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Development of Invasive Weeds *Ambrosia artemisiifolia* L. and *A. trifida* L. (Asteraceae) in Moscow Oblast

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Abstract—New data on the structure of seedlings, juvenile, immature, virginal, and generative individuals of invasive species *Ambrosia artemisiifolia* L. and *A. trifida* L. and the time of their transition to different age stages in Moscow and Moscow oblast have been obtained. These data can help in recognition of plants at different stages of their ontogenesis in nature and in their timely control. It has been shown that both species have a high germination rate; however, the pace of development differs, which affects the time of flowering and fruit ripening. For *A. artemisiifolia*, the duration of the growing season in Moscow and Moscow oblast is not enough to form mature seeds, while *A. trifida* in these conditions sets high-grade fruits and seeds with high germination capacity. The main propagation path of *A. artemisiifolia* fruits from the southern regions to the north is the railways. Seed drift of *A. trifida* is mainly associated with wheeled transport and transport and processing of grain. It has been suggested that *A. trifida* can potentially be a rather dangerous plant for the northeastern regions of Central Russia as an invasive species, which in the case of massive introduction of diaspores can occupy large areas in disturbed and natural communities and form stable self-renewing populations. The northward movement of *A. artemisiifolia* is more problematic. However, in consideration of wide adaptive potential of the species, including the shortening of development cycle and the formation of early maturing and female forms, it can be concluded that naturalization of the species in the northeastern regions of Russia is also possible.

Keywords: Ambrosia artemisiifolia, *A. trifida*, invasive species, ontogenesis, Moscow, Moscow oblast
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INTRODUCTION

The study of invasive species is very urgent for solving the problems of sustainable development of the regions; in particular, this concerns quarantine species, which in the European part of our country are first of all representatives of the North American genus *Ambrosia* L. Already in the middle of the last century *A. artemisiifolia* began to occupy a strong position in the disturbed communities of the southern regions of Russia; now the mass naturalization of the species has become a real tragedy for Stavropol krai and Rostov and Volgograd oblasts. Pollen of *A. artemisiifolia* is a strong allergen, which is why about 40% of the population of these regions suffer from pollinosis during the periods of its blossoming and actually find themselves in an incapacitated state (*Chernaya kniga*..., 2009). In this context, the active search for methods of species control and eradication from plant communities has been carried out for a long time (Vasiliev, 1958; Cherkashin, 1984; Kovalev et al., 1989; etc.). Much less studied (Khvalina, 1965), but no less dangerous for human health, are two more species—*A. trifida* and *A. psilostachya*—the detailed study of which began in Russia relatively recently (Esina, 2009).

The boundaries of the secondary habitats of the species under consideration are closely related to the biological characteristics of plants. Thus, *A. artemisiifolia* and *A. trifida* are long-lasting vegetative annuals with a development cycle of about 150–180 days, *A. psilostachya* is a perennial plant and all three species are short day plants (Allard, 1945). Allard (1945) showed that a long day stimulates the development of the male reproductive sphere, and a very short day stimulates the female reproduction. So, long days at the initial stage of flowering can stimulate the development of staminal flowers, and the shortening of the day length contributes to the formation of pistil flowers, so that late blooming individuals and the youngest side branches of early blooming plants contain more female flowers. As shown in an experiment on the ecology of *Ambrosia* seeds of different biotypes, the optimal temperature required for germination of seeds after stratification at low temperature should be as high as 25°C (Dinelli et al., 2013). These features allow species to grow and self-renew only in certain climatic conditions, which correspond to many southern areas of our country; progress to the north is limited, but recently it has been increasingly effective.

Monitoring of the process of expansion of the secondary range of quarantine ragweed species and the study of the ontogenesis features of plants in different geographical locations of this range are necessary to determine the time, pathways, and rate of invasions, as well as discover those mechanisms that contribute to the expansion of species in the northeastern regions of Russia (Petrova, 2012).

In this paper, we have conducted a detailed analysis of the distribution and individual development of two species—*A. artemisiifolia* and *A. trifida*—in a strategically important region, Moscow oblast.

MATERIALS AND METHODS

The distribution of *Ambrosia artemisiifolia* L. and *A. trifida* L. on the territory of Central Russia was analyzed on the basis of the collections presented in the herbaria of the Moscow State University (MW) and Tsitsin Main Botanical Garden of the Russian Academy of Sciences (MHA); special attention was paid to the findings from Moscow and Moscow oblast.

To study ontogenesis, seeds of *A. artemisiifolia* and *A. trifida* collected in 2014 in the city of Sterlitamak (Bashkortostan) and provided by S.R. Mayorov (Chair of Higher Plants, Faculty of Biology, Moscow State University) were sown outdoors toward winter in 2014 at the experimental site in the Sergiev Posad district of Moscow oblast, 5.5 km east of the village of Buzhaninovo. Observation of plant development in 2015 lasted from the beginning of germination to the death of most individuals, with the dates of transition from one age group to another noted, with individuals of different ages being dug up, described, photographed and fixed in 75% ethanol. At least five individuals were studied in each age group. By the end of the growing season, seeds covered with woody cover were harvested from the plants and then planted in soil boxes toward winter of 2015 to track and determine their germination capacity.

In order to provide a more detailed morphological analysis, the recorded plants of different ages were also studied under laboratory conditions using an IBS-1 binocular microscope, specifying the details of the structure and identifying the criteria for the main age states of the plants. The large life cycle was carried out using the technique proposed by Rabotov (1950), taking into account some subsequent clarifications and additions (*Ontogeneticheskii atlas*..., 2000).

RESULTS

Distribution in Moscow and Moscow Oblast

In Moscow and Moscow oblast, the regions where we studied the features of plant development, the following collection sites are known.

Ambrosia artemisiifolia

Moscow (Fig. 1), near the subway station Scherbakovskaya (now Alekseevskaya), Alekseevskoye, weedy places in poplar plantations, several tens of specimens at different stages of development (June 26, 1977) and strongly littered places along the fences, near the Yaroslavl market (September 4, 1977), as well as a small debris wasteland on the corner of Novoalekseevskaya and Staroalekseevskaya streets, one specimen (August 8, 1981), V.V. Makarov (MHA); Kuntsevsky district, on the lawn along Istrinskaya street (October 1, 1980) (MW) and (October 3, 1981 and October 14, 1981) (MHA), M.S. Ignatov; northeast, between P. Korchagin street and Yaroslavskaya street, in the crevice of asphalt near a house, one specimen (August 24, 1981), V.V. Makarov (MHA); along the fence at the Yaroslavl market, August 8, 1981, V.V. Makarov (MHA); on a railway area at station Kanatchikovo, October 20, 1982, M.S. Ignatov (MHA); Vladykino, on a roadbed and on a garbage heap, in the area between the Riga cinema, a fence of the main botanical garden, and a district railway (September 14, 1984), V.V. Makarov (MHA); Degunino, Oktyabrskaya Railway, near the Mosselmash platform (October 13, 1987), M.S. Ignatov and V.V. Makarov (MHA); Kursk Railway, near Lublino station, near Lublinskie ponds, on the embankment of the railway, colony (October 13, 1987), Lublinskaya street, in the area of Zhdanovsky market, waste dump between the street and the Kursk Railway (among *Helianthus annuus*), colony (October 13, 1987) and sorting station Lublino (near the Depot platform), on the roadbed of the railway, 55°40′52″ N, 37°43′92″ E (August 27, 2013), V.D. Bochkin (MW, MHA), and also near the railway station Lublino, on the rocky wasteland (October 5, 1996), A. Sukhorukov (MW); Kazanskaya Railway, 700 m away from the Plyushchevo platform (away from Moscow), along the railway bed (October 5, 1988), V.D. Bochkin (MHA); Kursk Railway, 980 m from Textilshchiki station (away from Moscow), meadows on the slope of the embankment of the railway in front of the overpass (near the Lublinskie ponds) (October 17, 1988), V.D. Bochkin (MHA); Moscow, Kursk Railway, near the Textilshchiki platform, along the roadbed, at the edge of the platform (October 2, 1989 and September 21, 1989), V.D. Bochkin (MHA); Malaya Okruzhnaya Railway, 300 m from Kozhukhovo sorting station, toward Ugreshskaya station, along the roadbed (September 22, 1989) and along the bed of Kozhukhovo station, several plants (September 22, 1989), V.D. Bochkin (MHA); Malaya Okruzhnaya Railway, sorting station Ugreshskaya, along the roadbed, colony (September 22, 1989), Bochkin V.D. (MHA); branch from the Testovskaya platform, Belorusskaya Railway, toward the sorting station Moscow-Smolenskaya (to Moscow), in the area of confluence with the railway branch from the sorting station Presnya, Malaya Okruzhnaya Railway, along the roadbed, in mass, over 1.5 m high (November 7, 1989), V.D. Bochkin (MHA); Malaya Okruzhnaya Railway, 200 m from the Lihobory marshalling yard toward the Vladykino marshalling yard along the roadbed (October 17, 1989 and November 7, 1989), V.D. Bochkin (MHA); Malaya Okruzhnaya Railway, Andronovka sorting station, along the roadbed, scattered (November 5, 1989) and 400 m from the Andronovka sorting station (from the intersection with the Kazan Railway) to the Lefortovo sorting station, triangle formed by three railway branches, wasteland of 2 ha, northeastern part of the wasteland, scattered, 55°44′893″ N, 37°44′341″ E (September 27, 2013), V.D. Bochkin (MHA); Malaya Okruzhnaya Railway, Cherkizovo sorting station, along the roadbed, scattered (November 6, 1989), V.D. Bochkin (MHA); Malaya Okruzhnaya Railway, along the roadbed of Brattsevo station (October 17, 1989 and November 7, 1989), V.D. Bochkin (MHA); Kursk Railway, 300 m from Bitza platform to Krasny Stroitel platform, along the railway line, colony (September 9, 1990), V.D. Bochkin (MHA); Novoslobodskaya street, on the balcony of a residential house (October 11, 1998), G.I. Peshkova (MHA); Textilshchiki, in the flower bed of the Rosgiproles Institute, one very large specimen (September 25, 2006), T.A. Rumyantseva (MHA); west, Initsiativnaya street 8 (near Aminevskoye highway), near the entrance to the house, one plant (September 26, 2007), V.D. Bochkin (MHA); park on the left bank of the Gorodnya River, just below the Borisovo metro station, on the lawn, several specimens up to half a meter high (August 26, 2012), Y.A. Nasimovich and K.Yu. Teplov (MHA); Kuzminki-Lublino Park, square 10, near the intersection with Stavropolskaya street, in a weedy place, a lot, 55°41′06″ N, 37°47′01″ E (August 9, 2012) (MW, MHA), and the meadow along Stavropolskaya street (opposite the entrance to the Lublin Cemetery), second-year lawn above the high pressure gas pipeline, 55°40′89″ N, 37°47′29″ E (September 11, 2013), V.D. Bochkin (MHA); North Orekhovo-Borisovo, Shipilovsky proezd 22, lawn at the roadside, one specimen, 55°36′54″ N, 37°41′40″ E (September 23, 2008 and September 11, 2013), K.Yu. Teplov (MHA); southeast, Gorkovskaya Railway, middle of Karacharovo platform, on a weedy place, one plant (September 27, 2013), V.D. Bochkin (MHA).

Moscow oblast (Fig. 2), Kolomenskiy district, on the railway tracks of Golutvin station (September 4, 1974), N. Oktyabreva and A. Chichev (MW); Podolskiy district, 1 km to Papino village, roadside of Starokaluga highway, individually (September 8, 1991), V.D. Bochkin (MHA); Krasnogorskiy district, Petrovo-Dalneye settlement, near bus stop, one plant (September 12, 2003), V.D. Bochkin (MHA); Mytishchinskiy district, 92 km of Moscow Okruzhnaya Railway, Gardener market on Taininka, on wasteland, colony (October, 15, 2004), V.D. Bochkin (MHA); Odintsovo district, Matveykovo settlement, construction market, several plants (October 4, 2003), V.D. Bochkin (MHA); Odintsovo district, Nemchinovo settlement, the 3rd Zaprudnaya street, roadside meadow, one plant, 55°43′36″ N, 37°22′32″ E (September 23, 2008), V.D. Bochkin (MHA); Egorievskiy district, Egorievsk, forest park (Zhukova Gora, adjoins Egorievsk from the south), on the right bank of the Guslitsa River just above the mouth of the Knyazevskiy Brook and at the same time on the southwest bank of the flooded quarry, on a low grass meadow near the trail, a small local population on the site of 1×0.5 m^2 (October 5, 2015), Yu.A. Nasimovich (MHA); Solnechnogorsky district, near Novye Khimki, cottage settlement Golden Domes, weedy on the site no. 277, several plants, 55°55′5″ N, 37°19′17″ E (October 16, 2015), V.D. Bochkin (MHA).

Ambrosia trifida

Moscow (Fig. 1), south, wasteland near the outer side of the Moscow Ring Road near the birch grove to the right of Bittsa station of Kursk Railway, September 24, 2005, V. Kuvaev (MW, MHA).

Moscow oblast (Fig. 2), Krasnogorsk district, between Dedovsk station and Malinovka platform, on railway embankment (August 18, 1977), A. Chichev (MW).

Ontogenesis

Ambrosia artemisiifolia

Virginal period, seedlings (Fig. 3*A*). Aboveground germination is hypocolyllar. Hypocotyl brings two assimilating cotyledons to the surface. The cotyledon laminae are naked, about 4–5 mm long and 2 mm wide, ovate-round, all-edged, green, somewhat fleshy, so that the side veins from the surface do not stand out. Petioles are naked, wide, and short, about 0.3–0.5 mm long. Hypocotyl in a fully developed seedling can reach 0.8–1 cm in length and 0.1 cm in diameter; its upper part is usually located above the ground and has a pinkish purple color. The main root is white, up to 8 cm long, with a diameter of about 0.1 cm at the bottom and is thinner below. Lateral roots are only of the first order, long, white; the largest number of them develops on the root neck.

In this development phase, most individuals were present by May 16. In the population, a significant temporal polyvariance in the appearance of seedlings was observed.

Juveniles (Fig. 3*B*). Plants move into the juvenile phase of development when the first real leaves appear. Leaves are opposite, the laminae are pubescent, about 7 mm long and 5 mm wide, oblong or ovate, with large pinnatisect edges (usually two segments); lower segments are set aside, so that the lamina acquires a tripartite structure; the veining is pinnate-meshed, the top is acuminate, the bottom is wedge-shaped, turning into a short about 5 mm long petiole. Cotyledons by this time reach the final dimensions, their laminae are 7 mm long and 5 mm wide;

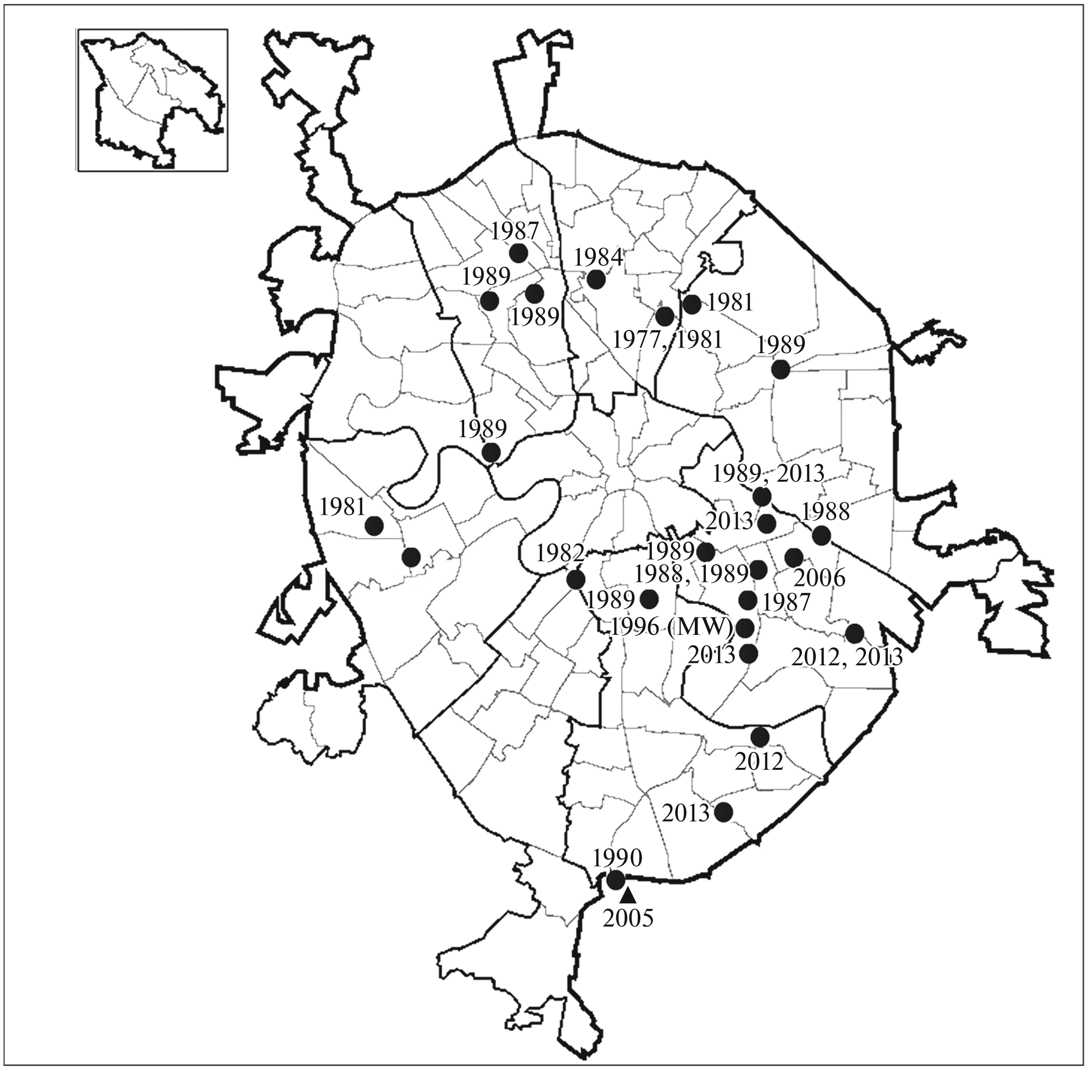

Fig. 1. Distribution of *Ambrosia artemisiifolia* (●) and *A. trifida* (▲) plants on the territory of the Moscow (within its old borders) according to the results of the study of the herbarium of the Tsitsin Main Botanical Garden, Russian Academy of Sciences (MHA). Findings from the herbarium of the Moscow State University, not duplicated in the MHA, are marked on the map as MW.

petiole is about 2 mm long. The first one is followed by a second pair of juvenile leaves. The shoot is up to 2 cm high by this time, with a distinctly pronounced epicotyl and the first real internode. The second pair of juvenile leaves have 1.2 cm long and 1.2 cm wide lamina, which is simple pinnate with two side segments; the petiole reaches 7 mm in length. At the occurrence of the third–fourth pair of leaves of transition type, the plant enters the immature period of development. The main root of juveniles is about 5–7 cm long and will branch intensively up to the first order. The longest roots, up to 6 cm long, are located on the root neck.

In this phase of development, most individuals were present by May 25. In the population, there was a significant polyvariance in the timing of transition to the juvenile phase of development, which is associated with different dates of germination.

Immature plants (Figs. 3*C* and 3*D*). Immature plants are characterized by the appearance of more complex dissected leaves with 3–4 lateral segments, the lower of which become incised, which is typical of the third or fourth pair (Fig. 3*C*). Cotyledons are dying when they get to this age state. The growth rate of shoots and stretching of internodes are increased significantly. By the middle of the immature phase of development, the shoot is clearly elongated, up to 40 cm high, with densely pubescent internodes and 5–7 pairs of opposite leaves, the lower ones of which are of juvenile type (Fig. 3*D*). The third pair of leaves is of the transition type, with pubescent lamina, 3 cm long and 2.5 cm wide, and the laminae are simple pinnate with three pairs of lateral segments; the lower ones of which are notched. Leaf lamina of upper leaves are pubescent, pinnately dissected, with 4–6 pairs of segments, the lower of which are pinnately dissected. Petioles are

Fig. 2. Distribution of *Ambrosia artemisiifolia* (●) and *A. trifida* (▲) plants on the territory of Moscow oblast.

half the length of the lamina. The main root is white, up to 8 cm long, with a diameter of about 0.1 cm at the base, and thinner below. The lateral roots are of the 1st order only, long, white, the largest number of them develops on the root neck.

In this phase of development, most individuals were present by June 20. In the population, there was a significant polyvariance in the timing of transition to the immature phase of development, which is associated with different germination periods.

Virginal plants (Fig. 3*E*). In this developmental phase, the leaves unfold in turn, so that the change of phyllotaxis from the opposite to the spiral can be a criterion for transition from one age state to another. The structure of these leaves is similar to that of the definitive leaves. Leaf laminae are pubescent, 8.5 cm long and 6 cm wide, oblong-ovoid or ovate in general, double pinnatisected, with 6–8 lateral segments of the first order, the lower of which are also pinnately dissected. Veins are pinnate-meshed. Petioles are 4–4.5 cm long. The lower two or three pairs of the opposite leaves begin to dry out. The shoot is elongated, about 45 cm long, and usually has up to 9–13 internodes by the end of this phase. In this age state, lateral shoots from the buds of the upper leaves begin to be realized, which so far only reach the vegetative phase of development. The main root is about 7 cm long, branching out to the second order. The longest roots are located near the root neck, many of which lie horizontally in the near-surface soil layer. All the roots are brown, covered with suber. The boundary between the virginal phase of development and the subsequent generative is morphologically indistinct, since the external vegetative appearance of the apex can begin to lay floral structures.

At this developmental phase, most of the individuals were found in July and by August 1. In the population, a significant polyvariance by the dates of transition to the virginal developmental phase was observed, which is connected with different dates of germination.

Generative period (Figs. 3*F* and 3*G*). The transition to the reproductive period begins with the appearance of the first flower primordium at the shoot apex. As the development of the inflorescence continues, how-

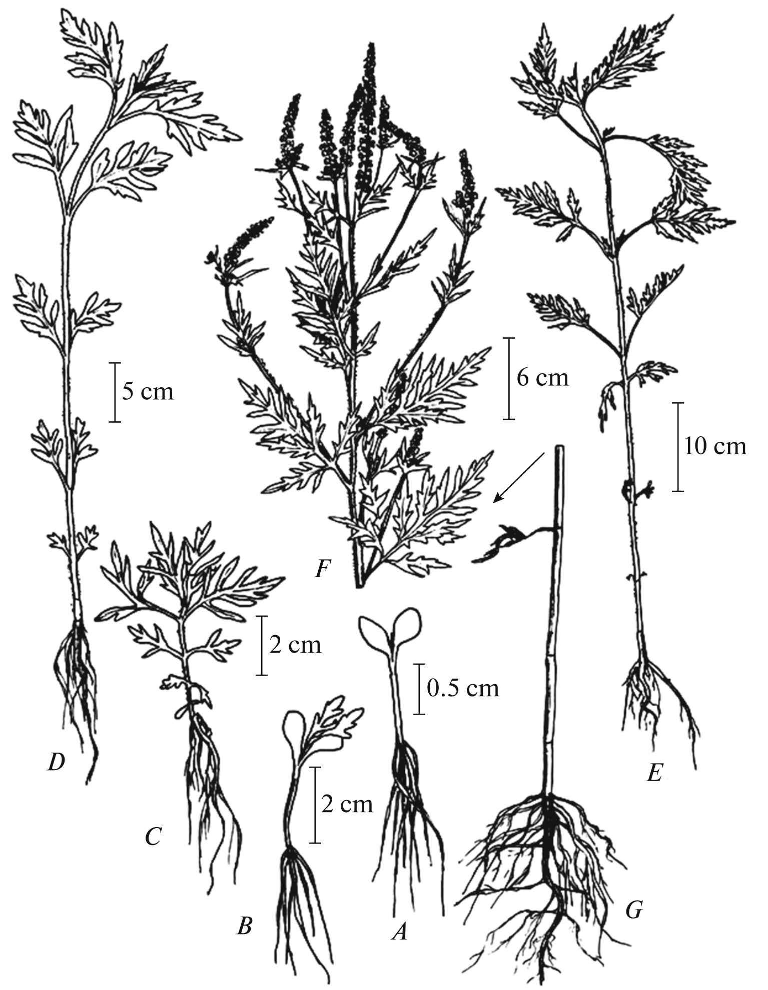

Fig. 3. Morphological features of *Ambrosia artemisiifolia* plant: (*A*) seedling; (*B*) juvenile plant; (*C*) immature plant in the early stages of development; (*D*) plant at the end of immature stage; (*E*) virginal, or adult, vegetative plant; (*F*) generative plant, the inflorescence; (*G*) lower part of the generative plant.

ever, many plants in our population were at the beginning of this stage even by September 20. As with most plants, *A. artemisiifolia* in this period can be distinguished by a phase of budding (by September 10–15), flowering (until the end of October), and fruiting with a stage of immature and fully ripe fruits. The beginning of active axillary branching coincides with floral differentiation. The shoot is elongated, 78–105 cm tall on average, bristly pubescent; its branching is mesotonic, rarely basimesotonic, and the longest on a fully developed generative shoot are the middle lateral branches.

The degree of branching depends on the conditions of growth; often lateral branches are formed starting from the third to fourth node. Up to the terminal inflorescence, 16 metamers are formed. Starting with the seventh metamer, the phyllotaxis usually changes to an ordinary or mixed arrangement. Leaf laminae of middle leaves are pubescent, 9–11 cm long and 8–10 cm wide, twice pinnatisected with 5–6 lateral segments of the first order, the lower of which are pinnately separate, and petioles are about 2.5 cm long. The lowermost metamers are leafless, as the leaves die on them at previous stages of development.

A. artemisiifolia is a monoecious plant, has unisexual, pistillate, and staminal flowers on the same individual. Each fully developed flower-bearing lateral shoot, or paraclady, includes at the base a female zone of several nodes with small (compared to the leaves of the main axis) pinnate covering vegetative leaves and female flowers, and a male terminal, consisting of a long brush without covering leaves. In the intermediate zone between the collection of male and female flowers in the most developed paracladiae, there may be an area of branching, where from the axils of covering leaves lateral shoots, or paracladia, of the second order, come out, having a structure similar to the maternal floral axis. The main axis of the branched out shoot usually ends with the most developed and longest brush only from male reproductive structures, at the base without female zone.

Female and male flowers are grouped into unisexual partial inflorescences (elementary floral units). Female partial inflorescences are single-flower baskets. The latter are grouped into more complex groups, arranged according to the type of complex dichasium, in which the first basket with the most mature flower is located in the center, on the sides of it in the axils of simple ovate flowers—on a single-flower basket of the second order, on the sides of which there are opposite floral bracts with the youngest axillary baskets of the third order. Such complex dichasia are located in the sinus of covering leaf of the maternal axis. Sometimes there is a whorl of three lateral dichasia around the main basket; in some cases there is not one, but two central baskets. Apparently, in the more successful southern populations, the collection of female baskets can be even more complex. Female flower is naked, enclosed in a long 3–5 mm, ovate, and narrowed at the top into a nose wrapper, in the middle part of the circle with 5–8 somewhat fleshy teeth, in the lower part with a rare bristle pubescence. The ovary is rounded and turns into a column, which is divided into two long stigmas. As the fruit ripens, the wrapper is solidified.

Male partial inflorescence is a multifloral (from 5–25 flowers) basket of 2.5–4.5 mm in diameter, surrounded by an integral, slightly toothed edge, with a rare, fine bristly pubescence, cover. The most mature flowers are on the periphery of the basket, and the youngest are in the middle. Male baskets are assembled at the top of the flower-bearing axes in a long spike-like racemes; they sit on short shoots, at the base of which there are no covering leaves. Male flowers with a diameter of 2–5 mm consist of a corolla tube, at the end of a five-toothed one, and 5 stamens with large anthers enclosed inside. Above the anthers, ovoid, peaky, flat stamen binders hang, covering them like a visor. There is also a strongly reduced ovary, which turns into a thick, short or equal in length to the length of the corolla tube, fringed column at the end.

The main root of the generative plant is short, brown, and branches up to the third order; the lateral roots are long, often outgrow the main one, and actively branch out. There is evidence in the literature that the root can penetrate to a depth of 4 m (*Chernaya kniga*..., 2009).

The final stage of the generative period—fruiting—occurs in late October—November; in Moscow oblast, many individuals did not have time to move into it, most likely because of the early onset of cold weather in 2015. In some female baskets, the fruits (multiple fruits) began to form, but they did not reach full maturity by the end of the growing season; that is, they did not go into a phase of maturity. Fruits harvested in November from the most complete specimens did not germinate. By November, most of the middle formation leaves had dried up, and with the onset of really cold weather, the stems began to bend to the ground, and with the beginning of winter, the plants completely died.

Ambrosia trifida

Virginal period, seedlings (Fig. 4*A*). Aboveground germination is hypocotyllar. Hypocotyl carries two assimilating seedlings quite high above the soil surface. Cotyledons have short petioles. Their laminae are naked, about 8 mm long and 6 mm wide, ovately rounded, all-edged, sometimes with slightly emarginate apex, intensively green, somewhat fleshy, so that lateral veins from the surface do not seem to stand out. Petioles are 1.5–3 mm long and about 1 mm wide. Hypocotyl in a fully developed seedling can reach 1–2 cm in length and about 1–1.5 mm in diameter; its upper part is usually located above the ground and has a pinkish purple anthocyanin color; the lower underground part is whitish. The main root is white, about 3–4 cm long, with the base up to 1 mm in diameter, and below it is sharply thinned to 0.5 mm. Usually the first lateral roots begin to appear at this time, the largest number of which is laid on the root neck.

In this developmental phase, most individuals were present by May 1–10. In the population, a significant polyvariance in the dates of appearance of seedlings was observed.

Juveniles (Fig. 4*B*). The first real leaves are opposite, located on the distinctly pronounced pubescent epicotyl. Shoot height at the end of stage is 3–3.5 cm. Laminae are pubescent, 1.7–2 mm long and 1.2–1.5 cm wide, oval-shaped, along the edges with two toothed notches, the lower ones slightly set aside, with a rounded whole tip and a wedge-shaped base, turning into a short petiole, about 6–10 mm long. The veins are pinnate-meshed; the lateral veins are not visible. At this stage, cotyledons reach their final sizes with laminae about 1.2 cm in length and 1 cm in width, and a petiole is about 7 mm in length. The main root branched out quite intensely. Lateral roots of the first order prevail and some of them begin to form second order roots near the apex. The greatest number, up to 15 lateral roots, is located on the root neck; they can reach a length of 8–15 cm. By the end of this age stage, another pair of real leaves develops. The latter have a triple-edged lamina at the bottom of the leaves, about 3.8 cm long and 2.3 cm wide, with a longer and more distant proximal lobe; along the edge, they are toothed, with a sharp tip and a wedge-shaped base that turns into petioles about 1.5 cm long.

In this phase, most individuals were present by May 16. In the population, a significant polyvariance by the dates of transition to the juvenile phase of devel-

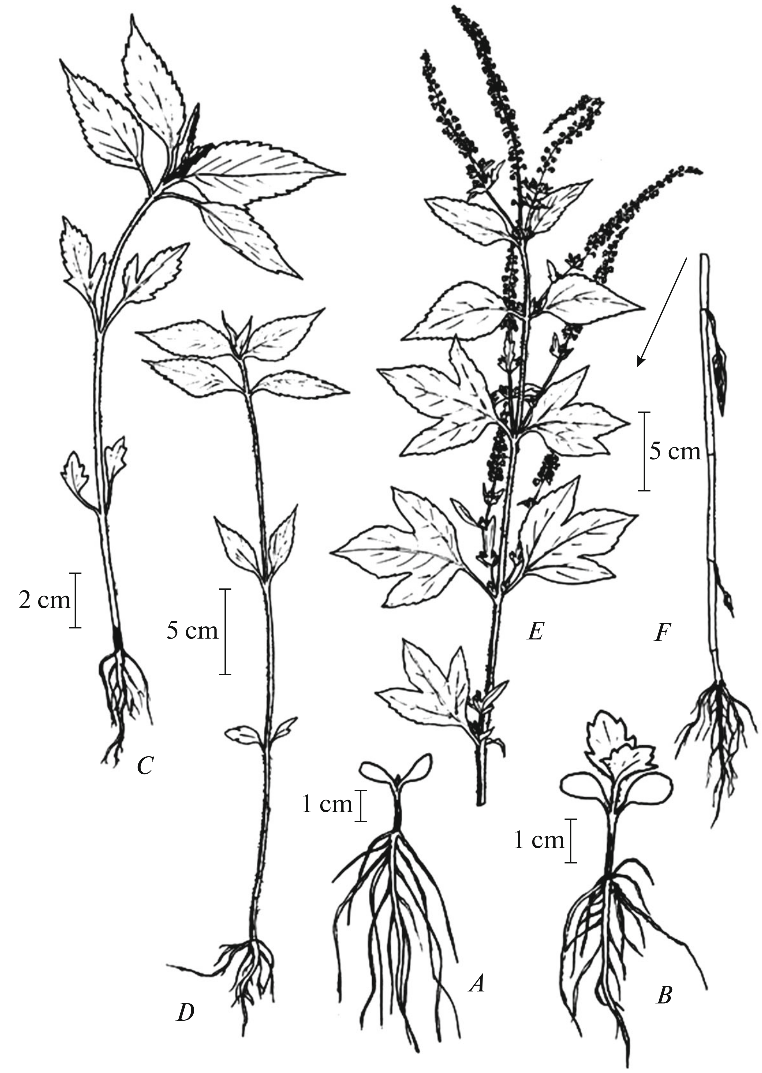

Fig. 4. Morphological features of *Ambrosia trifida* plant: (*A*) seedling; (*B*) juvenile plant; (*C*) immature plant; (*D*) virginal, or adult, vegetative plant; (*E*) generative plant, the inflorescence; (*F*) lower part of the generative plant.

opment was observed, which is connected with different dates of germination.

Immature plants (Fig. 4*C*). In this age group, leaves of a definitive type appear, usually the third pair of real leaves. They are pubescent, oblong-ovoid or broad lanceolate; they have a lamina serrated toothed along the edge, with pinnate-meshed vein, with a sharp tip and a wedge-shaped base, 6.5 cm long and 2.5 cm wide, and a short petiole of about 1.3 cm. The cotyledons are dying, and by the middle of the immature stage they are not visible. At this stage of ontogenesis, the shoot is strongly expanded out in length, especially in plants of a strongly thickened population. All internodes of the shoot are pubescent with whitish hairs, lengthened, usually in number of four by the end of the period. Buds are laid in the axils of all leaves.

This is the phase where the specimens pass by July 1. In the population, there was a significant polyvariance in the timing of transition to the immature phase of development, which is associated with different dates of germination.

Virginal plants (Fig. 4*D*). In this phase, plants usually have 4–5 upper pairs of live opposite leaves, the lower ones of which are yellowed, beginning to die, and 3 lower leafless nodes with dead juvenile leaves and cotyledons. Leaf laminae of the upper leaves are pubescent, 5–5.5 cm long, oblong or broad lanceolate, coarse toothed along the edge, with a pinnate-meshed veining, with a sharp tip and a wedge-shaped base that turns into a short petiole 0.8–1 cm long. Leaf structure variation was observed in the studied population; in particular, some individuals developed triple-bladed leaves on the seventh–eighth metamers.

The shoot is elongated, about 32 cm long. The main root is 12 cm long; the root neck has a chairlike inflection. Branching is observed up to the second order; the longest roots are located near the root neck. All the roots are brown, covered in cork.

The greatest number of individuals in this phase of plant development were obtained in July. In the population, a significant polyvariance in the dates of transition to the virginal phase of development was observed, which was connected with different dates of germination.

Generative period (Figs. 4*E* and 4*F*). The transition to the reproduction phase begins with the appearance of the first flower primordium at the apex of the shoot. As in the previous species, *A. trifida* in this period can be identified as having a phase of budding (most by August 1), flowering (most by August 7, the longest phase depends on the number of paracladiae), and fruiting with a stage of immature (early September) and fully formed fruits (by September 20 and until the end of October).

Floral differentiation coincides with the beginning of active axial branching. Shoot is elongated, rarely bristly pubescent, about 47 cm long, and is lignified at the end of this period at the root neck. The main root is 9–15 cm long, brown, and branches up to the second order, and in the root neck, it also becomes woody.

At the earliest stage of generative development, the plant has up to 4 pairs of normally developed upper opposite leaves, and the lower ones are yellow and usually withering; basal metamers are leafless, because the leaves die on them at the previous stages of development. Lateral shoots with 2–3 undeveloped metamers are clearly visible in the leaf angles of two to three middle pairs of leaves. Lateral shoots with inflorescences begin to appear in the axils of the uppermost leaves close to the terminal inflorescence. Leaf laminae of such leaves are oblong-oval, rarely pubescent from above and more densely bristly pubescent from below, about 11 cm long and 4–4.5 cm wide, toothed along the edge of leaf, with a pinnate vein, sharp pulled-out apex and wedge-shaped base, 1.5–2 cm long, slightly winged at the expense of the marginal part of the leaf. Variations in the leaf structure of the studied artificial population were rarely observed in the studied population, and the same is confirmed by the study of herbal specimens: often definitive leaves become triple-bladed with very large, lateral, put-aside laminae.

As the flowers continue to grow, there is a complete differentiation of flowers in the terminal inflorescence and extension of metamers, as well as the establishment of floral primordium on the lateral shoots (paracladia). Formed shoot with the height of about 116 cm, up to the terminal inflorescence has 8 metamers, all leaves are opposite, and only 4 upper pairs among them are live leaves. Shoot branching is mesotonic, with the longest median paracladiae on the fully developed generative shoot having 3–4 pairs of leaves of median formation up to the apical brush, in the leaf angle of which inflorescences also develop. The shortest of the lateral paracladiae, which are the first to lay inflorescences and do not have large developed leaves, are those adjacent to the terminal brush. In the studied population, changes in the morphogenesis of the shoot occurred as follows. By August 2, we had observed individuals at the earliest stage of their generative period that had just begun to develop cone-shaped male inflorescences: terminal (only 1–2 cm long) and downstream pair (7 mm long). By August 16, many individuals had a long, fully developed male terminal brush with baskets, in which the edge flowers were dusty and the central ones were in the bud phase, and with the only fully developed paracladia, both male and female, and the rest of the lateral inflorescences were in their embryonic state, most of them only with female baskets.

A. trifida, as well as *A. artemisiifolia*, is a monoecious plant with unisexual, pistillate, and staminal flowers on one side of the specimen. The reproductive area is similar to that of the previous species. Female and male flowers are grouped into unisexual partial inflorescences. Female partial inflorescence is a single flower basket, 2.5–5.5 mm long and 1–3 mm wide; sometimes, a second underdeveloped flower can be found. The baskets are aggregated into more complex of dichasial type located in the axil of the covering leaf of the main axis. Morphologically, the covering leaves of the baskets differ from the underlying median ones in that they have a narrower lamina of a smaller size. In such complexes, the central flowers are the first to be laid and developed, and the side flowers at the base have paired floral bracts. Female flower is naked, dressed in an ovate wrapper, pulled from above into a fringed nose at early stages of development, and along the perimeter in the middle part has 6–8 teeth. The oval ovary, narrowed to the bottom, about 1.5 mm long, goes into a short column, divided into two long stigmas. Male partial inflorescence is a multifloral basket, 4–4.5 mm in diameter, surrounded by a cup-shaped wrap, on the edges with wide teeth, with five veins, outside bristly pubescent. The most mature flowers are on the outside, on the edges of the basket, and the youngest ones are in the center. Male baskets are collected at the top of the flower-bearing axes in a long brush, without covering leaves at the base of the basket stem. Male flowers are actinomorphic and consist of a corolla expanding to the top, along the edge of a correctly five-toothed tube and five stamens with threads and large anthers covered with stamen binder from above growing at the base of the corolla tube. There is also a highly reduced ovary, which turns into a thick, short or equal in length to the length of the corolla tube column.

The final stage of the generative period is fruiting. By this time, many leaves of the median formation dry up. Male baskets also die and fall off, often leaving only the basket stems on the long axis of the brush. In the female reproductive sphere, fruits are being formed. Fruit is an obovate seed, enclosed in a woody wrapper about 9–11 mm in length (in fact, it is an infructescence). At the top of the cover, there is a clearly expressed spinelet (rostel); along the edges, there are 4–8 less developed spinelets, from which the convex ribs go down to the base; in the mature state, the seeds closely merge with the cover and it is difficult to separate them. In the artificial populations we studied, many individuals successfully entered the phase of full ripening of fruits. This stage in a number of selected individuals occurred by September 20. Seeds had time to be fully formed before the frosty weather and then, after sowing them in boxes with soil toward the winter, to give the next year good and even plantlets. With the onset of cold weather, the plants in the studied population began to dry out; their shoots bent to the ground and died at the beginning of winter.

DISCUSSION

As a result of the study of ontogenesis of two quarantine invasive species of ragweed—*A. artemisiifolia* and *A. trifida*—different age groups were characterized and the criteria of the main age groups were identified. In the virginal period of development, seedlings, juveniles, immature and virginal plants are described; in the generative period, plants are considered in the phase of budding, full anthesis, and fruiting. The data obtained can help to identify species at different stages of development and to take timely action to eliminate them. It is shown that both *A. artemisiifolia* and *A. trifida* germinate well after sowing freshly harvested seeds into the soil toward winter and develop normally in the north of Moscow oblast. However, the rate of development and morphogenesis of the two species varies, affecting the timing of flowering and maturation of fruits. Despite the fact that both plants are long-lasting vegetative annual plants with late blossoming and autumn tying of fruits, *A. artemisiifolia* is distinguished by a greater number of metamers and leaves on the shoots, as well as by a greater intensity of branching and, in general, a longer development time from germination to fruiting as compared to the early-ripening *A. trifida*. As a result, *A. artemisiifolia* does not have time to form ripe fruits, so that the collected seeds in autumn are not able to germinate in Moscow oblast, while *A. trifida* in this region forms ripe fruits and seeds with high germination. In general, in our experiment, the duration of the virginal period for *A. artemisiifolia* was about 120–140 days, and for *A. trifida*, it was about 90 days; the generative period for *A. artemisiifolia* was more than 90 days, and for *A. trifida*, it was about 80 days. In the south of the country, in the conditions of Adygea, the terms of prematurity of *A. artemisiifolia* are approximately the same, while germination begins a month earlier (in April), and the generative period lasts slightly less—about 60 days, and the plants have time to form fully mature seeds (Vasiliev, 1959). In Novocherkassk district of Rostov oblast, *A. artemisiifolia* shoots appear from the end of April to July; most of the shoots (up to 75%) occur in the second half of May, as in our case; flowering occurs in the second half of July and continues until October, and fruiting occurs from August to November and later (Bezruchenko and Chukarin, 1956). In Primorsky krai, the duration of the growing season for *A. artemisiifolia* is about 150 days (Moskalenko, 2001). In Canada, up to 90% of shoots appear by mid-June, flowering begins by August 7, and mature seeds appear in late August and early September (Bassett and Crompton, 1975), i.e., much earlier than in Moscow oblast. Bassett and Crompton (1975) showed that, in Canada, *A. artemisiifolia* is adapted to different day lengths, with more northern plants blossoming earlier and having a shorter vegetative period. Seedlings of *A. trifida* in Canada appear in March, April, or early May; blossoming begins in mid-July and lasts until late August or early September (Bassett and Crompton, 1982), as in the conditions of Moscow oblast.

The analysis of the literature and herbarium collections shows that, in the most fully studied Vladimir oblast, where the findings of *A. artemisiifolia* are quite common, the species is not retained in nature, and the new records are associated with the re-entry of seeds from the southern regions (Seregin, 2012). Here, as in our study in Moscow oblast, the species is not capable of self-renewal because of the late flowering dates (September–October), so that the fruits do not have time to mature as a result of the onset of cold weather (Seregin, 2010). This situation should probably be observed in all regions above 50°–55° N (outside the potential range) (Abramova, 1997). When we studied the herbarium, however, we noted an interesting specimen from the Ryazan oblast (Kasimov City): this is a low-length specimen (with only seven pairs of leaves), which is in full bloom at the beginning of August (while other specimens from the same region were still at the stage of buds or vegetation). The presence of super early forms from more southern regions is also repeatedly mentioned. In particular, D.S. Vasiliev discovered the following forms in the Krasnodar krai: seed maturation began in the first ten days of August. Just as dangerous as the super early form, the purely female specimens form only pistillate flowers. According to Vasiliev, such specimens can have whole bunches of seeds and productivity can reach 150000 seeds per plant, while the usual forms generate 1000 to 25000 seeds (Vasiliev, 1959), and in the least favorable conditions, they generate only from 5–13 to 96–118 seeds (Maryushkina, 1986). It follows that the reduction of the periods of development, a decrease in vegetative mass, earlier reproduction, and the formation of purely female individuals can potentially be a mechanism for stabilizing the species in high latitudes. Another important feature of *A. artemisiifolia* species, which opens up possible prospects for naturalization, is the ability of its seeds to move to a state of secondary biological dormancy, which, according to some reports, may range from 5–14 to 40 years (Maryushkina, 1986). In Moscow, the possibility of seed maturation and the presence of a seed bank of the species is indirectly confirmed by repeated records made in the same area (V.D. Bochkin, Moscow, Kursk Railway, near the Textilshchiki platform, 1987, 1988, 1989; MHA) and collection of specimens with mature fruits (V.D. Bochkin, Moscow, Okruzhnaya Railway, branch from the Testovskaya platform, November 7, 1989; MHA). The analysis of herbarium collections indicates that the main carrier of *A. artemisiifolia* fruits from the southern regions for a long time was the railways. However, in recent years, owing to the mass use of herbicides, ragweed plants on the railways have become rare (*Chernaya kniga*..., 2009; Mayorov et al., 2012).

The distribution of *A. trifida* seeds in the northern regions of Central Russia, judging by herbarium samples, is connected not only with railways, but mainly with wheel transport as well as with transport and processing of cereal crops. The most complete and regular collections made in Vladimir oblast indicate the possibility of annual seed self-renewal and the formation of stable, expanding populations (Seregin, 2010). This is due to earlier flowering dates (July–August) and successful ripening of fruits, which was revealed by us in the experiment with plants in Moscow oblast. Analysis of fresh collections from Penza oblast (Sukhorukov, 2010) (MW) indicates that the species can form mass accumulations, easily penetrating secondary vegetation groups emerging in the meadows and in floodplain communities. Monitoring of the distribution of *A. trifida* plants in the Republic of Bashkortostan showed (Abramova, 1997) that, within 10 years after the first invasion, the species became naturalized in ruderal communities and continued to actively expand its range. In many cases, *A. trifida* plants here occupied the first layer and displaced the native species to the lower one; at the same time its thickets could reach 1.5–2 m in height, and the plants formed a significant amount of seeds, which contributed to the further distribution of the species and the conquest of new spaces. As a result, the dominance of *A. trifida* species in some southwestern regions of Bashkiria has led to the formation of so-called derivative communities, i.e., communities in which atypical species dominate against the background of the usual floral combination (Abramova, 1997).

CONCLUSIONS

On the basis of our results, as well as the literature, we can assume that, despite the rarity of the findings of *A. trifida* plants in Moscow and Moscow oblast, the species can potentially prove to be a very dangerous invasive plant for these strategically important regions, capable of occupying significant territories in disturbed and natural communities in the event of mass overwintering of diaspores and forming stable self-renewing populations similar to those observed in *A. artemisiifolia* in southern regions (Abramova, 1997; *Chernaya kniga*..., 2009). Movement of *A. artemisiifolia* plants northward is more problematic; however, given the broad adaptive potential of the species, including the shortening of the development cycle, the formation of super early and female forms, etc. (Vasiliev, 1958; Abramova, 1997; Leiblein-Wild and Tackenberg, 2014), it can be assumed that its naturalization in Moscow oblast and a number of other northeastern regions is also possible. In this regard, it is necessary to monitor the breeding locations, abundance, distribution, and modification variability of both species.

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CONFLICTS OF INTEREST

The author declares that he has no conflict of interest.

COMPLIANCE WITH ETHICAL STANDARDS

The article does not contain any research with participation of live animals in the experiments performed by the author.

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