

The Structure of Absorbing Roots in Invasive and Native Maple Species

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Abstract—Specific structural features of absorbing roots have been studied in *Acer negundo* (an invasive species in the southern Cisural region), compared to native *Acer platanoides* and *A. tataricum*. A comparative analysis of the diameter of fine roots, stele and bark volumes, and the frequencies of roots with retained primary bark, root hairs, arbuscular mycorrhiza, and dark septate endophytes has been performed in the invasive and native species from four habitats (by two habitats in the forest–steppe and steppe zones). The roots of *A. negundo* have been additionally studied in trees from two monospecific stands. It has been found that the structure of fine roots significantly differs between the invasive and native species: the roots of *A. negundo* are larger, with relatively poorly developed root hairs and low occurrence of dark septate endophytes. In monospecific stands, the frequency of mycorrhiza in *A. negundo* roots is very low, with arbuscules and dark septate endophytes being totally absent. It is concluded that specific structural features of the belowground absorbing apparatus in *A. negundo* are accounted for mainly by traits autonomously formed in a plant, rather than by characteristics of symbiotic relationships, and that they are not consistent with the assumption that the invasive species can utilize soil resources more effectively or more rapidly than taxonomically close native species.

Keywords: *Acer negundo*, biological invasions, invasive plants, absorbing roots, fine roots, arbuscular mycorrhiza, dark septate endophytes, root hairs, southern Cisural region

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There is considerable uncertainty in knowledge of the functional features of invasive plants in the belowground sphere. For example, two recent reviews dealing with meta-analysis of the properties of invasive plants address only the most general parameters of belowground organs, namely, the belowground phytomass and belowground vs. aboveground phytomass ratio, while the set of aboveground traits included in analysis is markedly wider [1, 2]. It is considered that specific features of belowground organs in invasive plants have been studied to a lesser extent than those of aboveground organs [3].

Current views on the significance of mycorrhizal interactions for plant invasions are also ambiguous. On the one hand, many invasive species depend on the formation of arbuscular mycorrhiza (AM) [4], similar to the majority of other plants. Its formation in such species under new conditions is usually possible due to the cosmopolitanism and low specificity of AM fungi [4–6], and changes in AM fungal communities occurring after the invasion of new species may have favor-

able effects for the invaders [7]. On the other hand, a considerable proportion of invasive species in arid regions are nonmycorrhizal or facultatively mycorrhizal [8–10]. In the temperate zone, nonmycorrhizal invasive species usually colonize disturbed habitats, while mycorrhizal invaders are found in late successional communities [6].

The model plant used in this study is the boxelder maple *Acer negundo* L., an American species spreading rapidly in Eurasia [11, 12], particularly in the forest–steppe and steppe zones, which invades native plant communities and transforms them. Our initial assumption was that *A. negundo* as a transformed species may possess certain features of the belowground absorbing organs that allow it to utilize soil resources more effectively or more rapidly than do native species. The purpose of this study was to reveal specific structural features of absorbing roots in *Acer negundo*, compared to native *Acer platanoides* L. and *A. tataricum* L., in different habitats in order to take into account ecological variability.

Table 1. Characteristics of habitats

Habitat no.	Geographic coordinates	Biotope	Soil	Crown closure, %	HDSC*
Foothills: vicinity of Tashla, Tyulganskii district; <i>A. negundo</i> , <i>A. platanoides</i>					
I	52°24'52" N, 56°14'04" E	Dendropark, upper slope of Mt. Shikhan	Medium-humus leached chernozem	70–80	20–30
II	52°24'14" N, 56°13'23" E	Broadleaf forest margin, slope base of Mt. Lushnaya	Medium-humus leached chernozem	30–50	50–70
Plain: vicinities of Orenburg; <i>A. negundo</i> , <i>A. tataricum</i>					
III	51°42'04" N, 54°44'28" E	Protective forest strip, smooth hillslope in Ural–Ilek interfluve	Low-humus southern chernozem	50–70	50–70
IV	51°43'50" N, 54°36'25" E	Sparse floodplain forest, first terrace above Ural floodplain	Medium-humus ordinary chernozem	30–50	70–80
Monogroups: closed monospecific <i>A. negundo</i> stands in Orenburg					
V	51°44'21" N, 55°05'40" E	<i>Acer negundo</i> stand under motorway bridge	Ordinary chernozem transformed into urbiquasizem	60–70	0–5
VI	51°44'51" N, 55°05'37" E	<i>Acer negundo</i> stand on highway roadside	Ordinary chernozem transformed into urbiquasizem	70–90	0–2

* Herb–dwarf shrub coverage, %.

The absorbing roots were examined (a) for traits autonomously developed by a plant (root diameter, occurrence of root hairs, and retention of primary bark) and (b) characteristics of symbiosis, such as signs of mycorrhiza formation and occurrence of dark septate endophyte (DSE) mycelium. Some of these parameters were recommended for use in studies on the functional properties of plants [13]. There are data on AM formation in *A. negundo* within its native range [14, 15]. In Eurasia, this species can form AM [16–18] but may also remain nonmycorrhizal [19].

MATERIAL AND METHODS

The material was collected in Orenburg region from two habitats in the Southern Urals foothills and four habitats in the central, plain part of the region (in Orenburg and its vicinities) in the third 10-day period of June 2016 (Table 1).

The foothill region is characterized by low-mountain landscapes with elevations of 400–660 m a.s.l., and the plain region (90–100 m a.s.l.) has undulating or flatland topography. The climate is sharply continental, with hot summers ($T_{\text{July}} = 20.4\text{--}22.2^\circ\text{C}$) and cold winters ($T_{\text{January}} = -15.4$ to -13.7°C). The sum of temperatures above 10°C is 2300–2400°C in the foothills and 2600–2700°C in the plain; annual average precipitation in the respective regions amounts to 420 and 370 mm. The prevalent soils are podzolized and leached chernozems in the foothills and ordinary and southern chernozems in the plain. The former region is in the forest–steppe subzone with broadleaf, birch, and aspen forests and meadow steppes; the latter, in the subzone of typical motley grass steppes with birch

and aspen forest islands and floodplain stands. Landscapes of central Orenburg region have been extensively transformed by agricultural activities (plowed or used for livestock grazing).

Acer negundo appeared in the study region long ago. The proportion of this species in tree stands of Orenburg city parks increased from 20% in 1936–1938 to 40–60% in 1971 [20]. Its active invasion to ecosystems of the region was promoted by the planting of the state protective forest strip extending from Mt. Vishnevaya to the Caspian Sea (1949–1952). *Acer negundo* was subsequently planted in local protective woodland belts, from which it has expanded to floodplain and urbanized biotopes throughout the region, invading natural tree stands and displacing the Norway maple *A. platanoides* [21, 22]. In our study, *A. negundo* was compared with two species: *A. platanoides*, which is common in broadleaf forests growing in the foothills and floodplains, and the Tatarian maple *A. tataricum*, which sporadically occurs as a wild-growing species in floodplain forests of the region but is mainly found in various artificial tree stands.

In four habitats, the invasive and one of the two native species grow together. In the foothill region (habitats I and II), *A. negundo* was compared with *A. platanoides*; in the plain region (habitats III and IV), with *A. tataricum*. In Orenburg (habitats V and VI), *A. negundo* was studied in its monospecific closed stands (below, referred to as monogroups).

Samples of last-order roots in each habitat were taken from four to five generative trees, which is considered sufficient for studying structural features of belowground plant organs [13]. For reliable species identification, the connection between fine roots,

Table 2. Results of three-way ANOVA (F -test/significance level, P) for traits of absorbing roots in species of the genus *Acer* in habitats with *A. negundo* growing together with *A. platanoides* or *A. tataricum* ($n = 39$)

Trait	Factors			
	Invasive status ($dF = 1$)	Region ($dF = 1$)	Habitat within region ($dF = 2$)	Invasive status \times region ($dF = 1$)
Root diameter	10.90/0.0023*	0.70/0.4075	0.43/0.6566	1.00/0.3243
Stele diameter	4.04/0.0525	1.54/0.2241	0.23/0.7948	0.19/0.6646
Partial bark volume	0.79/0.3769	0.48/0.4944	1.47/0.2436	2.05/0.1614
Occurrence frequency:				
primary bark	3.11/0.0871	5.93/0.0205	2.48/0.0991	0.11/0.7457
root hairs	13.00/0.0010*	1.54/0.2238	2.37/0.1092	5.22/0.0289
all AM structures	0.02/0.8981	0.02/0.8881	36.60/<0.0001*	0.05/0.8290
arbuscules	0.11/0.7408	1.18/0.2844	47.79/<0.0001*	0.79/0.3814
vesicles	0.51/0.4804	8.10/0.0076	12.73/0.0001*	0.65/0.4251
DSE mycelium	14.68/0.0005*	15.82/0.0004*	1.16/0.3244	4.56/0.0403

* Differences are significant with account of the Benjamini–Yekutieli correction for multiple testing.

higher-order roots, and tree stems was traced during sampling.

Root and stele diameters in each plant were measured in transverse cryotome sections (15–20 μm) of last-order roots that had no signs of degradation. Mycorrhizal colonization was evaluated by analyzing 15 randomly selected 1-cm fragments of fine roots of the last and second-last orders. The roots were macerated in KOH for 1 h and stained with aniline blue to make squashed preparations, which were analyzed under a Leica DM 5000 microscope at 100 \times magnification. In each fragment, five microscopic fields were examined for the presence of the following structures: (a) preserved primary bark, (b) root hairs, (c) any AM structures (hyphae, vesicles, or arbuscules), (d) arbuscules, (e) vesicles, and (f) the mycelium of dark septate endophytes (DSE), a low-specialized group of fungal root symbionts [23].

The results were processed statistically using the Statistica 8.0 package. Interspecific differences in the occurrence of test traits were evaluated by hierarchical (nested) ANOVA and multivariate ANOVA (MANOVA). In all cases, an individual tree was used as the statistical unit, with fractions being arcsine-transformed prior to analysis.

RESULTS

General features of root structure in invasive *A. negundo*, compared to the native species, were evaluated by one-way MANOVA of datasets compiled in two ways: taking into account (1) data on the nine test traits of absorbing roots only in plants from habitats I–IV, where *A. negundo* grew together with *A. platanoides* or *A. tataricum*, or (2) the total data from all habitats, including those with *A. negundo* monogroups. In both cases, significant differences were revealed between

the invasive and native species: for the first dataset, $\lambda = 0.33$, $F_{(9, 29)} = 6.68$; $P < 0.0001$; for the second dataset, $\lambda = 0.35$, $F_{(9, 38)} = 7.79$; $P < 0.0001$.

To find out in which particular traits, and with which amplitude, the absorbing roots of the invasive and native species differ from each other, subsequent analysis was performed taking into account not only species-dependent but also other factors of variability in root structure. In particular, the data on habitats I–IV (*A. negundo* + *A. platanoides* or *A. tataricum*) was analyzed with regard to two types (sources) of variability in the set of test traits: interspecific variability between invasive *A. negundo* and the two native species (factor “invasive status”) and variability between habitats. The latter was analyzed on two scales: geographic, since plant habitats were located in different geomorphological regions (factor “region”), and local (ecotopic), or ecological (factor “habitat” nested within “region”) (Table 2).

The diameter of absorbing roots and the occurrence frequency of root hairs differed between the species but not between habitats. The root diameter was greater in *A. negundo* than in *A. platanoides* and *A. tataricum*: 292–338 vs. 250–286 μm (here and below, the range of habitat-average values) (Fig. 1a). Conversely, root hairs in all habitats occurred more frequently in *A. platanoides* and *A. tataricum* than in *A. negundo*: 41–72 vs. 17–43% (Fig. 1d). The stele diameter and partial bark volume (stele-to-bark ratio) were conserved (Fig. 1b), and the sources of their variability remained obscure. The occurrence frequency of preserved primary bark in fine roots differed slightly between plants from the foothill and plain regions (83–98 vs. 75–96%) (Fig. 1c).

The occurrence frequencies of AM hyphae, vesicles, and arbuscules proved to depend on ecological

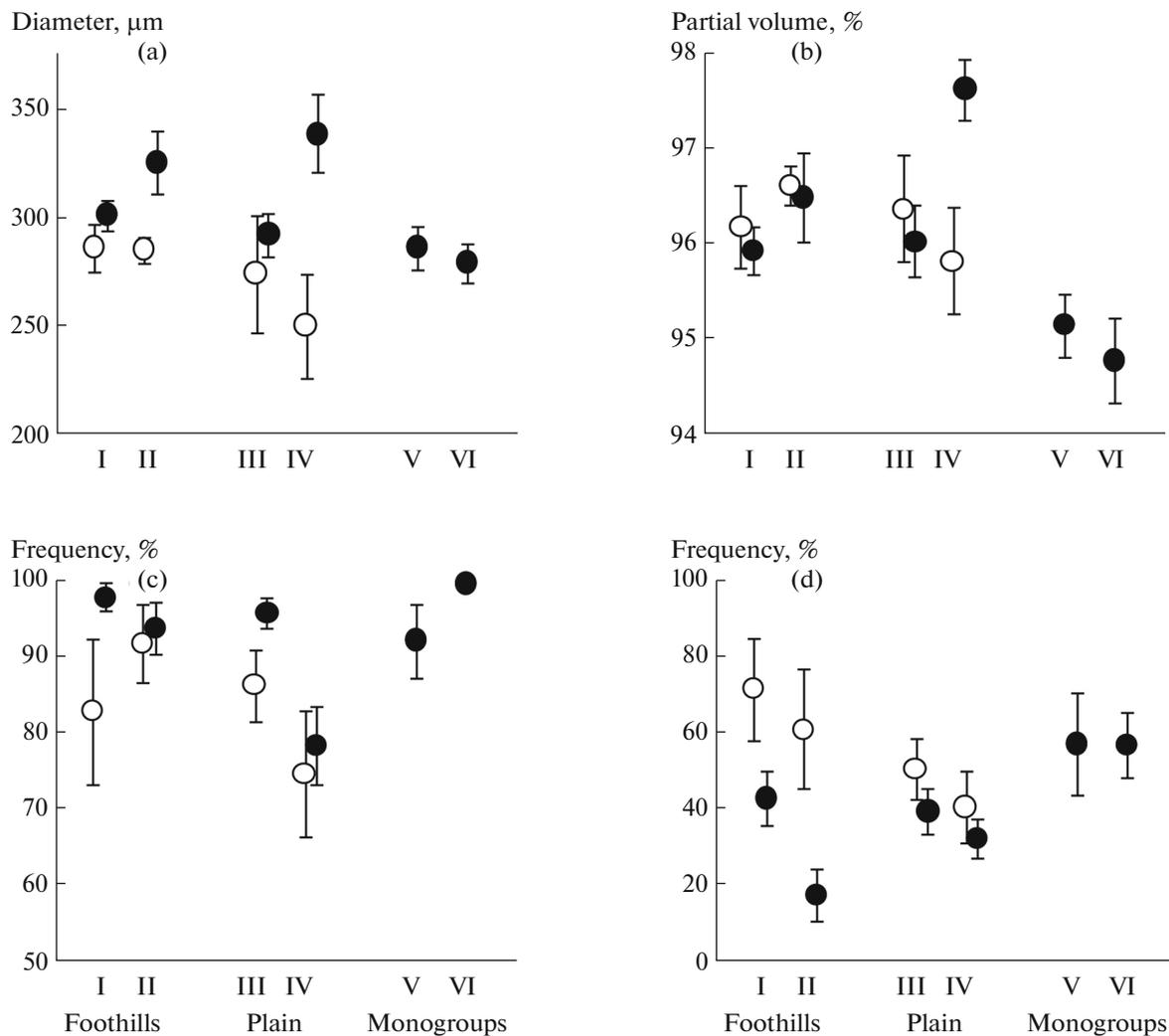


Fig. 1. (a) Root diameter, (b) partial bark volume, and occurrence frequency of (c) preserved primary bark and (d) root hairs in *Acer negundo* (solid circles) compared to *A. platanoides* and *A. tataricum* (open circles) in different regions and habitats, $m \pm SE$.

factors, since they differed mainly between habitats (Figs. 2a–2c). Characteristics of mycorrhization in the invasive and native species from the same habitat were similar and concordantly varied between habitats: for example, the frequencies of hyphae, arbuscules, and vesicles in *A. negundo* and *A. tataricum* were high in habitat III but low in habitat IV. The occurrence of DSE differed both between geographic regions and between tree species, being more frequent in the foothills than in the plain and in native *A. platanoides* and *A. tataricum* than in invasive *A. negundo* (in both cases, 1–10 vs. 0–2%) (Fig. 2d).

One-way ANOVA of data from habitats I–IV (*A. negundo* + *A. platanoides* or *A. tataricum*) confirmed all differences between the invasive and native species revealed with regard to factors of ecological variability.

A distinct relationship between root structure and ecological conditions was revealed when comparing

the traits of *A. negundo* roots in samples collected in mixed and monospecific stands (Table 4). The samples from monogroups were characterized by significantly smaller root diameter and partial bark volume (Figs. 1a, 1b), higher frequency of root hairs (Fig. 1d), lower frequency of total AM structures and arbuscules (Figs. 2a, 2b), and the absence of DSE (Fig. 2d). The following trend is noteworthy: in habitat III, where the highest AM frequency was recorded, *A. negundo* was planted artificially and has not been regenerating despite successful seed production; in habitats I, II, and IV (medium mycorrhization frequency), *A. negundo* is regenerating but has not displaced other species; and in habitats V and VI (monogroups), where *A. negundo* is absolutely dominant, the frequency of AM is minimum.

On the whole, specific features of particular habitats basically do not modulate the differences in absorbing root structure between trees from mixed and monospecific stands. This follows from the coinci-

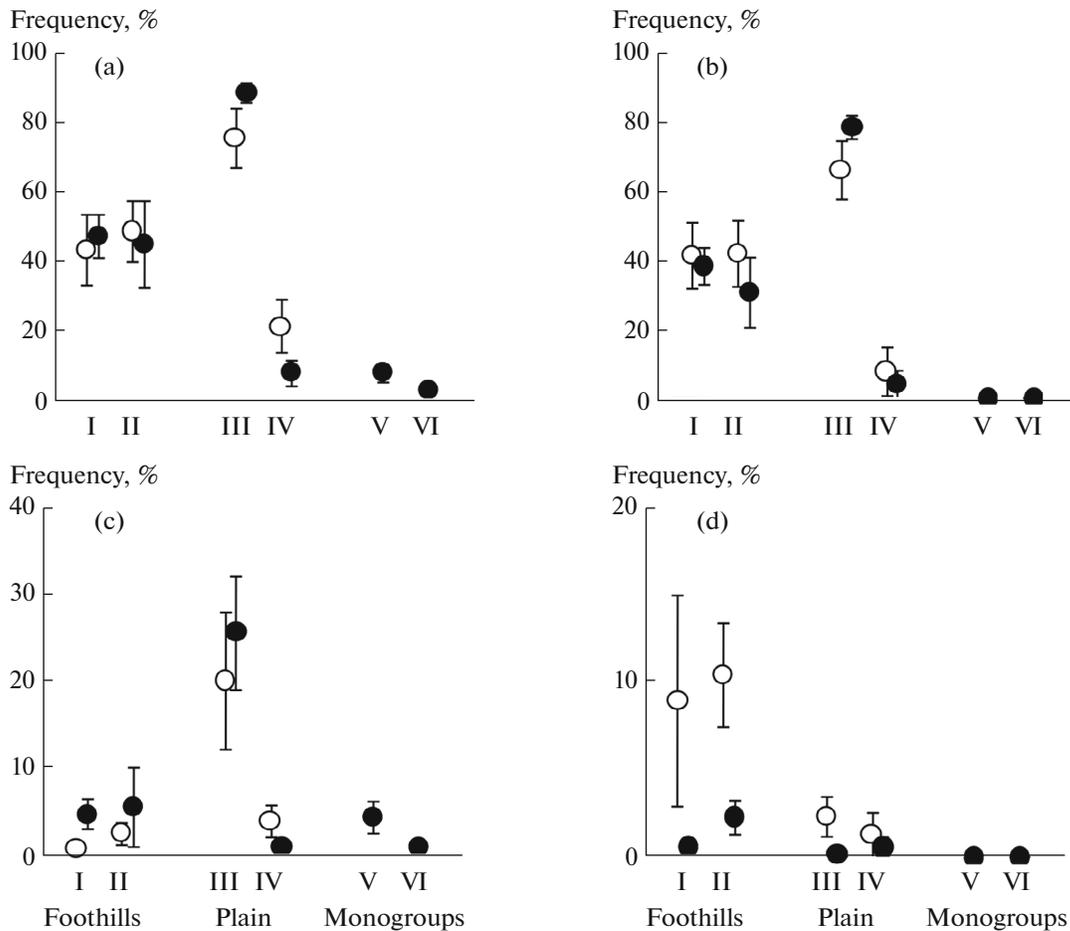


Fig. 2. Occurrence frequency of (a) arbuscular mycorrhiza structures, (b) arbuscules, (c) vesicles, and (d) dark septate endophyte mycelium in *Acer negundo* (solid circles) compared to *A. platanoides* and *A. tataricum* (open circles) in different regions and habitats, $m \pm SE$.

dence between the one-way and two-way ANOVA estimates of statistical significance for differences in the test traits between these stand types (Table 4).

DISCUSSION

The main result of this study is the conclusion about differences in the traits of absorbing roots between native and invasive tree species that are close both taxonomically and ecologically. Differences in root diameter and root hair development are most apparent. In mixed stands, the roots of invasive *A. negundo* have a greater diameter, while root hairs are formed more actively in the native species. Dark septate endophytes are also more frequent in the native species. In monospecific stands, however, root diameter in *A. negundo* is smaller than in mixed stands, and root hairs are more abundant.

Published data on specific features of root structure in invasive plants are ambiguous: compared to native species, root diameter and specific length of

last-order roots in these plants may be either greater or smaller [3, 24, 25].

On the whole, our results provide conclusive evidence for the existence of certain distinctive features in the structure of belowground absorbing apparatus in the invasive and native maple species, but these features cannot as yet be interpreted unambiguously. In particular, differences in the size of absorbing roots can be explained in different ways. On the one hand, their diameter may be positively correlated with the rate of tree growth, since it is known that the roots are larger in fast- than in slow-growing plants [26]. Hence, it is possible that the increased root diameter in *A. negundo* is due to a high growth rate, which is implied by the invasive status of this species. On the other hand, the diameter of fine roots is generally greater in mycorrhizal than in nonmycorrhizal plants [27], but this factor is unlikely to account for the observed differences: the frequency of AM does not differ between the invasive and native species, mycorrhization, and the partial bark volume in all these spe-

Table 3. Results of one-way ANOVA (F -test/significance level, P) for traits of absorbing roots in invasive and native species of the genus *Acer* ($dF = 1$) in habitats with *A. negundo* growing together with *A. platanoides* or *A. tataricum* ($n = 39$)

Trait	F	P
Root diameter	11.52	0.0017*
Stele diameter	4.40	0.0429
Partial bark volume	0.73	0.4000
Occurrence frequency:		
primary bark	2.77	0.1047
root hairs	10.01	0.0031*
all AM structures	0.01	0.9320
arbuscules	0.02	0.8889
vesicles	0.21	0.6473
DSE mycelium	9.20	0.0044*

* Differences are significant with account of the Benjamini–Yekutieli correction for multiple testing.

cies is within the range typical of mycorrhizal plants (91–96% [28]) or even higher.

This study has revealed no evidence that *A. negundo* has any morphologically distinct features of the absorbing apparatus that allow it to utilize soil resources more completely or more rapidly, compared to taxonomically close native species. Functional traits related to the capacity for absorbing substances from the soil—root hairs and arbuscular mycorrhiza—in *A. negundo* are developed no better than in the native species, and the equal ratios of stele and bark volumes is indicative of similarity in the absorptive, symbiotic, and transport functions of fine roots between *A. negundo*, *A. platanoides*, and *A. tataricum*.

We already studied mycorrhiza formation in *A. negundo*, but without comparing it with native species [18]. Here, we have made such a comparison taking into account geographic and ecological variability of fine roots and revealed no critical features of mycorrhiza formation differentiating invasive *A. negundo* from the native species. It is important, however, that such differentiation has been revealed with respect to other traits of absorbing roots. Our failure to reveal distinguishing features of mycorrhization in different maple species is largely explained by high variability in the level of AM formation between different habitats. This variability in *A. negundo* is higher than in the native species and approaches the theoretically possible limits: its absolute range in *A. negundo* is 0.03–0.89 (without monogroups, 0.08–0.89), compared to 0.22–0.76 in the native species. The prevalence of ecological component in the overall variability of AM formation unequivocally indicates that this proves is strongly determined by environmental conditions. This is in agreement with modern views on mycorrhizal symbiosis as a means to fine-tune the absorbing apparatus of plants for the functioning under given soil conditions.

Our data suggest that the more favorable are the conditions for *A. negundo* to express its properties as a transformer plant, the less close are its mycorrhizal connections and, in general, its symbiotic relationships in the belowground sphere. The properties of *A. negundo* as a species transforming autochthonous communities are better expressed in monospecific stands, where its roots proved to contain no arbuscules whose presence is regarded as a criterion of functional symbiosis [29]. The roots of *A. negundo* in monospecific stands also contain no DSE but have well-developed root hairs. Such a combination of traits is indic-

Table 4. Results of ANOVA (F -test/significance level, P) for traits of *A. negundo* absorbing roots in mixed and monospecific stands ($n = 29$)

Trait	One-way ANOVA for factor “stand type” ($dF = 1$)	Nested two-way ANOVA for factors	
		stand type ($dF = 1$)	habitat within stand type ($dF = 4$)
Root diameter	7.51/0.0107	8.77/0.0070*	2.39/0.0805
Stele diameter	4.96/0.0344	4.82/0.0386	1.04/0.4092
Partial bark volume	15.34/0.0006*	22.43/0.0001*	4.43/0.0084
Occurrence frequency:			
primary bark	2.49/0.1264	3.34/0.0805	5.03/0.0046*
root hairs	10.83/0.0028*	12.27/0.0019*	1.96/0.1340
all AM structures	15.36/0.0005*	60.07/<0.0001*	21.56/<0.0001*
arbuscules	21.41/0.0001*	107.01/<0.0001*	28.27/<0.0001*
vesicles	1.90/0.1795	3.17/0.0881	6.93/0.0008*
DSE mycelium	4.83/0.0368	5.86/0.0238	2.51/0.0696

* Differences are significant with account of the Benjamini–Yekutieli correction for multiple testing.

ative of an autonomous, nonsymbiotic strategy of soil nutrient acquisition.

It is an established fact that the same species may have different patterns of root system organization. For example, in *Pinus sylvestris* L. (a typical ectomycorrhizal species), the root systems and roots of juvenile trees in postpyrogenic habitats are formed as in weakly mycorrhizal plants [30]. The modes of soil nutrient acquisition in trees of the genus *Acer* is also potentially diverse. In the mycorrhizal intensity database for the territory of the former Soviet Union, *A. negundo* is classified as a facultative mycorrhizal species [19]; i.e., capable of either forming AM or remain nonmycorrhizal; *A. platanoides* and some other maple species may be nonmycorrhizal or form AM or ectomycorrhizae [19, 31].

Thus, the absence of arbuscules observed in monospecific *A. negundo* stands does not contradict previous data on mycorrhiza formation in trees of the genus *Acer*. Nevertheless, the conclusion about low mycorrhization of *A. negundo* in monospecific stands is untrivial, because it is considered that nonmycorrhizal and facultative mycorrhizal species are usually characteristic of the initial succession stages [32]. In particular, this is true of successions in dendrocenoses in the taiga zone [33] and herbaceous plant successions in the steppe zone [34–36]. However, there also are opposite examples where tree species with well-developed AM are replaced in the course of succession by species with a low frequency of mycorrhiza [37].

In our opinion, the low mycorrhization level in *A. negundo* from monogroups is an important fact, since it may be associated with changes in the communities of arbuscular mycorrhizal fungi [7, 38, 39]. For example, adverse effects on the native communities of these fungi have been observed upon invasion of the nonmycorrhizal European species *Alliaria petiolata* in North American forests [38].

CONCLUSIONS

The structure of absorbing roots in invasive *A. negundo* is significantly different from that in *A. platanoides* and *A. tataricum*, which are native in the region. Species-specific features of absorbing roots in *A. negundo* are consistently expressed independently of the properties of a given habitat. Their specificity is accounted for mainly by a complex of traits autonomously formed in a plant, such as root diameter and the frequency of root hairs, rather than by characteristics of development of symbiotic structures. Absorbing roots of the invasive species are characterized by greater diameter, relatively poorly developed root hairs, and low occurrence of dark septate endophytes. Apparently, *A. negundo* in certain situations can successfully grow without actively functioning AM. High variability in the occurrence frequencies of AM and root hairs and, to a lesser extent, in root diameter and the stele/bark ratio is consistent

with the concept of increased morphological plasticity of invasive species in the belowground sphere [25] and in general [2]. It may well be that the wide reaction norm of the traits of belowground organs is a component of the overall invasive syndrome associated with the ability of *A. negundo* to expand and compete with native species in habitats with different combinations of environmental conditions.

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