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Original Article

Ecological condition and invasiveness of *Fraxinus pennsylvanica* in different ecotopes of the arid Caspian region

Condição ecológica e invasividade de *Fraxinus pennsylvanica* em diferentes ecótopos da região árida do Cáspio

M. K. Sapanov[a,b], M. M. Elekesheva[b*], M. L. Sizemskaya[a] and A. V. Kolesnikov[a]

[a]Institute of Forest Science of the Russian Academy of Sciences, Uspenskoe, Moscow region, Russia
[b]Zhangir Khan West Kazakhstan Agrarian Technical University, Uralsk, Kazakhstan

Abstract

The study investigated ash development in an arid region, focusing on its invasive spread mechanisms at organismic and ecosystem levels under varying moisture conditions. Conducted in the Northern Caspian region's Volga-Urals interfluve, it examined the effects of arid climate, soil salinity, and limited moisture on plant communities. The features of ash functioning at the organismal and ecosystem levels with permanent and partial deficiency of productive moisture in the soil, as well as with its optimal availability, were investigated. It is shown that on automorphic soil types, ash cultures, subject to appropriate forestry technologies, can exist for many decades even during periodic soil droughts due to premature harmless dumping of leaf mass. In hydromorphic floodplain conditions, ash is not only well preserved in cultures, but also effectively introduced into meadow and forest ecosystems by lowering the relief. Trees in a new place, especially in meadows, begin to bear fruit after 6-10 years and spread the seeds to other territories. Such a nomadic strategy of stepwise dispersed multiple dispersal of ash contributes to the rapid formation of its secondary invasive areas and eliminates the possibility of effective control against it. Therefore, the use of ash in industrial plantings in floodplains is highly inadvisible.

Keywords: arid region, forest cultures, Pennsylvania ash, seed renewal, seed spreading, invasion, secondary habitat.

Resumo

O presente estudo investigou o desenvolvimento do freixo da Pensilvânia em uma região árida, concentrando-se nos mecanismos de sua propagação invasiva a nível organísmico e ecossistêmico, sob condições variáveis de umidade. Realizado no interflúvio Volga-Urais da região norte do Cáspio, foram examinados os efeitos do clima árido, da salinidade do solo e da umidade limitada nas comunidades vegetais. As características do funcionamento do freixo a nível de organismo e de ecossistema foram investigadas tanto em relação à deficiência permanente e parcial de umidade produtiva no solo, quanto a sua disponibilidade ideal. Foi possível observar que culturas de freixo sujeitas a tecnologias florestais apropriadas podem existir por muitas décadas em solos não-hidromórficos, mesmo durante secas periódicas, devido ao seu processo de desfolha precoce e inofensiva. Além de apresentar uma boa adaptação em culturas com condições de solos hidromórficos em planícies aluviais, a introdução do freixo em ecossistemas de prados e florestas é igualmente bem-sucedida após a nivelação do relevo. Árvores plantadas em um novo local, especialmente em prados, começam a frutificar após 6-10 anos e assim disseminam suas sementes para outros territórios. Tal estratégia nômade de dispersão múltipla e gradual contribui para a sua rápida invasão de áreas secundárias e elimina a possibilidade de um controle eficaz contra o freixo. Portanto, o plantio de freixo em cultivos para fins industriais em planícies aluviais é altamente desaconselhável.

Palavras-chave: região árida, culturas florestais, freixo da Pensilvânia, renovação de sementes, propagação de sementes, invasão, habitat secundário.

1. Introduction

Fraxinus pennsylvanica Marsh. growing naturally in North America has been introduced long ago into the landscapes of Europe and Asia. Its usage in cultures is conditioned by good survival in different habitat conditions. However, its capacity to form an invasive habitat, especially in floodplains, is alarming. At the same time, the mechanisms of its introduction and spread on different types of soils are poorly covered in the literature (Kennedy Junior, 1990; Csiszár and Bartha, 2004; Dudkin and Ivanov, 2014; Drescher and Prots, 2016; Mayer et al., 2017; Campagnaro et al., 2018; Vicherek et al., 2000; Grigorèvskaya et al., 2013; Kholenko and Semenishchenkov, 2021; Rode, 1961).

*e-mail: elekesheva@inbox.ru
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The available publications provide certain aspects of the life strategy of its existence: information on the territorial occurrence, age and taxation structure of stands, high reproductive capacity, features of seed germination, structure of root systems, damage to stands by xylophages (Dudkin and Ivanov, 2014; Drescher and Prots, 2016; Mayer et al., 2017; Campagnaro et al., 2018; Vicherek et al., 2000; Grigorèvskaya et al., 2013; Rode, 1961; Knight et al., 2013; Orlova-Bienkowskaja, 2013; Burr and McCullough, 2014; Darbaeva and Chukalina, 2011; Darbaeva et al., 2020). It is worth noting in particular its weak salt resistance, good tolerance of summer droughts and short-term flooding (Kholenko and Semenishchenkov, 2021; Orlova-Bienkowskaja, 2013; Tselniker, 1960; Gomes and Kozlowski, 1980; Tang and Kozlowski, 1984; Abrams et al., 1990; Izhevskii and Mozolevskaya, 2010; Sapanov, 2003, 2010).

In arid regions, on treeless zonal soil types, the cultivation of trees and shrubs is possible only if they are provided with additional soil moisture due to snow accumulation, surface inflow of meltwater and stormwater, or the availability of fresh groundwater (Galkin et al., 2023; Asadulagi et al., 2024), whereas for the native herbal phytocenoses growing here, an insignificant reserve of accumulated autumn-winter moisture in the soil is sufficient, and when exhausted, plants can end their seasonal growth with the death of the aboveground part already in the middle of summer (Olovyannikova, 2004; Sizemskaya et al., 2009; Sapanov and Sizemskaya, 2020).

In the Caspian lowland between the Volga and Ural rivers, Pennsylvania ash has been widely used in protective afforestation since the middle of the XX century. At the present stage, few cultures have been preserved on zonal soil types; the best of them are located at the Dzhanybek Research Station of the Institute of Forest Science of the Russian Academy of Sciences, and in the intrazonal conditions of river valleys they are ubiquitous. In floodplains, the condition of ash cultures is much better, moreover, there is an intensive penetration of self-seeded ash specimens into native ecosystems.

The purpose of our investigation is to present a summary and identify the features of the state and development of ash in the arid region at the organismic and ecosystem levels in different conditions of soil moisture supply in order to reveal the main mechanisms of formation of the secondary invasive area.

2. Materials and Methods

2.1. Natural and climatic conditions of the study area

The research was carried out in the interfluve of the Volga and the Urals within the Northern Caspian region. The diversity of zonal landscapes is regulated there by the aridity of the climate, the salinity of soils (the former bottom of the Caspian Sea) and the degree of availability of productive moisture to plant phytocenoses, which is provided here only by meager atmospheric precipitation and their redistribution over the area. The existing intrazonal conditions with natural forest ecosystems are confined to the valleys of the lower reaches of the Ural River and the Volga-Akhtuba floodplain.

2.1.1. Climate

The climate of the region is sharply continental, with dry hot summers and little snow, cold winters, often with strong winds. The average air temperature is +7.1 °C, in winter months it can drop to -41 °C, in summer it can rise to +40 °C. The average annual precipitation is 300-350 mm, which falls almost equally in the cold and warm periods of the year, with the evaporation rate of the growing season about 900 mm (Nikitin, 1957; Doskach, 1979).

2.1.2. Characteristics of zonal automorphic soil types

The research was carried out at the Dzhanybek Research Station of the Institute of Forest Science of the Russian Academy of Sciences (49.3980°N, 46.7960°E), which was established in 1950 on the border of Russia and Kazakhstan (Figure 1A). The research station territory (about 1,500 hectares) is representative of the landscapes of the subboreal semi-deserts of the Northern Caspian region with a total area of about 2.9 million hectares. According to the botanical and geographical zoning, it belongs to the Volga-Kazakhstan province of the Eurasian steppe region, to the district of desert pyrethrum- and white wormwood-turf-grass steppes (Doskach, 1979).

The flatness of the heavy-loamy territory is disturbed by local saucer-shaped meso- and micro-depressions, which determine the shallow contour and complexity of the soil and vegetation cover. On microelevations (the main territory), solonchakous solonetzes with desert vegetation were formed, light-chestnut soils with dry-steppe vegetation on microslopes, meadow-chestnut (dark-colored chernozem-shaped) soils with steppe grasses in micro- and mesodepressions (flat-bottom steppe depression) of the relief.

Groundwater, saline to 7-10 g/l, lies at a depth of 5-6 m. The thickness of the capillary fringe of groundwater is about 2.5 m. Only in the mesodepressions there are fresh water lenses that have a common water table with saline groundwater (Olovyannikova, 2004; Kamenetskaya, 1952; Rode and Polskii, 1961; Gordeeva and Larin, 1965).

The first object of research in this area are forest strips with ash trees, which are grown on reclaimed solonchakous solonetzes. Here, the root systems of trees are located in soils that have previously been reclaimed by reclamation plowing and washed from easily soluble salts. The thickness of the root-inhabited soil layer does not exceed 100 cm (Figure 2A, B) (Bazykina and Olovyannikova, 1996; Sizemskaya, 1996).

To increase the water supply area of each tree, they were planted in the form of several single-row forest strips at a distance of 6-10 m from each other, and wide aisles are plowed annually to destroy weeds.

The second object is plantations grown on meadow-chestnut soils in the form of small closed multi-row arrays. Here, the entire soil profile down to the fresh water lens does not contain toxic salts (Figure 2C), so ash trees can already partially use water from its capillary fringe. Exactly partially because ash trees have a shallow root system and do not penetrate deeper than 300 cm into the soil, whereas tree species with anchor roots (oak, poplar, elm) form a second layer of conductive and sucking roots in the capillary zone and use this water in full measure (Rode, 1961; Sapanov, 2003).

Figure 1. Locations of key sites with Pennsylvania ash: (A) on a native treeless plain territory; (B) in the valley of the floodplain of the Ural River.

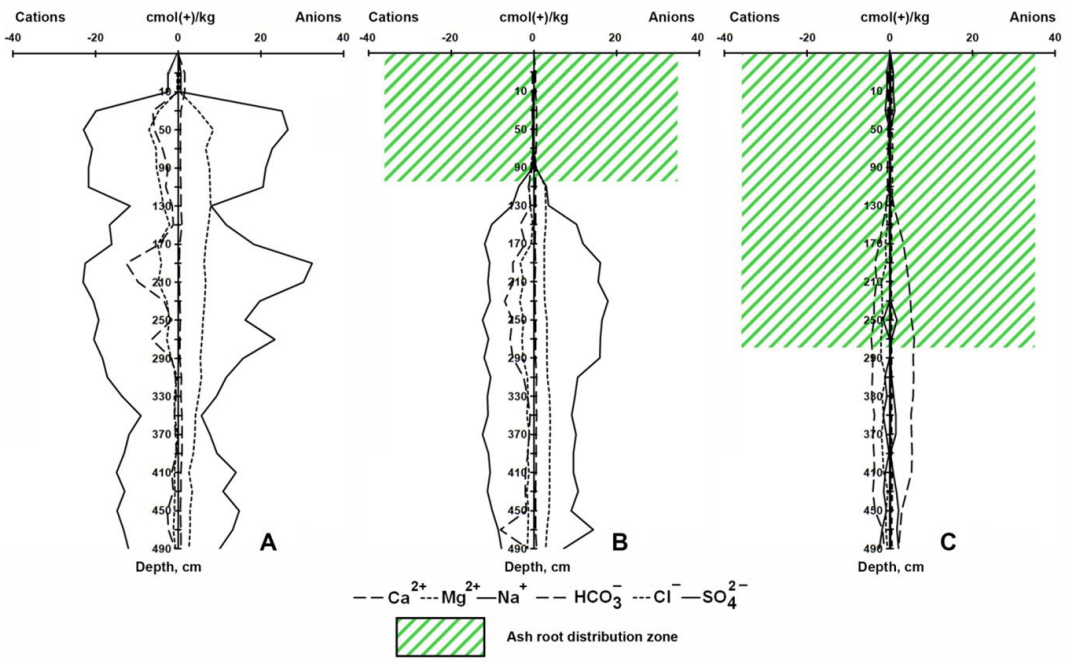

Figure 2. Salt profile and thickness of the soil horizon with ash root systems: (A) and (B) solonchakous solonetz in virgin and ameliorated condition, respectively; (C) meadow-chestnut soils.

2.1.3. Characteristics of intrazonal hydromorphic alluvial floodplain soils

The sites of study are located in the valley of the Ural River and, according to soil and hydrological conditions, are representative of the floodplain conditions of its lower course (Figure 1C). The relief of the floodplain is ridged and cut through by former bayous, old river beds. The high part of the floodplain rises 5-8 m above the low water level of the river, the low one - above 1-3 m. The sediments contain a layered thickness of loam, sand and clay. Periodically, the

floodplain is flooded by spring flood waters (Nikitin, 1957; Galperin et al., 2008; Sergaliev et al., 2013; Auezov et al., 2022).

The main dominant forest areas in terms of species composition and location in the floodplain of the Ural River are represented by: white (*Populus alba* L.) and black poplar (*P. nigra* L.) and white willow (*Salix alba* L.). Grass ecosystems are developed in treeless near-forest clearings and near-floodplain spaces, the species diversity of which (from meadow to marshy communities) depends primarily on the degree of availability of groundwater (Darbaeva and Chukalina, 2011; Darbaeva et al., 2020; Nikitin, 1957; Khlyustov et al., 2017, 2019).

In the conditions of the floodplain, the peculiarities of the growth, condition and seed renewal of ash in the created cultures, willow-poplar forests and meadows were studied.

The presented objects allow us to assess the degree of naturalization of Pennsylvania ash in the arid Caspian region in a wide soil-hydrological regional amplitude: (1) with constantly insufficient moisture supply, when water is used only for spring accumulation, (2) with periodic moisture deficiency, after its exhaustion from the entire root zone and partial consumption from deep-lying groundwater, (3) with optimal moisture consumption from close-lying groundwater.

2.2. Methods

The methodological basis of the research is comparative observations of the adventive Pennsylvania ash in conditions of its geographical and ecological inconsistency with the conditions of the Caspian arid region, in order to identify the mechanisms of its invasive spreading. Traditional methods of forest ecology and taxation were used to study the functioning of ash stands. On the ground, test sites were laid in planted ash cultures on different types of soils and in natural meadow and forest ecosystems with spontaneously penetrated seed specimens of Pennsylvania ash.

On these sample plots, the location on the terrain, the features of micro- and mesorelief, soil cover, and the regime of moisture supply of vegetation were noted. Taxation and photographing of planted and natural stands were carried out. In small stands (curtains), the so-called "upper height" was determined by measuring the heights and diameters of median trees in an amount of at least 10 units, which are located inside the stand. This method allows us to estimate objectively the potential of a stand without taking into account the other development of marginal individuals. The parameters of self-seeding specimens were determined: their number on plots of 2×2 m, heights, diameters, age, condition and fruiting were recorded. The minimum age of fruiting onset in young female specimens was determined separately.

Characteristic places with invasive ash in floodplain areas were found on publicly available satellite images (Google Earth) during the autumn color of ash leaves in yellow, visualized on the ground and marked on the maps of the forestry. Its condition was noted after periodic flooding and fires. The presence and level of spring flooding of the plots were recorded by a whitish bloom at the bases of the tree trunks.

If necessary, the data obtained were processed by well-known mathematical methods. It should be pointed out that the work also summarizes long-term researches of the bioecology of forest cultures at the Dzhanybek Research Station. The plantations created there since the 1950s differ in the variety of tree and shrub species, soil preparation methods, and methods of planting pure and mixed stands on different types of soils (Knight et al., 2013; Sapanov, 2003; Sizemskaya et al., 2021).

3. Results

3.1. The condition and renewal of ash on plain automorphic soil types

Pennsylvania ash, due to its drought resistance, has been widely used in protective afforestation since the middle of the XXth century. The main testing ground for its testing and study on zonal soil types between the rivers of the Volga and the Urals is the Dzhanybek Research Station, where there are unique forest cultures of 50-70 years old, created both on ameliorated solonchakous solonetzes and meadow-chestnut soils. There are no other plantations of this age at the Caspian Lowland now.

3.1.1. Ash cultures on ameliorated solonchakous solonetzes

These conditions are the most extreme in terms of aridity due to the constant shortage of soil moisture for trees, therefore, annual agrotechnical tending in the aisles is mandatory in the created cultures. Such a costly, in fact garden method of growing trees is not used in practice. Thus, in industrial protective plantations, ash cultures completely die after 5 ... 9 ... 15 years, after the termination of soil cultivation.

Only at the Dzhanybek Research Station have 48-year-old forest belts preserved to date, which are grown for scientific purposes in compliance with this technology (Figure 3A). But even in this case, they exist on the limit of survival. The entire period of their preservation can be conditionally divided into two periods. The first period lasted up to 20-25 years, when the trees for the most part reach significant sizes. The second period is characterized by their gradual drying out (Table 1).

This is due to the fact that an adult tree has a period when the increased leaf biomass begins to exhaust productive moisture from the soil faster, so, premature yellowing and leaf fall is noted, for example, already in the middle of summer. It is surprising that the ash tree remains alive, even with the annual repetition of such a scenario (Figure 3B). Obviously, this is due to the fact that it is one of the few tree species that manages to accumulate spare substances by this time in the process of photosynthesis for subsequent trunk respiration and the beginning of vegetation for the next year (Tselniker, 1960). However, such a soil drought on a ameliorated solonchakous solonetz still causes a gradual weakening (impotence, wilting) of adult trees, which is recorded by the gradual thinning of the crown and the drying of the trunk with the appearance of numerous epicormic shoots from dormant buds. First, the apical part of the trunk

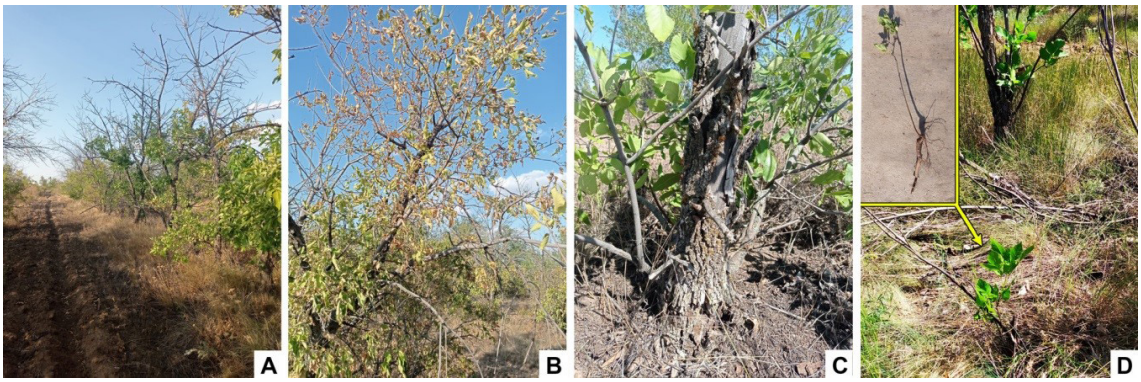

Figure 3. State of the 47-year–old forest strip of Pennsylvania ash on a reclaimed solonchakous solonetz: (A) a general view of shrinking trees; (B) live epicormic (secondary) shoots at the base of the shrinking trunk; (C) yellowing of ash leaves in early August 2023; (D) a long-term self-seeding specimen ash trees with a periodically drying out aboveground part.

Table 1. Taxation indicators of ash trees in forest cultures grown on reclaimed solonchakous solonetz and meadow-chestnut soil (average of 10 measurements ± standard deviation).

Soil	Type of stand	Age, years	Height (H), m	Diameter (D), cm	Note
Solonetz	Planted trees	47	8.5 ± 2.03	13.4 ± 3.34	Trunks dried off by more than half
	Self-seeding	2-5	--	--	Non-viable, single
Meadow-chestnut	Planted trees	71	11.5 ± 1.58	17.7 ± 4.22	Drying of trunk tops (staghead)
	Self-seeding	≤ 35	4.2 ± 1.87	5.2 ± 2.04	Viable, 0.9 units/m^2

dies, last of all, the perennial epicormic shoots at its base die (Figure 3B, C). It is in such a permanently weakened state that ash cultures have existed in recent decades on the ameliorated solonchakous solonetz.

Self-seeding specimens of ash in such plantings appear singularly. At the same time, their aboveground part dies off many times, so they are stunted and cannot replace planted trees (Figure 3D). In forestry, such shoots are referred to as "self-seedlings of delayed development/dying off".

3.1.2. Ash cultures on meadow-chestnut soils

At the Dzhanybek Research Station, ash cultures already exist in relief depressions in the form of multi-row close-set strips, in which agrotechnical soil cultivation was discontinued at the age of 8-10 (Figure 4A).

The taxation parameters of these 71-year-old stands (forest outliers) are better than those grown on reclaimed salt flats due to better moisture availability (Table 1). However, here, over time, the apical part of the ash's trunk also dies off. This is related to the periodic deterioration of the moisture supply of trees due to a shortage of productive moisture in the aeration zone of the soil and the forced separation of their root systems from the capillary border, due to the annual lowering of the level of fresh water due to evapotranspiration of vegetation of the entire landscape (Sapanov, 2003).

It should be noted that in the future, the crown of trees can be restored by the rapid growth of replacement lateral branches (Figure 4A). This is best done during a period of a sharp increase in annual trunk growth in height and diameter in exceptionally favorable years, which arise by a climatogenic increase in the moisture content of the territory and a gradual annual rise in the groundwater table. However, such periods occur quite rarely (Sapanov, 2020).

The separation of the capillary border from the root systems of ash trees was most clearly manifested in a small array measuring 30×30 m, which was planted surrounded on three sides by highly spirited stands of oak (*Quercus robur* L.), white poplar and elm (*Ulmus pumila* L.). At the age of 30-40, this closed stand reached 10-12 m in height, with an average trunk diameter of 13-15 cm. However, then the trees began to staghead and gradually die off according to the same scenario as on ameliorated solonchakous solonetzes. This was because the severe desuction of nearby forest plantations lowers the overall table of fresh water already in June. Therefore, for ash, water from a fresh lens turned out to be inaccessible very early, which was recorded by the absence of daily pulsation in groundwater table, whereas, for example, under oak cultures its amplitude could exceed 12 cm (Sapanov, 2003, 2020).

In the best-developed ash forest outliers, seed self-renewal is quite common, and the undergrowth reaches significant sizes (Figure 4C, Table 1). However, there is no reason to believe that it is capable of long-term retention of this territory both in quantity and in their condition. In the future, apparently, the demutation process here will be aimed at its displacement by native species of herbaceous vegetation, as happened with the ash-leaved maple (*Acer negundo* L.), which formed a pure stand of different ages with no live ground cover in the decayed poplar stand. However, after 25 years, the maple was completely replaced by native species of herbaceous vegetation (Sapanov and Sizemskaya, 2021).

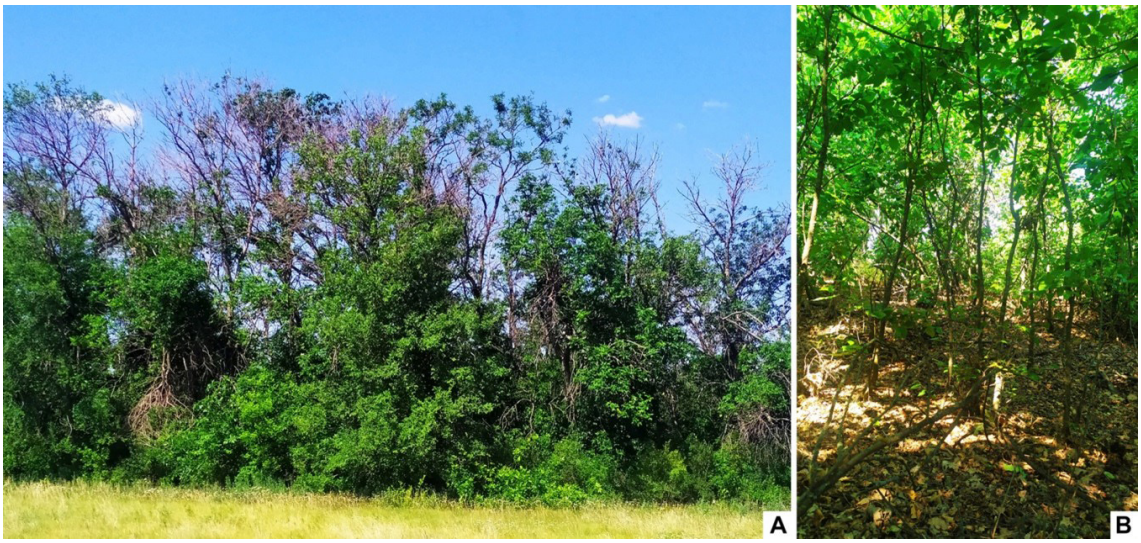

Figure 4. Condition of Pennsylvania ash on meadow-chestnut soils: (A) periodic drying of the tops of tree trunks and their replacement restoration by side branches in 70-year-old cultures; (B) self-seeding shoots of ash under the canopy of cultures.

It is appropriate to mention here the natural settlement and existence for 40 years of the Pennsylvania ash on the territory of the research station in an overgrown unused wet artificial mesodepression – a pond, in which an intrazonal natural willow-oleaster-poplar forest community of quasi-riparian appearance with weed-wet meadow grass was spontaneously formed. The arboretum of the Dzhanybek Research Station became the source of the imported seeds (Sizemskaya et al., 2009). This once again indicates that for the long-term preservation of ash, much more productive moisture is needed and that under optimal moisture conditions it can successfully compete with other plant species.

3.2. Features of ash stands functioning in floodplain conditions

The soil and hydrological conditions of each floodplain site are different and difficult to study due to the heterogeneity of the mechanical composition of the soil, the presence or absence of buried fertile horizons in them, and the significant dynamics of the groundwater table. Nevertheless, for adventive ash, it is quite possible to determine the degree of suitability of certain specific floodplain ecotopes by comparing the features of their condition and development with similar stands that are grown on plain automorphic soil types.

3.2.1. Features of the growth and development of ash cultures in the floodplain of the Ural River

To identify the mechanism of invasion (in terms of survival, range of distribution, and concentration characteristics in different ecotopes), two floodplain sites of the same structure were studied in the Ural Forestry of the Department of Natural Resources of the West Kazakhstan Region, which differ only in the number of ash cultures created on them: in the Ural Forestry with the largest number of cultures created (51.21302°N, 51.40996°E) and the Yanaikino Forestry (50.70244°N, 51.13563°E) with the least amount of it, since the Budarin State Biological (Zoological) Reserve is located there.

In the Ural Forestry, the research was conducted in a separate bend of the Ural River, in the so-called "Perevalochnaya Roshcha", where only 706 hectares of area are covered with forest in 16 forest compartments, of which 103 hectares (12.7%) account for pure and mixed ash cultures. Each subcompartment (57 units) occupies a small area of 2.2 ± 1.53 hectares. The average age of the cultures is 58.7 ± 11.0 years, the trees in them have reached an average height of 14.9 ± 2.7 m, with an average tree diameter of 22.8 ± 6.7 cm. The cultures are in a sparse state (average stand density is 0.41 ± 0.11).

In the Yanaikino Forestry, whose territory covers 6707 hectares, of the entire forested area of 2906.8 hectares, the same ash cultures account for 12.8 hectares (0.4%), which are planted on 14 subcompartments.

Forestry work in the river valley is always carried out only in treeless areas. Old-age forest plantations located on elevated terrain areas, on the so-called "high floodplain", are usually in a disturbed state, or completely die, while those created in low floodplain conditions successfully grow and develop for many decades according to the III-IV site class (Table 2).

In many cultures self-seeding is absent, in others it occurs in an amount of 0.8-1.3 units/m2, while the leader shoots can reach a height of 3-5 m (Figure 5A, B). Spring fires, which occur quite often here, do not destroy the ash tree; the restoration of the stand occurs due to the regrowth of the ground part of the plants in the same year (Figure 5C).

Unfortunately, we cannot predict the trends of further successions in all these cultures, since there are no analogues with the complete disintegration of the planted stand against the background of its gradual replacement with self-seeding specimens. At the same time, it is clear that the best cultures will serve as a seedbed for a long time.

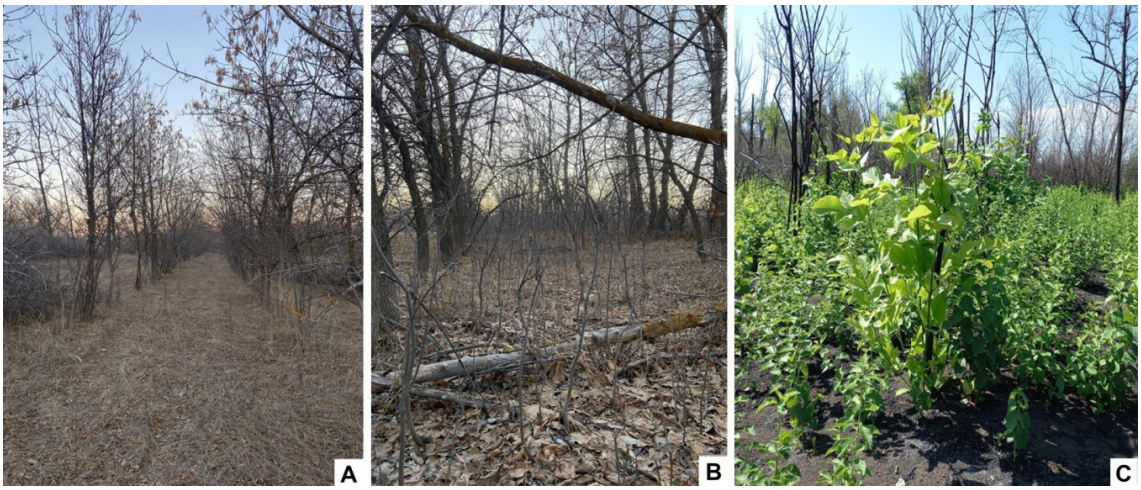

Figure 5. Self-seeding in 40-year-old Pennsylvania ash cultures (autumn 2022) and in 58-year-old cultures (summer 2023) grown at different levels of groundwater table (A, B, respectively), the regeneration of ash in cultures after the spring fire (2023) (C).

Table 2. Taxation characteristics of typical forest cultures involving Pennsylvania ash in the Yanaykino forestry (according to the 2016 forest management data).

Compartments /Plot	Area, ha	Composition	Species/ age, years	Height, m	Diameter, cm	Site class	Density
39/1	0.2	8Up2Fp+Eo	Up 51	9	10	4	0.5
			Fp 51	10	10		
			Eo 51	7	8		
40/47	0.6	10Fp	41	10	10	3	0.6
43/28	0.7	10Fp	33	9	10	3	0.5
127/11	11	10Fp	2	2	2	-	0.4

Note: Fp: Pennsylvania ash (*Fraxinus pennsylvanica* Marsh.); Up: elm (*Ulmus pumila* L.); Eo: oleaster (*Elaeagnus oxycarpa* Schltdl.).

3.2.2. Features of the penetration of ash into forest ecosystems

First of all, we note that the natural forests of the lower reaches of the Ural River have a complex structure of stands with a small number of forest-forming species. For example, in the Yanaikino forestry, the main main species are poplars (white and black) and white willow, which grow in 49 compartments. In the total structure of 365 subcompartments (plots), stands grow mainly in a sparse state according to the 5th site class (Table 3).

A distinctive feature of these forests is the horizontal thinning and high vertical closeness of the crown space of the stands. In the first layer, poplars are most often found: white and black (41% and 39%, respectively), as well as white willow (20%), in the second layer and in the undergrowth European white elm (*Ulmus laevis* Pall.) (53%), buckthorn (*Rhamnus cathartica* L.), Caspian willow (*Salix caspica* Pall.), blackthorn (*Prunus spinosa* L.) and rosehip (*Rosa* sp.) (19%, 12%, 10%, 6%, respectively).

Let's consider some scenarios for the introduction of ash into these willow-poplar forests. Most often it settles along their edges, along cleared strips, glades, in the canopy windows of dead trees. In such limited areas, the amount of viable self-seeding varies significantly depending on age (0.1... 3...5 units/m2). The most interesting forest area is represented by a 25-year-old ash tree in the amount of 1.2 units/m^2, which formed the lower layer in a stand about 7-8 m high (Figure 6A).

Also of interest are the forest poplar areas, where, next to the previously introduced single fruiting ash trees with a height of 5-8 m, there are numerous juvenile undergrowth of different ages up to 1-2.5 m high. In our opinion, such a scenario indicates a stepwise occupation of living space in forest stands.

Unfortunately, due to the youth of the naturalizing ash, we cannot determine the degree of its influence on native forest species and predict a further successional scenario, but the fact that ash transforms natural biogeocenotic processes is quite obvious (Dudkin and Ivanov, 2014; Darbaeva and Chukalina, 2011; Rusakova and Zabolotnaya, 2011).

3.2.3. Features of the distribution and condition of ash trees in treeless areas

The general picture of the settlement of meadows with ash is easily systematized. During the survey, single groups of several specimens or free-standing trees are most often found (Figure 6B), as well as small curtains with an area of several tens or hundreds of square meters. Ash is mainly embedded in natural micro- and mesodepressions of the

Figure 6. Pennsylvania ash in the Ural floodplain: (A) inside a willow-poplar stand (autumn 2022); (B) in a meadow (summer 2022); (C) on the wet slope of water body (summer 2023).

Table 3. Typical forest areas in the Yanaikino forestry according to the results of forest management in 2016.

No.	Compartments	Plot	Area	Composition Formula	Layer	Species	Diameter	Height	Age	Site class	Density
1	47	16	2.7	7Pn1Pa2Sa	1	Pn	32	18	60	5	0.5
					1	Pa	28	18	50		
					2	Sa	20	13	40		
2	49	24	3.4	8Pa1Sa2Pn	1	Pa	32	15	50	5	0.5
					1	Sa	22	14	45		
					1	Pn	32	18	50		
3	40	32	2.7	8Sa2Pn	1	Sa	18	13	40	5	0.7
					1	Pn	28	15	40		

Note: Pn: black poplar (*Populus nigra* L.); Pa: white poplar (*Populus alba* L.); Sa: white willow (*Salix alba* L.).

relief, including in the depressions of meander bends, as well as in gullies, trenches, ditches, on old arable lands and along roads. It is often found along the shores of permanent and drying reservoirs (Figure 6C).

The specifics of the ash spreading outside the established cultures must be divided into the physical spreading of seeds (1), their rooting (2) and the long-term existence (3).

(1) In floodplain conditions, anemo- and hydrochoric spreading of ash winged fruits is most common (Burns and Honkala, 1990; Schmiedel and Tackenberg, 2013; Yuferev and Taranov, 2020). Wind travel over long distances is difficult due to obstacles: high herbage and the presence of nearby forest areas. However, we have repeatedly observed the plucking of winged fruits from branches during a blizzard and their transfer over the snow. In flooded floodplains, fruits are also easily transported by water.

(2) Ash shoots appear in places with additional moisture. We found seedlings and juvenile plants in the depressions of the relief, on the wet slopes of permanent reservoirs and the edges of drying puddles. The rooting and successful competition of ash seedlings with dense meadow vegetation is amazing. Apparently, this is because its seedlings appear early in spring, even before the complete snowmelt and the beginning of vegetation of any other vegetation.

(3) The continued existence of trees obviously depends on the degree of their moisture supply during the entire growing season. Many self-seeding specimens die in the early years, but a significant part lives for decades, and only after reaching a certain size, by analogy with trees growing on automorphic soil types, begins to staghead and die. Apparently, it is this process of ash exodus in meadows that, at least to some extent, delays its spread in certain originally treeless territories.

In the meadows, groups of several ash trees with leading individuals 9-12 m high are most noticeable, many of which are beginning to staghead or have already died. There are also numerous free-standing adult trees (H = 5-8 m) with varying degrees of trunk shrinkage. Dense curtains are quite common: for example, in one of them there are 17.3 ± 3.3 units/m2 of trees, with an average height of H = 3.7 ± 0.2 m and a diameter of D = 1.9 ± 0.1 cm. At the same time, the dominant specimens reach 6 m in height.

Here you can also find small pure forest outliers of different ages in the lowlands. There are more than 500 individuals in one of them form a stand with an average height of 12 ± 6 m, with a trunk diameter of 12 ± 6 cm. At the same time, there are 7 units of dominant trees with a trunk diameter of 45-50 cm. The curve of the distribution of trees in 4 cm thick steps differs from the normal one in the direction of right-sided asymmetry, which indicates their continued intensive differentiation (Figure 7). Under the canopy of the crowns of this stand, a secondary natural renewal of ash with a shoot height of up to 1 m in the amount of 4-5 units/ m2 was noted. The features

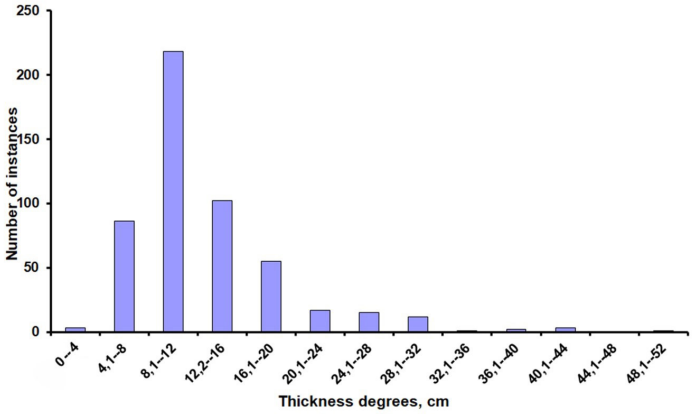

Figure 7. Distribution of ash tree trunks by 2 cm thick steps in the Yanaikino Forestry.

of the functioning of this stand indicate the possibility of forming full-fledged natural ecosystems in some native treeless mesodepressions of the relief.

The fruiting of the ash tree that has penetrated into the meadows begins quite early. Self-seeding female specimens in curtains begin to bear fruit at the age of 6 with an average height of H = 1.98 ± 0.1 m and a diameter of trunks at the root neck D = 2.25 ± 0.19 cm (n = 10). Abundant fruiting is observed from 10-12 years of age in trees with a height of H = 3.57 ± 0.23 m and a diameter of D = 4.45 ± 0.48 cm.

On average, the number of fruiting individuals in the curtains varies. There are even such stands in which only a few trees bear fruit. For example, in one of them, with a density of 0.2 pcs./m2 out of 40 individuals (Hav. = 9.1 ± 0.4 m, Dav. = 8.0 ± 0.6 cm), in 2022 only one 24-year-old tree with a height of 9.5 m and a diameter of 8.5 cm was fruiting.

4. Discussion

The importance of studying the influence of biotic and abiotic conditions on ecosystem resilience (or resistance), as well as ecological and evolutionary processes, is widely discussed in the literature (Ansabayeva, 2023; Serekpayev et al., 2016; Yernazarova et al., 2023). The global spread and increasing abundance of some invasive alien species outside their natural range have caused biodiversity declines, agricultural yield reductions, and ecosystem service impairments (Pyšek and Richardson, 2010; Vilà et al., 2011; Eschen et al., 2023; Ye et al., 2023; Shaldybayeva et al., 2023). It is noted that plant invasions need to be studied at different scales of space and time to gain new insights into the importance of species traits and long-term community dynamics in invaded ecosystems (Gioria et al., 2023). However, identifying the conditions and traits that allow introduced species to grow and spread, from initial rarity to abundance (defined as invasiveness), is the essence of invasion ecology (Cavieres, 2021). Invasiveness can be measured as the size of opportunity niches (positive invasiveness in trait space) given abiotic environmental conditions (Hui et al., 2023). In practice, invasibility reflects a loss of community stability and can be signaled by temporary changes in composition, especially the appearance and loss of rare species (Hui et al., 2023). The manifestation of high or low invasive activity of an introduced species with functional traits similar to the functional traits of a widespread species in the community largely depends on the basic functions of productivity and the strength of interactions with traits and environmental conditions (Cavieres, 2021). In this regard, the studied experience and inevitable failures in the use of introduced Pennsylvania ash in afforestation in arid regions are indicative.

4.1. Features of the functioning of ash stands

In the arid natural and climatic conditions of the Caspian Lowland, ash cultures were created only in treeless territories. The work shows their different living conditions depending on the conditions of soil moisture supply: from the worst automorphic soils of a plain area to the best hydromorphic floodplain soils. The research was conducted in order to study the features of the penetration, spreading and long-term existence of its seed individuals in different growing conditions in order to identify its regional invasive danger. Studies in this context confirm and expand the general known results on the peculiarities of the functioning of ash trees at the organismic and ecosystem levels of their self-organization.

The features of the gradual death of a tree from a gradual deterioration of moisture supply against the background of the presence of amazing adaptive properties to soil drought are shown. This manifests itself in the safe premature yellowing and leaf fall, for example, already in early August. Obviously, by this time the ash tree manages to accumulate spare substances in the process of photosynthesis in the right amount for subsequent respiration of the trunk and the beginning of vegetation for the next year. In general, the condition of the tree is gradually degrading due to an increase in its biomass against the background of using moisture from only 250-300 cm of the soil layer by its surface root system.

In general, as the size of the tree increases, frequent soil drought causes thinning of the crown and drying of part of the trunk, starting from the top. Last of all, the secondary

shoots at the base of the trunk dry out. Nevertheless, with the observance of forest culture technologies, an ash tree with a partially shrunken trunk can exist for many decades. The best condition of ash is observed on hydromorphic floodplain soils with a close occurrence of the groundwater table.

4.2. Features of the ash tree spreading

On a plain territory, it is possible for seed specimens of ash to appear only in established cultures, whereas in river valleys it easily forms a secondary invasive area. The scale of the invasion in similar conditions, for example, in the Volga-Akhtuba floodplain, is evident because ash is already considered one of the main secondary forest-forming species there (Rusakova and Zabolotnaya, 2011; Yuferev and Taranov, 2020).

In the natural willow-poplar forests of the floodplain of the Ural River, ash is inhabited by single specimens, which subsequently, after the beginning of fruiting, give self-seeding around themselves. It is also possible to root numerous self-seeding in forest clearings, which later forms a second layer in the form of a stable undergrowth. Apparently, the removal of ash winged fruits outside these polydominant natural stands will be difficult due to the high vertical closeness of the crowns. However, it can be argued that the fruiting ash rooted in the forest represents a kind of "insurance fund" in case of its death in other places.

In floodplains, due to the transfer of winged fruits by wind and water, ash randomly inhabits meadows, regardless of the distance to fruit-bearing trees. The penetration of ash into native meadow ecotopes indicates a high degree of its invasive aggressiveness, relative to local species of trees and shrubs that never settle here. Such a disorderly settlement makes it difficult to determine the most important parameter – the speed of ash spreading through the territory. Nevertheless, we proceeded from the following obvious provisions: each fruiting ash tree or group of trees spreads seeds and gradually randomly saturates a limited area around itself, including penetrating into the nearest forest ecosystems. After 6-10 years, new fruiting specimens grow in the meadows, which increase the area of further dispersed distribution. It is precisely this explosive nomadic strategy of ash tree settlement with a frequency of 6-10 years, combined with hydrochory that makes it possible to quickly master ecologically optimal growing conditions, forming a stable secondary habitat.

In the Ural Forestry in the territory we are studying ("Perevalochnaya Roshcha"), over several decades, ash has increased its spreading area (from 12.5% of the culture area) by more than two times and has become a common species far from these plantings (Figure 8A, B).

The distribution of ash is easily identified on satellite images by the autumn characteristic yellow the aspect of leaf coloring on trees. In the Yanaikino forestry, on the territory of which the state reserve is located, according to the visual expert assessment of our group, as well as local forestry workers, ash has become a common dominant species in many places.

As we can see, in floodplain forest conditions, from an invasive point of view, the use of ash in industrial forest cultures, especially in specially protected areas, is contraindicated from the point of view of changing the species diversity of vegetation, as well as unwanted transformation of habitats and food supply of protected animal species.

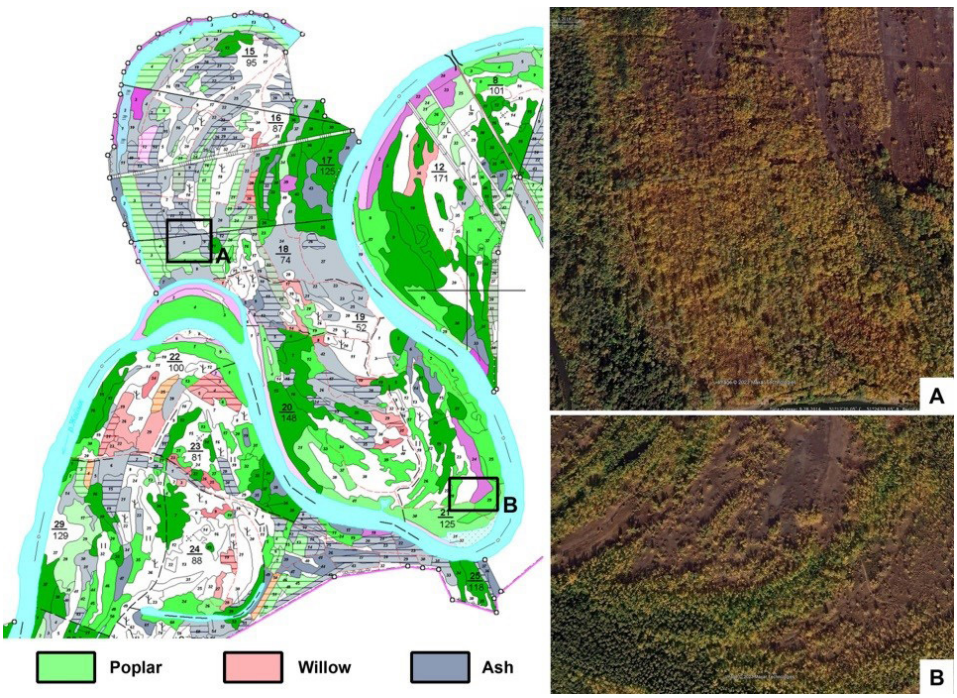

Figure 8. Diagnosis of Pennsylvania ash in the "Perevalochnaya Roshcha" of the Ural Forestry based on autumn leaf color (yellow): (A) in plantations; (B) on invasion-transformed territories.

5. Conclusions

In arid natural and climatic conditions, the features of the functioning of artificial and natural ecosystems from Pennsylvania ash in the ecological range of soil moisture supply from conditions with a minimum amount of available soil moisture (spring accumulation in the upper soil horizons of ameliorated solonchakous solonetzes) to alluvial floodplain soils with constantly available groundwater are considered. Comparative observations have shown, on the one hand, a high degree of adaptation of ash to soil drought, on the other – to short-term flooding and survival in conditions of complete soil moisture saturation.

It is shown that the use of ash in protective afforestation on zonal soil types is quite justified and environmentally friendly. While on intrazonal floodplain soils, its use will necessarily cause the uncontrolled formation of a secondary invasive area by the explosive spread of winged fruits across floodplain meadows with penetration into natural forest ecosystems. The mechanism of rapid dispersed spreading is a stepwise, multiple, nomadic strategy of spreading through micro- and mesodepressions of the relief as the trees reach the age of fruiting in the developed area every 6-10 years. Such a scenario of ash spreading excludes the possibility of effective control of it in floodplains, therefore, it cannot be used in industrial plantations in these areas.

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