plant species

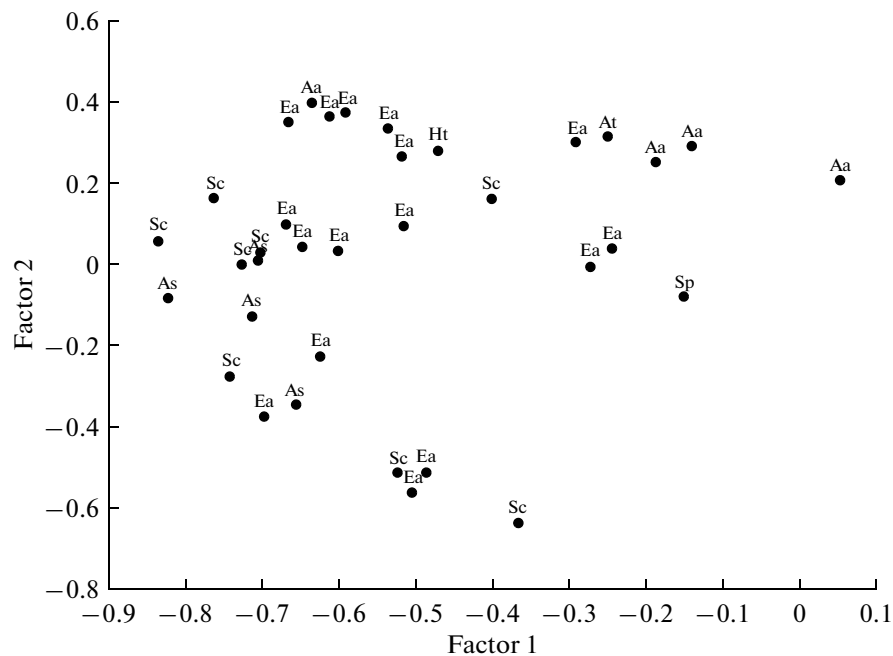
Dominant	<i>n</i>	<i>N</i>	<i>S</i>	<i>F</i>	<i>N_a</i>	<i>S_a</i>	<i>F_a</i>
<i>Erigeron annuus</i> (L.) Pers.	16	28.3	12.8	0.43	2.3	1.0	0.47
<i>Solidago canadensis</i> L.	8	27.0	9.2	0.30	3.9	1.1	0.24
<i>Ambrosia artemisiifolia</i> L.	4	23.3	10.6	0.45	2.3	1.1	0.49
<i>Asclepias syriaca</i> L.	4	29.5	11.8	0.38	2.8	1.2	0.44
<i>Helianthus tuberosus</i> L.	1	31	14.5	0.45	4	2.1	0.53
<i>Abutilon theophrasti</i> Medikus	1	26	8.7	0.31	7	2.8	0.40
<i>Silphium perfoliatum</i> L.	1	27	13.4	0.48	2	0.7	0.35

species composition of the studied communities in fallow lands. This conclusion is confirmed by the results of ordination of the described fallow lands by the method of factor analysis (Fig. 1). It was performed on the basis of only accompanying species (both adventive and aboriginal), and none of the adventive dominants was taken into account. As is demonstrated in the figure, the sites of fallow lands do not form well isolated assemblies in the factor space by the character of the dominating species.

As follows from Table 2 in plots of 0.5 m², the minimum average species richness was recorded for cenoses with the predominance of *Solidago canadensis* and *Abutilon theophrasti*, and the maximum average species richness was recorded for cenoses with the predominance of *Silphium perfoliatum* and *Helianthus*

tuberosus. The minimum number of species in plots of 15 m² was found in cenoses with the predominance of *Ambrosia artemisiifolia*, and the maximum number was found in cenoses with the dominance of *Helianthus tuberosus*. So, as is seen from the table, the plots of fallow lands with the maximum and minimum average values of the cover is not obligatorily characterized by higher or lower average values of species richness.

The highest number of adventive plant species was documented in plots with the dominance of *Abutilon theophrasti* and their lowest number was documented in plots with the dominance of *Silphium perfoliatum*. The minimum average frequency of species is typical of plots with the dominance of *Solidago canadensis* and *Abutilon theophrasti*; the maximum average frequency of species is typical of plots with the domi-

**Fig. 1.** Ordination of phytocenoses in fallow lands with the predominance of different adventive plant species by the method of factor analysis.

Dominating species: Sc—*Solidago canadensis*, Aa—*Ambrosia artemisiifolia*, Ea—*Erigeron annuus*, As—*Asclepias syriaca*, Ht—*Helianthus tuberosus*, At—*Abutilon theophrasti*, Sp—*Silphium perfoliatum*.

Table 3. The relationship between the cover of dominating adventive plant species, species richness, and average frequency of species in plots of fallow lands

Dependent parameter	<i>n</i>	<i>r</i>	<i>r_s</i>	<i>R</i> ²
<i>N</i>	35	-0.251	-0.326*	0.063
<i>N_n</i>	35	-0.327*	-0.424**	0.107
<i>N_a</i>	35	0.313*	0.359**	0.098
<i>S</i>	35	-0.521***	-0.531***	0.271
<i>S_n</i>	35	-0.547***	-0.566***	0.299
<i>S_a</i>	35	0.032	-0.013	0.001
<i>F</i>	35	-0.507***	-0.509***	0.257
<i>F_n</i>	35	-0.427**	-0.480***	0.182
<i>F_a</i>	35	-0.319*	-0.320*	0.102

Note: *n* is the number of plots; *r* is the Pearson correlation coefficient; *r_s* is Spearman's rank correlation coefficient; confidence level: (***) <0.01, (**) <0.05, (*) <0.1; absence of the superscript indicates the confidence level greater than 0.1; *R*² is the coefficient of determination.

nance of *Silphium perfoliatum*. The average frequency of aboriginal and accompanying adventive species of plants does not differ significantly between plots. The frequency of aboriginal species is somewhat higher in

plots with the predominance of *Solidago canadensis* and *Silphium perfoliatum*, and it is lower in other plots.

Table 3 and Fig. 2 present the results of the comparison of the average cover of the most abundant adventive plant species with different components of the species richness and the frequency of species in sites of fallow lands. As is seen, the communities with higher cover of the adventive dominant are characterized by a lower species richness on the whole, lower number of aboriginal species, and average frequency of both aboriginal and adventive species. In all cases, the interdependence is not high (this factor determines the variation of dependent parameters by 10–30%). But it should be noted that the negative effect of adventive dominants on the number of aboriginal species is less pronounced in sites of less area. It agrees with the results of earlier studies which indicate that (1) the effect of adventive species on diversity of aboriginal species is more manifested in small plots occupied by communities (Brown and Peet, 2003; Fridley et al., 2004; Herben et al., 2004; Réjmánek et al., 2005); (2) the effect of the degree of dominance of any species (not only adventive) on the species richness of plant communities decreases with the increase in the area of the studied plots (Akatov, 2010a). This can probably be related to changes in the relative role of local (competitive exclusion) and regional (immigration) processes in determination of the species

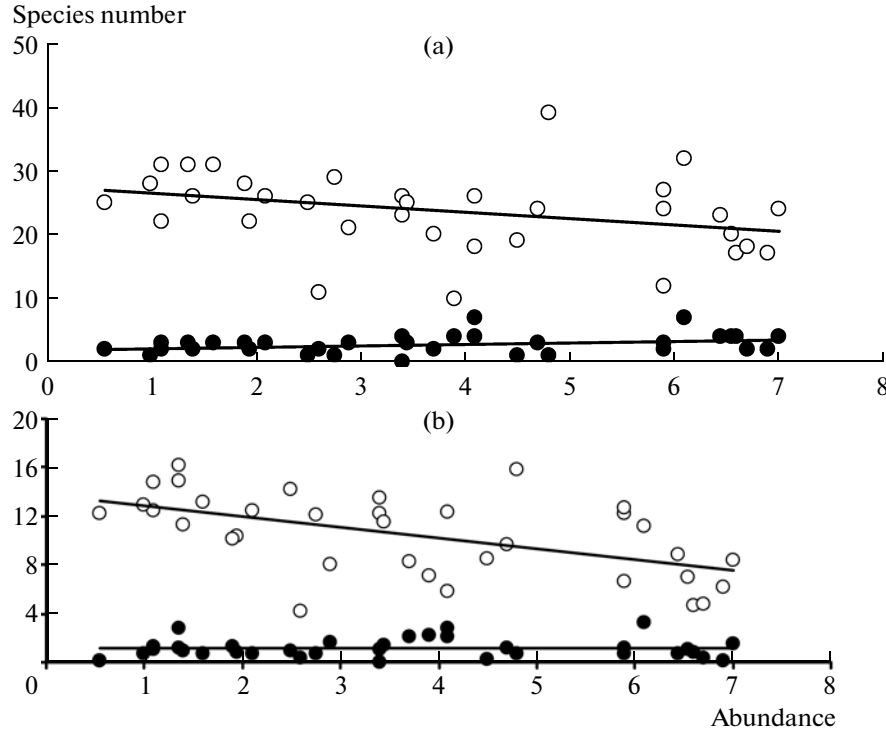


Fig. 2. The relationship between the abundance of the adventive dominant and the number of aboriginal and accompanying adventive species of plants in plots of 15 m² (a) and 0.5 m² (b).

The abundance of the dominant species is expressed as an average point value of the projective cover. White circles denote the number of aboriginal species; black circles denote the number of accompanying adventive species.

richness of communities in the area gradient (Brown and Peet, 2003; Akatov, 2010a).

The relationship between the abundance of adventive dominants and the number of adventive species in plots is also weak but positive. The negative relationship between the abundance of adventive species and the average frequency of species apparently supports the fact that the decrease in the species richness of the communities is not the result of the ecosystem forming activity of adventive plants which prevents growing of one aboriginal species and, correspondingly, favors higher abundance of other aboriginal species (the effect of compensation or ecological release (Soule, 1986; Chernov, 2005; Gonzalez and Loreau, 2009; etc.)). This is supported by a relatively weak specific effect of concrete adventive species dominants on the species composition of communities, which was demonstrated above.

In conclusion, we touch briefly on the importance of our results for the purpose of nature conservation. In publications devoted to the problems of invasive ecology, much attention is paid to the effect of adventive species of organisms, including plants, on the species richness of acceptor communities. But the understanding of the consequences of the introduction of nonnative plants (in contrast to invasions of animals) into natural and seminatural cenoses for aboriginal species is vague. Thus, according to the published data, almost half of the species that were included in the Endangered Species Act (United States) became rare as a result of their competition with adventive species (Flather and Sieg, 2008). Sometimes in works published in our country, examples are given of displacement of aboriginal species by adventive ones, for example, of populations of aboriginal species of the genus *Bidens* by North American beggar ticks *Bidens frondosa* (Vinogradova, 2003; 2008; Vasilieva and Papchenkov, 2011). In some publications, it is shown that invasions of nonnative species take place without displacement of aboriginal species (Sax and Gaines, 2003; Sax et al., 2005; Kravtsova et al., 2010). It is necessary to note that the frequency of references to competition of adventive plants among factors limiting the number of species of vascular plants that were included in the Red Books of the Russian Soviet Federative Socialist Republic (1988) and the Russian Federation (2008) is less than 1% (Akatov, 2010b).

The communities in fallow lands are not significant cozoologically since they rarely include endemic, rare, and endangered plant species. But as was mentioned above, this is the type of communities in the Western Caucasus where adventive species reach the highest number and abundance and dominate in many sites. Thus, phytocenoses in fallow lands can be considered as the model for the situation where as a result of expansion of the ecologic-cenotic spectrum of adventive species in the region they become dominant in other cozoologically significant types of communities. By their example, the consequences of high abun-

dance of adventive species for aboriginal species can be evaluated.

As follows from the results of our studies, when reaching a high abundance, the adventive species have a negative effect on diversity and frequency of aboriginal species, but such an effect is little specific, is not strong, and decreases upon increasing the size of plots from 0.5 to 15 m². Therefore, it can be suggested that, in plots of a larger area, such an effect is not appreciable. It is interesting to compare these data with the results of analysis of displacement of aboriginal dominants in arboreal and shrub layers in forests located along river channels in the Western Caucasus (*Populus nigra* L., *Alnus incana* (L.) Moench, *Salix alba* L., *Swida australis* (C.A. Mey.) Pojark. ex Grossh., *Euonymus europaea* L., etc.) by adventive species (*Ailanthus altissima* (Miller) Swingle, *Ficus carica* L., *Robinia pseudoacacia* L., *Acer negundo* L., and *Amorpha fruticosa* L.) (Akatov et al., in press). The relationship between the degree of dominance and the species richness in sites of tree communities of the area of 300 m² and shrubs of the area of 15 m² was stronger than between the abundance of adventive plants expressed by the average point value of cover and the species richness in plots of fallow lands of 0.5 and 15 m² (Pearson's correlation coefficient varied from 0.662 to 0.777, $P < 0.001$). However, the average abundance of adventive dominants (*Ailanthus altissima*, *Ficus carica*, and *Robinia pseudoacacia*) was not higher than that of aboriginal species in similar habitats, and the species richness of communities in plots of 300 m² was not lower. On the contrary, the displacement of aboriginal dominants by maple ash (*Acer negundo*) led to a decrease and by false indigo (*Amorpha fruticosa*) led to a substantial decrease in the number and average density of populations of aboriginal species of trees. Apparently, this took place not only as a result of capture of most of the food resources by adventive dominants as compared to aboriginal ones but also because adventive species provoked keen competition of other (accompanying) species for the remaining resources (Akatov et al., in press). But in this case too, it is necessary to take into account the spatial scale since upon increasing the area of plots by a factor of ten (from 300 m² to 0.3 ha) the role of the degree of dominance in variation of the species richness of the tree layer in forest phytocenoses in the Western Caucasus decreases by a factor of three (Akatov, 2010a).

CONCLUSIONS

On the basis of the results, the following conclusions and suggestions can be made:

1. Adventive dominants do not have a significant specific effect on the species composition of fallow communities in the region under study.
2. Communities of fallow lands with more abundant adventive dominants consist mainly of a fewer

number of aboriginal species and a greater number of adventive ones. In this case, the effect of this factor on the species richness of communities is relatively weak and decreases with the increase in the area of plots.

3. The abundance of adventive dominants has a negative effect on the average frequency of both aboriginal and adventive species. It can be suggested that the decrease in the species richness of fallow communities in the gradient of the increase in values of this factor is not the consequence of the ecosystem forming activity of adventive dominants but is the result of the competition for resources.

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research, grant no. 07-04-00449.

REFERENCES

- Akatov, V.V., Importance of Local and Regional Process in Species Diversity Formation of Wood Layer in the Western Caucasian Different Size Areas, *Issledovano v Rossii*, 2010a, no. 40, pp. 479–486. <http://zhurnal.ape.relarn.ru/articles/2010/040.pdf>
- Akatov, V.V., Rare and Endangered Plant Species of Russia, Krasnodar Krai and Adygei Republic: Key Factors and Treats by Experts' Opinion, in *XVI Mezhdunar. nauch.-prakt. Konf. "Ekologicheskie problemy sovremennosti. Ratsional'noe prirodopol'zovanie i sokhranenie bioraznoobraz'ya"* (The XVI International Scientific-Practical Conference on contemporary Ecological Problems. Rational Nature Management and Preservation of Biodiversity), Maikop: MGTU, 2010b, vol. 3, pp. 105–115.
- Akatov, V.V., Akatova, T.V., and Eskina, T.G., Variation Factors of the Number of Adventive Species in Grass Communities of Western Caucasus, *Ekologiya*, 2010, no. 5, pp. 344–351.
- Akatov, V.V., Akatova, T.V., and Shadzhe, A.E., Species Diversity of Wood and Shrubby Layers in Riparian Forests of Western Caucasus with Domination of Alien Species, *Ekologiya* (in press).
- Brown, R.L. and Peet, R.K., Diversity and Invisibility of Southern Appalachian Plant Communities, *Ecology*, 2003, vol. 84, no. 1, pp. 32–39.
- Callaway, R.M. and Ridenour, W.M., Novel Weapons: A Biochemically Ased Hypothesis for Invasive Success and the Evolution of Increased Competitive Ability, *Frontiers Ecol. Environ.*, 2004, no. 2, pp. 433–436.
- Chernov, Yu.I., Species Diversity and Compensatory Processes in Communities and Biotic Systems, *Zool. Zh.*, 2005, vol. 84, no. 10, pp. 1221–1238.
- Flather, C.H. and Sieg, C.H., Species Rarity: Definition, Causes, and Classification, in *Conservation of Rare or Little-Known Species: Biological, Social, and Economic Considerations*, Raphael, M.G. and Molina, R., Eds., Washington, 2008, pp. 40–66.
- Fridley, J.D., Brown, R.L., and Bruno, J.E., Null Models of Exotic Invasion and Scale-Dependent Patterns of Native and Exotic Species Richness, *Ecology*, 2004, vol. 85, no. 12, pp. 3215–3222.
- Gonzalez, A. and Loreau, M., The Causes and Consequences of Compensatory Dynamics in Ecological Communities, *Annu. Rev. Ecol. Evol. Syst.*, 2009, vol. 40, pp. 393–414.
- Hejda, M. and Pyšek, P., What is the Impact of *Impatiens glandulifera* on Species Diversity of Invaded Riparian Vegetation?, *Biological Conservation*, 2006, vol. 132, pp. 143–152.
- Hejda, M., Pyšek, P., and Jarosik, V., Impact of Invasive Plants on the Species Richness, Diversity and Composition of Invaded Communities, *Journal of Ecology*, 2009, vol. 97, pp. 393–403.
- Herben, T., Mandak, B., Bimova, K., and Munzbergova, Z., Invasibility and Species Richness of a Community: A Neutral Model and a Survey of Published Data, *Ecology*, 2004, vol. 85, pp. 3223–3233.
- Houlihan, J.E. and Findlay, C.S., Effect of Invasive Plant Species on Temperate Wetland Plant Diversity, *Conservation Biology*, 2004, vol. 18, no. 4, pp. 1132–1138.
- Hulme, P.E. and Bremner, E.T., Assessing the Impact of *Impatiens glandulifera* on Riparian Habitats: Partitioning Diversity Components Following Species Removal, *Journal of Applied Ecology*, 2006, vol. 43, pp. 43–50.
- Krasnaya kniga Rossiiskoi Federatsii (Rasteniya i griby)* (Red Book of Russian Federation), Moscow: Tov. Nauch. Izd. KMK, 2008, 855 p.
- Krasnaya kniga RSFSR. Rasteniya* (Red Book of RSFSR. The Plants), Moscow: Rosagropromizdat, 1988, 591 p.
- Kravtsova, L.S., Izhboldina, L.A., Mekhanikova, I.V., Pomazkina, G.V., and Belykh, O.I., Naturalization of *Elodea canadensis* Mich. in the Baikal Lake, *Ros. Zh. Biol. Invaz.*, 2010, no. 2, pp. 2–18.
- Kunte, K., Competition and Species Diversity: Removal of Dominant Species: Increases Diversity in Costa Rican Butterfly Communities, *Oikos*, 2008, vol. 117, pp. 69–76.
- McKane, R.B., Johnson, L.C., Shaver, G.R., Nadelhoffer, K.J., et al., Resource-Based Niches Provide a Basis for Plant Species Diversity and Dominance in Arctic Tundra, *Nature*, 2002, vol. 415, pp. 68–71.
- Meiners, S.J., Pickett, S.T.A., and Cadenasso, M.L., Effects of Plant Invasions on the Species Richness of Abandoned Agricultural Land, *Ecography*, 2001, vol. 24, pp. 633–644.
- Mills, J.E., Reinartz, J.A., Meyer, G.A., and Young, E.B., Exotic Shrub Invasion in an Undisturbed Wetland Has Little Community-Level Effect over a 15-Year Period, *Biol. Invasions*, 2009, vol. 11, pp. 1803–1820.
- Mirkin, B.M. and Naumova, L.G., *Nauka o rastitel'nosti (istoriya i sovremennoe sostoyanie osnovnykh kontseptsiy)* (The Science of Vegetation (History and Present Status of General Conceptions)), Ufa: Gilem, 1998, 413 p.
- Reinhart, K.O., Greene, E., and Callaway, R.M., Effects of *Acer platanoides* Invasion on Understory Plant Communities and Tree Regeneration in the Rocky Mountains, *Ecography*, 2005, vol. 28, pp. 573–582.
- Réjmanek, M., Richardson, D.M., and Pyšek, P., Plant Invasions and Invisibility of Plant Communities, in *Vegetation Ecology*, van der Maarel, E., Ed., Oxford: Blackwell, 2005, pp. 332–355.
- Sagoff, M., Do non-Native Species Threaten the Natural Environment?, *Journal of Agricultural and Environmental Ethics*, 2005, vol. 18, pp. 215–236.

- Sax, D.F., Brown, J.H., White, E., and Gaines, S.D., The Dynamics of Species Invasions: Insights into the Mechanisms that Limit Species Diversity, in *Species Invasions: Insights into Ecology, Evolution and Biogeography*, Sax, D.F. and Sunderland, S.D., Eds., Massachusetts: Sinauer Associates, 2005, Ch. 17, pp. 447–465.
- Sax, D.F. and Gaines, S.D., Species Diversity: From Global Decreases to Local Increases, *Trends in Ecology and Evolution*, 2003, vol. 18, no. 11, pp. 561–566.
- Silliman, B.R. and Bertness, M.D., Shoreline Development Drives Invasion of *Phragmites australis* and the Loss of Plant Diversity on New England Salt Marshes, *Conservation Biology*, 2004, vol. 18, pp. 1424–1434.
- Soule, M.E., Community Processes, in *Conservation Biology: The Science of Scarcity and Diversity*, Soule, M.E., Ed., Sunderland, Massachusetts: Sinauer Associates, 1986, pp. 304–308.
- Uitteker, R., *Soobshchestva i ekosistemy* (Communities and Ecosystems), Moscow: Progress, 1980, 327 p.
- Vasil'eva, N.V. and Papchenkov, V.G., Influence Mechanisms of Invasive *Bidens frondosa* L. on Domestic Species of the Bur-Marigold, *Ros. Zh. Biol. Invaz.*, 2011, no. 1, pp. 15–22.
- Vinogradova, Yu.K., Experimental Studies of the Plant Invasions (by an Example of Genus *Bidens*), in *Problemy izucheniya adventivnoi i sinantropnoi flory v regionakh SNG* (Problems of Study of Adventive and Synanthropic), Moscow: Botanicheskii Sad MGU, 2003, pp. 31–33.
- Vinogradova, Yu.K., Invasive Capacity of Natural Phytocenoses and Competitive Relations between Domestic and Invasive Species, in *Bioraznoobrazie: problemy i perspektivy sokhraneniya. Materialy konferentsii* (Proceedings of the Conference on Biodiversity: Problems and Perspectives of Preservation), Penza, 2008, pp. 17–19.