

Shading and Light Interception in Thickets of Invasive *Acer negundo* and *Sorbaria sorbifolia*

D. V. Veselkin^a, D. I. Dubrovin^a, O. S. Rafikova^a, Yu. A. Lipikhina^a, N. V. Zolotareva^a,
E. N. Podgaevskaya^a, *, L. A. Pustovalova^a, and A. V. Yakovleva^a

^a Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia

*e-mail: enp@ipae.uran.ru

Received April 30, 2021; revised September 9, 2021; accepted November 5, 2021

Abstract—The purpose of the work was to establish how much the illumination conditions change under the crowns (canopy of leaves) of *Acer negundo* and *Sorbaria sorbifolia*, two invasive plant species in the Middle Urals. In June–August 2020, we performed 8370 illumination measurements in forest parks (at a height of 1.5 and 0.5 m, that is, above and below the canopy of the leaves of the invasive shrub *S. sorbifolia* and the local shrub *Rubus idaeus*; at random points under the crowns of *Pinus sylvestris*; in glades, trails, and near forest boundaries) and in urban habitats (at a height of 1.5 and 0.5 m in dense thickets of the invasive tree *A. negundo* and other tree species) using a portable light meter. The average illumination intensity was as follows: $4 \pm 1 \text{ lx} \times 10^2$ under *S. sorbifolia*; $7 \pm 1 \text{ lx} \times 10^2$ under *R. idaeus*; $13 \pm 2 \text{ lx} \times 10^2$ in stands of *A. negundo*; $25 \pm 4 \text{ lx} \times 10^2$ in urbanized plantations from other types of trees; $80 \pm 10 \text{ lx} \times 10^2$ under the canopy of urban pine forests; $96 \pm 14 \text{ lx} \times 10^2$ at the edge of the forest. Dense clumps of *A. negundo* intercept about 94% of the light from their crowns, and *S. sorbifolia* intercepts about 93%. This level is significantly higher than the level of light interception in control habitats: crowns of other tree species of highly urbanized habitats intercept about 89%, and thickets of *R. idaeus* intercept about 82%. Thus, invasive plants reduce the amount of light available to other species in communities significantly more strongly than native plants.

Keywords: invasive plants, light regime, light intensity, shading, urbanized habitats

DOI: 10.1134/S2075111722010155

INTRODUCTION

In some cases, alien invasive plants are capable of exhibiting the properties of strong edificators (Richardson et al., 2000). Environment-forming influences from such alien species, which alter the conditions or the amount of resources available to native species, are taken into account as a leading explanation in several hypotheses of their success: Global Competition Hypothesis—GCH; Sampling Hypothesis—SPH; Ideal Weed Hypothesis—IWH (Catford et al., 2009). The effects of invasive plant species can be realized by influencing the light regime of communities, the cycle of nutrients, and various components of the biota.

The idea that the availability of light determines the structure of plant communities is trivial: it is a central concept of plant ecology that does not require any special evidence. However, there are also numerous experimental confirmations that lighting conditions determine the productivity of the ground cover (Gilliam and Roberts, 2014; Landuyt et al., 2019) and its species composition (Canham, 1994; Knight et al., 2008). There is a lot of evidence that invasive plants create a denser canopy of leaves than native ones (Reinhart et al., 2006; Nilsson et al., 2008; Cusack and

McCleery, 2014; Berg et al., 2017). It is often concluded that shading is an active mechanism of the influence of invasive plants on indigenous communities (Reinhart et al., 2006; Nilsson et al., 2008; Bravo-Monasterio et al., 2016). However, sometimes higher shading under the crowns of alien plants is not confirmed (Lanta et al., 2013; Dyderski and Jagodziński, 2019).

With regard to specific invasive species, the hypothesis about the effect on light conditions requires a separate verification. Thus, the shading effect of *Acer negundo* L. in the secondary range is not unambiguous: it may be stronger than that of local trees (Saccone et al., 2010; Bottollier-Curtet et al., 2012), or it may not differ with *A. negundo* and native trees (Berg et al., 2017). Also, no evidence of a special shading effect of the invasive *Sorbaria sorbifolia* (L.) A. Braun in comparison with the local shrub *Rubus idaeus* L. was found earlier (Lanta et al., 2013).

Purpose of the work was to establish the extent to which the lighting conditions change under the crowns (canopy of leaves) of two species of invasive plants, *Acer negundo* and *Sorbaria sorbifolia*. We compared the illumination under the crowns of *A. negundo* and *S. sorbifolia* with the illumination in different urban-

ized habitats, microhabitats, and communities, including specially selected communities that can be considered as controls to communities dominated by the studied invasive species.

MATERIALS AND METHODS

Location. Yekaterinburg (56°50' N, 60°35' E) is a city in Russia with a population of 1.5 million people, the administrative center of Sverdlovsk Region. Yekaterinburg is located in the southern taiga subzone of the boreal forest zone. Pine (*Pinus sylvestris* L.) forests on sod-podzolic soils and burozems dominate in the vegetation cover (Kulikov et al., 2013). The climate is temperate continental; winter is long and cold with a stable snow cover; summer is short. The average annual temperature is +3.0°C, the average January temperature is –12.6°C, and the average July temperature is +19.0°C. The average annual precipitation is 550–650 mm. The maximum precipitation occurs during the warm season (May–August), during which about 60–70% of the annual amount falls. The height of the standing of the sun at true noon in June–July, when the measurements were taken, is 52°–56°.

Invasive plants. *Acer negundo* is a tree up to 20 (25) m high and 90 (100) cm in diameter. Its natural range is North America from the Rocky Mountains to the Atlantic coast and from Canada to Florida (Rosario, 1988). Deliberately brought to Europe in the 17th century, it has been known in Russia since the second half of the 18th century. At present, *A. negundo* is included in the list of the most dangerous invasive species in Europe (Pyšek et al., 2009), Belarus (*Chernaya kniga...*, 2020), and Russia (Vinogradova et al., 2009). In its primary range, it grows in floodplain, mesotrophic deciduous and coniferous forests, in open oak forests, in various prairies, and in fields and bogs (Rosario, 1988). In the secondary range, it inhabits coastal phytocenoses, mesophytic oak forests, and pine forests and colonizes a wide range of seminatural habitats (Vinogradova et al., 2009; *Chernaya kniga...*, 2020). In Sverdlovsk Region, *A. negundo* is actively introduced into natural and seminatural communities as a dominant and edicator species (Tretyakova, 2016), where it forms single-species thickets, prevents the regeneration of species of natural flora, and leads to the transformation of biocenoses.

Sorbaria sorbifolia is a shrub 1–3 m high. The natural range of *S. sorbifolia* includes Western and Eastern Siberia, the Far East, Kamchatka, Japan, Korea, China, and Central Asia (*Flora Sibiri...*, 1988). It has been known in cultivation since the middle of the 18th century and is widely used in landscaping (Koropachinsky and Vstovskaya, 2002). In the secondary range, *S. sorbifolia* is an invasive colonophyte species, listed in the Black Book of Flora of Central Russia (Vinogradova et al., 2009). The introduction into natural communities was found in Poland (Tomaszewski, 2001), Latvia (Jurševska, 2007), Lithuania (Dobravol-

skaitė and Gudžinskas, 2011), Finland (Lanta et al., 2013), and Belarus (*Chernaya kniga...*, 2020). Occurrences of *S. sorbifolia* in Yekaterinburg are located 1000 km west of the western border of its natural range (*Flora Sibiri...*, 1988; Koropachinsky and Vstovskaya, 2002).

In Sverdlovsk Region, *S. sorbifolia* disperses and naturalizes in disturbed habitats (Tretyakova, 2016). It has been found that *S. sorbifolia* forms continuous thickets under the forest canopy in the forest parks of Yekaterinburg and displaces native species (Veselkin et al., 2020). In a number of regions of the European part of Russia, *S. sorbifolia* persists for a long time in places of cultivation, naturalizes (runs wild), and forms extensive thickets (Vinogradova et al., 2009).

Areas and habitats. Illumination was measured in different habitats and microhabitats. Habitats were continuous, relatively homogeneous areas of vegetation, the size of which was sufficient to accommodate one or several test plots (TPs) 10 × 10 or 20 × 20 m. Microhabitats are small with a linear size from tens of centimeters to several meters, areas located continuously (small glades, paths) or intermittently (areas under the crowns of individual individuals). TPs were not used during the study of microhabitats; instead, 20–50 measurements of illumination were made in different parts of forest parks. Measurements were performed as follows:

(1) inside forest parks (forest parks: Southwest; Foresters of Russia; Uktusky; Shartashsky; Kalinovsky) and urbanized forests; according to the EUNIS classification (EUNIS..., 2021), X11 type of habitats: large parks:

(a) in the darkest microhabitats at a height of 0.5 m from the soil surface, which were specially selected as a positive control for subsequent comparison with the results of measurements in other conditions; as a rule, areas under the crowns of dense low shrubs, both local (*Salix* spp., *Ribes* spp.) and alien (*Cotoneaster* spp., *Syringa* spp.) were chosen;

(b) above the canopy (at heights of 1.5–1.8 (2) m above the soil level; hereinafter, the unified designation 1.5 m is used in the text) and below (at a height of 0.5 m) the canopy of *S. sorbifolia* leaves in several clumps with an area of 300–4000 m²; TP 10 × 10 m.

(c) above (at a height of 1.5 m) and below (at a height of 0.5 m) the canopy of leaves of the local shrub *Rubus idaeus* in several clumps of 300–1500 m² in different forest parks; PP 10 × 10 m; these measurements were used as control measurements in *S. sorbifolia* thickets;

(d) in random places with an average crown density of *Pinus sylvestris*; at a height of 0.5 and 1.5 m; TP 20 × 20 m;

(e) in microhabitats on small glades and trails and in habitats near the forest boundaries at the TP 20 × 20 m (0–20 m inside from the edge of the stands);

(2) in urban habitats (according to EUNIS: small green areas completely or almost surrounded by buildings (X22) or roads (X23); large parks (X11)); measurements on the same TPs were repeated in 2 rounds, in June and at the end of July—early August:

(a) in dense thickets of *A. negundo* with an area of 500–10000 m² at a height of 1.5 and 0.5 m; TPs 20 × 20 m; when choosing plots with *A. negundo*, we were guided by its absolute predominance in the crown cover: 75–100% of the total crown cover;

(b) in dense thickets of other species, both local (*Prunus padus* L., *Pinus sylvestris*, *Salix alba* L., *Sorbus aucuparia* L., *Tilia cordata* Mill.) and alien (*Malus baccata* (L.) Borkh and *Ulmus laevis* Pall.) tree species at a height of 1.5 and 0.5 m; TPs 20 × 20 m; these measurements were used as control measurements in *A. negundo* thickets.

The investigated forest parks and urbanized forests are the remnants of conventionally native forests of *Pinus sylvestris* of the same age, which arose before the start of intensive urban development. Forests were in a zone of active development 40–60 years ago; the age of trees of the main generation is 90–120 years (Veselkin et al., 2015; Shavnin et al., 2016). The investigated plant communities of urban forests are represented by two groups. Pine forests are less numerous, the grass-shrub layer of which is composed of typical forest and forest-edged species with dominating *Calamagrostis arundinacea* (L.) Roth and *Vaccinium myrtillus* L. or forbs. The herbaceous layer of most urbanized forests is dominated by forest-edge and ruderal-forest nitrophiles: *Glechoma hederacea* L., *Urtica dioica* L., *Aegopodium podagraria* L. Urban forests are characterized by a low density of the tree layer (0.5); the presence of a layer of tall shrubs and low trees (average density of 0.3) with dominating *Sorbus aucuparia*; the presence of a shrub layer (average coverage of 15%), the basis of which is formed by *Rubus idaeus*, *Rosa acicularis* Lindl., and *Cotoneaster lucidus* Schlecht.; and a low projective cover of the grass-dwarf shrub layer (average projective cover of 50%). Inner-city plantations with *A. negundo* and their control, as a rule, were located near buildings and infrastructure facilities. The origin of the stands was both artificial and natural.

The local species *R. idaeus* was used as a control for *S. sorbifolia* because of their phylogenetic proximity, similarity of life forms (creeping-rooted shrub), and the possibility of picking up clumps of *S. sorbifolia* and *R. idaeus* in close proximity to each other. The areas dominated by *S. sorbifolia* and control areas with *R. idaeus*, as well as areas dominated by *A. negundo* and control areas with dominance of other tree species, were selected in such a way that they formed a linked pair: they were maximally homogeneous and located in close proximity to each other, in the same landscape element, in the same cenotic environment with similar levels of urbanization and disturbance. In

addition, plots with *A. negundo* and control plots were selected so that they had similar levels of crown density.

Names of taxa are given according to the database World Flora Online (World..., 2021).

Illumination measurement. A total of 8370 illumination measurements (Table 1) were performed with a TKA-PKM-42 luxmeter, which measures illumination in the visible region of the spectrum of 380–760 nm. All measurements were performed in the period from June 22 to August 3, 2020. The time interval of measurements during the day was from 10:00 to 15:00. In all cases, control measurements were made in an open place, 15–20 m from the nearest buildings, structures, and the edge of the forest, with an interval of no more than 10–20 min before or after measurements inside forest parks or inside urban areas occupied by trees. During each cycle of measurements in each habitat or microhabitat or on each sample plot, the nature of cloudiness was recorded, reducing it to three gradations: cloudy, partly cloudy, and clear.

Data analysis. The average value of 20–50 initial measurements of illumination on one test area (plot, habitat, microhabitat) for one round was the unit of observation. Two quantities were used as the illumination characteristic. The graphs and text show the untransformed values of the illumination intensity (L , in lux × 10²). However, the transformation of illumination intensity by means of the natural logarithm $\ln(L)$ was used in statistical comparisons. In addition, the I_L index or the characteristic of the relative light contentment was used (Larcher, 1978), which was defined as the ratio of the illumination intensity in the habitat to the closest measurement of the illumination intensity in an open place $I_L = L_{\text{location}}/L_{\text{open place}}$. It was assumed that this parameter is less dependent on the weather, that is, cloud conditions, than L . Arcsine-transformed I_L values were used in statistical comparisons. To compare the characteristics of illumination in communities dominated by *S. sorbifolia* and control communities with *Rubus idaeus* and in communities dominated by *A. negundo* and control communities with other tree species in an urban environment, we used the t -test for pairwise related variables. The coefficient of variation (CV) was used to characterize the unevenness in the distribution of loci of different illumination within individual habitats and microhabitats. The averaged values given in the text are arithmetic averages with indication of the standard error of the mean (SE) through the symbol \pm .

RESULTS

Illumination intensity varied greatly between the studied habitats/microhabitats and within them (Table 2). Naturally, microhabitats, which we specially chose as the most shaded areas, were the darkest, and the open areas were the most illuminated. The total range (min–max) of the recorded L values was

Table 1. Places, dates and number of illumination measurements

Habitats and microhabitats	Density of the crowns of the tree layer	Measurement dates	Number of sites/trial plots	Number of measurements rounds on each site/trial plot	The number of measurements in each site/trial plot in each round	Number of measurements		
						at a height of 0.5 m from the soil surface	at a height of 1.5 m from the soil surface	in an open place
Forest parks and urbanized forests (EUNIS: X11)								
The darkest microhabitats	40–90	July 24–August 3	5	1	25	125	0	75
Thickets of <i>Sorbaria sorbifolia</i>	30–80	July 10–23	6	1	25	150	150	75
Thickets of <i>Rubus idaeus</i>	30–80	July 10–23	6	1	25	150	150	75
Areas with medium crown density	40–90	June 3–July 15	28	1	40–50	440	1300	480
Glades, trails, forest boundaries	0–70	June 3–August 3	20	1	25–50	0	705	175
Urban habitats (EUNIS: X11, X22, X23, F9)								
Thickets of <i>Acer negundo</i>	70–95	June 22–30, July 24–August 3	12	2	20	480	480	480
Thickets of other tree species	65–95	June 22–30, July 24–August 3	12	2	20	480	480	480

Table 2. Illumination intensity (range of average, $\text{lx} \times 10^2$) in different habitats and microhabitats and at different heights above soil level

Habitats and microhabitats	Height above soil surface	
	1.5 m	0.5 m
Open places	34–946	No measurements
Forest parks and urbanized forests		
Darkest microhabitats	No measurements	1–4
Thickets of <i>Sorbaria sorbifolia</i>	13–112	1–7
Thickets of <i>Rubus idaeus</i>	21–57	5–9
Areas with medium crown density	11–342	11–354
Glades, trails, forest boundaries	10–302	No measurements
Urban habitats		
Thickets of <i>Acer negundo</i>	4–29	3–24
Thickets of other types of trees	5–85	3–63

1–946 $\text{lx} \times 10^2$, that is, three orders of magnitude. Within one type of habitat or microhabitat, the range of L values ranged from 3 to 30 times at one height above the soil level and from 7 to 110 times when taking into account the variability between measurements at heights of 0.5 and 1.5 m above the soil surface.

The intensity of the illumination was expectedly dependent on the cloud cover. In open places, the range of illumination values was $L = 350\text{--}946 \text{ lx} \times 10^2$

under a clear sky, $L = 184\text{--}726 \text{ lx} \times 10^2$ with variable cloud cover, and $L = 34\text{--}269 \text{ lx} \times 10^2$ in cloudy weather. Thus, the differences in the intensity of the incident light depending on the cloudiness can reach an order of magnitude or slightly more. Similar differences in illumination intensity are also noticeable under the canopy of the crowns (Fig. 1). The average illumination intensity under the canopy of urbanized pine forests in clear weather is 2.8 times higher than the average illumination intensity in cloudy weather

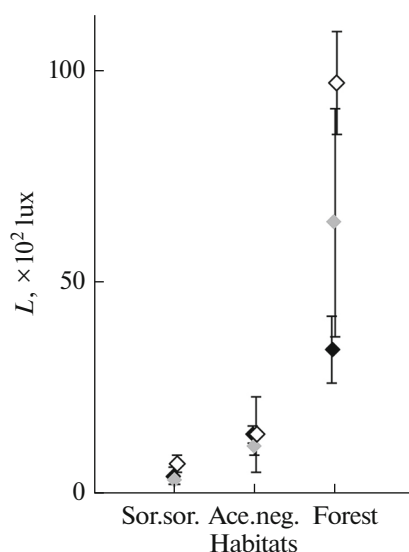


Fig. 1. Illumination intensity at a height of 0.5 m in the thickets of *Sorbaria sorbifolia* (Sor.sor.), at a height of 1.5 m in the thickets of *Acer negundo* (Ace.neg.) and at random locations under the canopy of urbanized pine forests during clear weather (◇) and with variable (◆) and full (◆) cloud cover. Vertical lines show the SE.

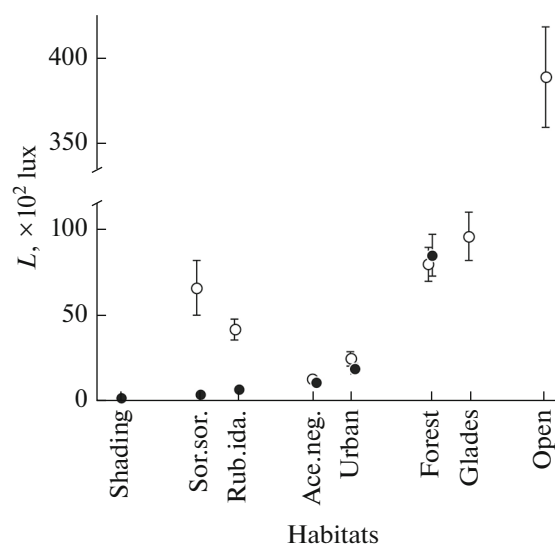


Fig. 2. Illumination intensity at a height of 0.5 m (●) and 1.5 m (○) in different habitats and microhabitats (the darkest places (shading); thickets of *Sorbaria sorbifolia* (Sor.sor.), *Rubus idaeus* (Rub.ida.), *Acer negundo* (Ace.neg.), and other urban trees (urban); random points under the canopy of urbanized pine forests (forest), edges of stands and glades (glades), and open spaces (open)). Vertical lines show the SE.

and about 1.5 times higher than under variable cloudiness. However, the illumination under the canopy of *Sorbaria sorbifolia* (at a height of 0.5 m) and *Acer negundo* (at a height of 1.5 m) depends little on cloudiness. The average range is $2\text{--}7 \text{ lx} \times 10^2$ in the first case and $11\text{--}14 \text{ lx} \times 10^2$ in the second case.

Measurements of L in each type of habitat and microhabitat were performed under a clear sky and with variable and full cloud cover. Therefore, it was possible to compare the differences in illumination intensity in different habitats and microhabitats, taking into account the state of cloudiness (Fig. 2). Average illumination intensity in open areas was $L = 389 \pm 29 \text{ lx} \times 10^2$. In comparison with this value, the illumination in specially selected most shaded microhabitats was lower by more than two orders of magnitude, almost 200 times less: $L = 2 \pm 1 \text{ lx} \times 10^2$. Strong shading is also created in the forests under the canopy of *S. sorbifolia* ($L = 4 \pm 1 \text{ lx} \times 10^2$) and *R. idaeus* ($L = 7 \pm 1 \text{ lx} \times 10^2$) at a height of 0.5 m from the soil. It is slightly lighter in the stands of *A. negundo* ($L = 13 \pm 2 \text{ lx} \times 10^2$ at a height of 1.5 m) and other tree species ($L = 25 \pm 4 \text{ lx} \times 10^2$ at a height of 1.5 m). There is noticeably more light under the canopy of urban pine forests ($L = 80 \pm 10 \text{ lx} \times 10^2$ at a height of 1.5 m), especially in the marginal zones ($L = 96 \pm 14 \text{ lx} \times 10^2$ at a height of 1.5 m).

Pairwise comparisons with adequate controls were performed to make a strong conclusion about the shading produced by invasive plants. The illumination

intensity differs significantly at a height of 0.5 m under the canopy of *S. sorbifolia* and *R. idaeus* ($t = 2.91$; $P = 0.0336$; $dF = 5$) and under the canopy of *A. negundo* (at a height of 1.5 m: $t = 3.37$; $P = 0.0027$; $dF = 23$; at a height of 0.5 m: $t = 3.05$; $P = 0.0057$; $dF = 23$).

Along with the assumption that invasive plants produce, on average, high shading, we also tested the assumption about the change in the uniformity of illumination under them. Thus, we estimated how large the scatter of L estimates in each habitat was. The average values of CV_L were as follows: $CV_L = 50 \pm 6\%$ in urbanized forests at a height of 1.5 m; $CV_L = 64 \pm 13\%$ in inner-city tree plantations from different tree species; $CV_L = 59 \pm 12\%$ in inner-city tree plantations of *A. negundo*; $CV_L = 35 \pm 4\%$ at a height of 0.5 m under the canopy of *R. idaeus*; $CV_L = 46 \pm 2\%$ at a height of 0.5 m under the canopy *S. sorbifolia*.

Thus, invasive *S. sorbifolia* and *A. negundo* create higher shading than native plants with a similar growth pattern. At the same time, the degree of uniformity in the distribution of loci with increased and decreased illumination in communities dominated by local and invasive plants does not differ.

The proportion of light from illumination in an open place. The I_L values were relatively high in cloudy weather (Fig. 3). In particular, $4 \pm 1\%$ of light under the canopy of *S. sorbifolia*, $10 \pm 1\%$ under the canopy of *A. negundo*, and $25 \pm 2\%$ under the canopy of pine forests penetrated from an open area under full cloud cover. In clear weather and variable cloudiness, the

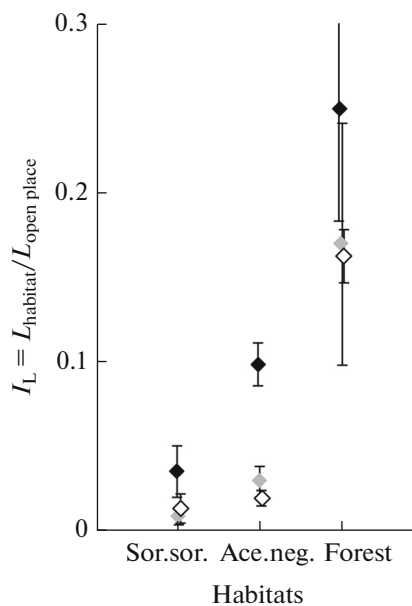


Fig. 3. The proportion of light penetrating at the height of 0.5 m in the thickets of *Sorbaria sorbifolia* (Sor.sor.), at the height of 1.5 in the thickets of *Acer negundo* (Ace.neg.), and at random points under the canopy of urbanized pine forests (forests) during clear weather (○) and with variable (◆) and full (◆) cloud cover. Vertical lines show the SE.

values of the fraction of light penetrating under the canopy were lower: about 1% of light from an open area penetrated under the canopy of *S. sorbifolia*, 2–3% under the canopy of *A. negundo*, and 17–18% under the canopy of pine forests.

On average, $24 \pm 3\%$ of light from illumination in an open place penetrated into the marginal zones and small edges of urban forests; under the canopy of urban forests, it was, on average, $18 \pm 2\%$ at a height of 1.5 m and $17 \pm 2\%$ at a height of 0.5 m (Fig. 4). Under the crowns of *A. negundo*, 5–6% of light from illumination in an open place penetrated; 8–11% penetrated in thickets of other tree species. Under the canopy of *S. sorbifolia*, $2 \pm 1\%$ of light from the illumination in an open place penetrated, and $4 \pm 1\%$ penetrated in the control variants with *R. idaeus*. The proportion of light in specially selected most shaded microhabitats of urban forests was expected to be minimal: $1 \pm 1\%$.

The I_L values differed significantly ($t = 2.94$; $P = 0.0322$; $dF = 5$) at a height of 0.5 m under *S. sorbifolia* and *R. idaeus*. The proportion of illumination under the canopy of *A. negundo* and other urban trees also significantly differed at a height of 1.5 m ($t = 2.19$; $P = 0.0393$; $dF = 23$), but not at a height of 0.5 m ($t = 1.93$; $P = 0.0657$; $dF = 23$).

Interception of light flux by invasive plants. The difference in the intensity of illumination above and below the canopy is a characteristic of the degree of interception of the light flux by the crowns. $L = 66 \pm$

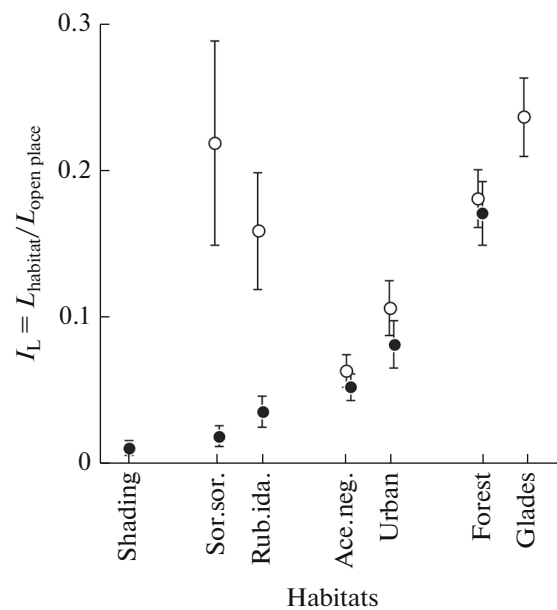


Fig. 4. The proportion of illumination from light in an open place at a height of 0.5 m (●) and 1.5 m (○) in different habitats and microhabitats (the darkest places (shading); thickets of *Sorbaria sorbifolia* (Sor.sor.), *Rubus idaeus* (Rub.ida.), *Acer negundo* (Ace.neg.), and other urban trees (urban); random points under the canopy of urbanized pine forests (forest), edges of stands and glades (glades)). Vertical lines show the SE.

16×10^2 , $I_L = 22 \pm 7\%$ above the leaf canopy of *S. sorbifolia*; $L = 42 \pm 6 \times 10^2$, $I_L = 16 \pm 4\%$ above the canopy of leaves of *R. idaeus* (Figs. 2–4). Consequently, *S. sorbifolia* is a slightly more light-loving species, which was found and studied in better illuminated habitats compared to *R. idaeus*, at least in the forest parks of Yekaterinburg.

The characteristic of the light flux interception by the crowns of *S. sorbifolia* and *R. idaeus* is the difference between the illumination at heights of 1.5 and 0.5 m. A similar characteristic for *A. negundo* and comparatively studied trees in an urbanized environment is the difference between the illumination in an open place and at a height of 1.5 m, since the effects of shading by tall grasses begin to have an effect at a height of 0.5 m. The amount of light interception in *S. sorbifolia* thickets is $93 \pm 1\%$ of the level falling on the crowns, and it is $82 \pm 3\%$ in *R. idaeus* thickets. These differences are significant ($t = 3.51$; $P = 0.0169$; $dF = 5$). The amount of light interception is $94 \pm 1\%$ in the thickets of *A. negundo* and $89 \pm 2\%$ in the thickets of other trees, and these differences are also significant ($t = 2.19$; $P = 0.0393$; $dF = 23$).

DISCUSSION

The results support the assumption that the illumination under the crowns (canopy of leaves) of two species of invasive plants, *Acer negundo* and *Sorbaria sor-*

bifolia, is lower than in similar habitats in which other woody plants dominated. The reliability of this conclusion is due to several circumstances. First, the conclusion about a high shading ability was obtained for both invasive plants. Secondly, many measurements have been analyzed. At the same time, the effects of shading in the communities of invasive and native plants of similar life forms were compared, and the illumination in a wide range of habitats was additionally compared. Third, the conclusion about the high shading effect of invasive plants was obtained with respect to both utilized characteristics of the light regime: both the illumination intensity and the proportion of light from illumination in an open place. The levels of light flux interception by the crowns of *A. negundo* and *S. sorbifolia* are significant at 93–94%, and the average illumination under invasive plants is 400–1300 lx, which approximately corresponds to the range of illumination levels from a cloudy day to the moment before sunset. The lighting conditions under the crowns of *S. sorbifolia*, apparently, are close to such conditions that they can be considered a sufficient explanation for the suppression of the under-canopy vegetation. For a positive carbon balance, the minimum photon flux density should be 0.5–1% of the density calculated for the community in the middle of the day (Zitte et al., 2007, p. 54).

The presented data confirm that the specific effect on the light regime is played by the real mechanism of the environment-forming influence of *A. negundo* in the secondary range (Saccone et al., 2010; Bottollier-Curtet et al., 2012). The presented data also confirm this mechanism for *S. sorbifolia*, although it was not confirmed earlier (Lanta et al., 2013).

It should be noted that the test plots in the stands with *A. negundo* and the control plots for them were selected taking into account such a criterion as similar values of crown density (Veselkin and Dubrovin, 2019). However, it is, on average, darker in *A. negundo* thickets than in similar communities dominated by other tree species. The ability to increase light interception can be explained by the dense crowns of *A. negundo* with a higher leaf area index (LAI) than in local species (Porte et al., 2011). It is possible that the growth form of *A. negundo* as a low multilateral tree with inclined trunks and low branches is also important (Kostina et al., 2016). It cannot be ruled out that the high crown density of *A. negundo* can be partly explained by the high preservation of leaves due to the low levels of damage to its leaves by phytophages in the secondary range. It is known that leaf damage by phytophages is qualitatively lower in *A. negundo* in comparison with the background southern-taiga deciduous trees *Betula pendula* Roth and *Salix caprea* L. (Veselkin et al., 2019).

The biological features of *S. sorbifolia* in the secondary range are apparently less studied than the analogous features of *A. negundo* in comparison with local

species. In Scandinavia, it was not possible to establish the specifics of the distribution of leaves and biomass in *S. sorbifolia*, as well as the amount of light penetrating under the canopy in comparison with local shrubs, primarily *R. idaeus* (Lanta et al., 2013). It was earlier shown that *S. sorbifolia* grows in the Middle Urals in areas with relatively sparse Scots pine stands (Veselkin et al., 2020), and direct estimates of illumination given in this work confirm this. Estimates of LAI and phytophage activity for *S. sorbifolia* in the secondary range are not known.

The morphology of crowns, clumps, or thickets and the way branches and leaves colonize the space are important for the formation of the light regime in communities. The degree of shading is obviously related not only to the total leaf area per unit area of the community but also to the size of the leaves and the way they are arranged in space. For example, it is expected that, with a decrease in the crown height, for example, in the order pine forests—thickets of *A. negundo* and other tree species—thickets of *S. sorbifolia* and *R. idaeus*, the degree of shading under them greatly increases. In the secondary range, *A. negundo* and *S. sorbifolia* are similar in their ability to form extended closed clumps with leaves densely located in approximately one layer. For temperate latitudes, where the sun is not at its zenith and there is long twilight, the ability to intercept lateral streams of light seems to be of great importance. Meanwhile, little is known about the structure of crowns and clumps of local and alien woody plants, and it is difficult to formalize this knowledge. An attempt to assess the heterogeneity of the illumination distribution, that is, to estimate the ratio of the loci of strong and weak shading, was associated with the desire to understand whether the effect of invasive plants could be implemented not only through strong shading but also through a decrease in the heterogeneity of the distribution of light spots. So far, this assumption has not been confirmed.

Among other factors not directly related to the biological characteristics of plants, but capable of influencing the level of light under the crowns, it is necessary to take into account the consequences of habitat fragmentation, which always accompanies urbanization. The availability of light, as the main resource required for plants, is increasing in the marginal zones of plant communities (Weathers et al., 2001; Vallet et al., 2010). Consequently, an increase in the degree of illumination in them with a decrease in the size of fragmented communities can be expected. However, the light intensity under them was low despite the fact that some studied communities dominated by *A. negundo* were highly fragmented.

The intensity of light in the visible spectrum, and not in the photosynthetically assimilated range, PAR, was calculated in the study. On one hand, the main parts of the ranges of visible light (380–780 nm wave-

length) and PAR (380–710 nm) coincide. Therefore, the regularities established when measuring the visible range and PAR should not differ greatly. On the other hand, it would still be justified to carry out measurements similar to those described in the PAR range. Then it will be possible to assess the degree of change in the spectral composition of light after selective absorption by leaves of waves of the red part of the spectrum in the range of 620–680 nm.

When interpreting the results obtained, it should be borne in mind that high shading due to a closed canopy of leaves can correlate with the active use of not only light but also other resources. For example, a lot of macro- and microelements are needed to build a large mass of leaves and their bearing branches and shoots. A lot of water is needed to maintain the turgor of the leaves and the transpiration process. Consequently, the increased shading created by invasive plants can indirectly indicate their high competitiveness with respect to the absorption of soil resources. In addition, a lot of leaf litter, which can also have an environment-transforming significance, is formed in communities with a large mass of leaves. Large shading caused by dense and/or low-lying crowns is also a possible indicator of isolation/closure of invasive plant thickets from the flow of diaspores of other organisms. Invasive plants usually contribute to a decrease in the diversity and size of seed banks in aboriginal communities (Gioria et al., 2012; Gioria and Osborne, 2014). In the Middle Urals, this fact was confirmed for *A. negundo* (Veselkin et al., 2018), but not for *S. sorbifolia* (Veselkin et al., 2020).

The suppression of vegetation in the undercrown space of invasive plants is an easily predictable and actually observed consequence of high shading, the possible efficient use of soil resources, and the limitation of the formation of soil seed banks. There is quite a lot of evidence for this fact (Maron and Marler, 2008; Hejda et al., 2009; Emelyanov and Frolova, 2011; Lanta et al., 2013; Kostina et al., 2016), including in the Middle Urals, both for *A. negundo* (Veselkin and Dubrovin, 2019) and for *S. sorbifolia* (Veselkin et al., 2020). It is significant that the disappearance of vegetative species under the canopy of *S. sorbifolia* was selective: relatively light-loving and relatively dry-loving species predominantly disappeared, while more shade-loving and moisture-loving species were resistant (Veselkin et al., 2020).

CONCLUSIONS

In accordance with the presented results, the amount of light under the crowns (canopy of leaves) of two invasive plant species, *Acer negundo* and *Sorbaria sorbifolia*, is lower than in strictly selected local control species. On one hand, this result seems somewhat trivial and intuitively easy to imagine. It corresponds to the feelings of an unbiased observer who at least once observed clumps of *A. negundo* and *S. sorbifolia* from

the inside, even with the naked eye. On the other hand, results that did not confirm the hypothesis about their specific change in light conditions were earlier published both for *A. negundo* and for *S. sorbifolia*. The main significance of the results lies in the quantitative characterization of the degree of shading and light interception in the thickets of *A. negundo* and *S. sorbifolia*. *A. negundo* intercepted about 94% of light from the level incident on its crowns, while *S. sorbifolia* intercepted about 93%. Compared with the average light interception by tree crowns in the urbanized forests of the Middle Urals at the level of 82%, this value indicates a significantly stronger shading caused by invasive plants. At the same time, the average (that is, averaged for different degrees of cloudiness) level of illumination is about 1300 lx in the thickets of *A. negundo* and about 400 lx in the thickets of *S. sorbifolia*. Thus, the ability of the studied alien plants to influence aboriginal communities in the Middle Urals is explained, at least, by a strong decrease in the amount of light available for other species in the communities under the influence of *A. negundo* and *S. sorbifolia*.

FUNDING

Various parts of the field measurements were carried out within the framework of the theme of the state assignment of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, no. AAAA-A19-119031890084-6; the Russian Foundation for Basic Research (RFBR), project 20-54-00024 (joint competition of RFBR and BFRF); and RFBR project no. 20-44-660013, jointly financed by the RFBR and the Government of Sverdlovsk Region.

CONTRIBUTION OF AUTHORS

D.V. Veselkin presented the idea and the development of the observation scheme, analysis and discussion of data, and preparation of the basis of the text; D.I. Dubrovin performed the development of the observation scheme, analysis and discussion of data, and field measurements; N.V. Zolotareva, Yu.A. Lipikhina, E.N. Podgaevskaya, L.A. Pustovalova, O.S. Rafikova, and A.V. Yakovleva performed field measurements and discussion of data. All authors have read the manuscript and agree with its content.

COMPLIANCE WITH ETHICAL STANDARDS

The authors declare no conflict of interest. This article does not contain any research involving humans or animals as research objects.

REFERENCES

- Berg, C., Drescherl, A., and Essl, F., Using relevé-based metrics to explain invasion patterns of alien trees in temperate forests, *Tuexenia*, 2017, vol. 37, pp. 127–142. <https://doi.org/10.14471/2017.37.012>

- Bottollier-Curtet, M., Charcosset, J., Poly, F., Planty-Tabacchi, A.M., and Tabacchi, E., Light interception principally drives the understory response to boxelder invasion in riparian forests, *Biol. Invasions*, 2012, vol. 14, pp. 1445–1458.
<https://doi.org/10.1007/s10530-011-0170-0>
- Bravo-Monasterio, P., Pauchard, A., and Fajardo, A., *Pinus contorta* invasion into treeless steppe reduces species richness and alters species traits of the local community, *Biol. Invasions*, 2016, vol. 18, pp. 1883–1894.
<https://doi.org/10.1007/s10530-016-1131-4>
- Canham, C.D., Finzi, A.C., Pacala, S.W., and Burbank, D.H., Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees, *Can. J. For. Res.*, 1994, vol. 24, pp. 337–349.
<https://doi.org/10.1139/x94-046>
- Catford, J.A., Jansson, R., and Nilsson, C., Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework, *Divers. Distrib.*, 2009, vol. 15, pp. 22–40.
<https://doi.org/10.1111/j.1472-4642.2008.00521.x>
- Chernaya kniga flory Belarusi: chuzherodnye vredonosnye rasteniya* (The Black Data Book of the Flora of Belarus: Alien and Noxious Plants), Parfenov, V.I. and Pugachevskii, A.V., Eds., Minsk: Belaruskaya Navuka, 2020.
- Cusack, D.F. and McCleery, T.L., Patterns in understory woody diversity and soil nitrogen across native- and non-native-urban tropical forests, *For. Ecol. Manag.*, 2014, vol. 318, pp. 34–43.
<https://doi.org/10.1016/j.foreco.2013.12.036>
- Dobravolskaitė, R. and Gudžinskas, Z., Alien plant invasion to forests in the vicinity of communal gardens, *Bot. Lithuan.*, 2011, vol. 17, nos 2–3, pp. 73–84.
- Dyderski, M.K. and Jagodziński, A.M., Similar impacts of alien and native tree species on understory light availability in a temperate forest, *Forests*, 2019, vol. 10, no. 11, p. 951.
<https://doi.org/10.3390/f10110951>
- Emelyanov, A.V. and Frolova, S.V., Ash-leaf maple (*Acer negundo* L.) in coastal phytocenoses of the Vorona River, *Russ. J. Biol. Invasions*, 2011, vol. 2, nos. 2–3, pp. 161–163.
<https://doi.org/10.1134/S2075111711030052>
- EUNIS Habitat Classification Descriptions. <https://www.eea.europa.eu/data-and-maps/data/eunis-habitat-classification>. Accessed April 20.
- Flora Sibiri. Rosaceae* (The Flora of Siberia: Rosaceae), Novosibirsk: Nauka, 1988, 2021.
- Gilliam, F.S. and Roberts, M.R., Interactions between the herbaceous layer and overstory canopy of eastern forests, in *The Herbaceous Layer in Forests of Eastern North America*, Gilliam, F.S. Ed., Oxford, UK: Oxford Univ. Press, 2014, pp. 233–254.
<https://doi.org/10.1093/acprof:osobl/9780199837656.003.0009>
- Gioria, M. and Osborne, B.A., Resource competition in plant invasions: emerging patterns and research needs, *Front. Plant Sci.*, 2014, vol. 5, no. 501.
<https://doi.org/10.3389/fpls.2014.00501>
- Gioria, M., Pyšek, P., and Moravcová, L., Soil seed banks in plant invasions: promoting species invasiveness and long-term impact on plant community dynamics, *Preslia*, 2012, vol. 84, pp. 327–350.
- Hejda, M., Pyšek, P., and Jarošík, V., Impact of invasive plants on the species richness, diversity and composition of invaded communities, *J. Ecol.*, 2009, vol. 97, no. 3, pp. 393–403.
<https://doi.org/10.1111/j.1365-2745.2009.01480.x>
- Jurševska, G., Invasive tree taxa in major dendrological plantations in Jelgava district, *Acta Biol. Univ. Daugavpiliensis*, 2007, vol. 7, no. 2, pp. 149–158.
- Knight, K.S., Oleksyn, J., Jagodzinski, A.M., Reich, P.B., and Kasprowicz, M., Overstorey tree species regulate colonization by native and exotic plants: a source of positive relationships between understorey diversity and invasibility, *Divers. Distrib.*, 2008, vol. 14, pp. 666–675.
<https://doi.org/10.1111/j.1472-4642.2008.00468.x>
- Koropachinskii, I.Yu. and Vstovskaya, T.N., *Drevesnye rasteniya Aziatskoi Rossii* (Woody Plants in Asian Russia), Novosibirsk: Geo, 2002.
- Kostina, M.V., Yasinskaya, O.I., Barabanshchikova, N.S., and Orlyuk, F.A., Toward an issue of box elder invasion into the forests around Moscow, *Russ. J. Biol. Invasions*, 2016, vol. 7, no. 1, pp. 47–51.
<https://doi.org/10.1134/S2075111716010069>
- Kulikov, P.V., Zolotareva, N.V., and Podgaevskaya, E.N., *Endemichnye rasteniya Urala vo flore Sverdlovskoi oblasti* (Plants Endemic to the Urals in the Flora of Sverdlovsk Region), Yekaterinburg: Goshchitskii, 2013.
- Landuyt, D., Lombaerde, E.D., Perring, M.P., Hertzog, L.R., Ampoorter, E., Maes, S.L., Frenne, P.D., Ma, S., Proesmans, W., Blondeel, H., et al., The functional role of temperate forest understorey vegetation in a changing world, *Glob. Change Biol.*, 2019, vol. 5, pp. 3625–3641.
<https://doi.org/10.1111/gcb.14756>
- Lanta, V., Hyvönen, T., and Norrdahl, K., Non-native and native shrubs have differing impacts on species diversity and composition of associated plant communities, *Plant. Ecol.*, 2013, vol. 214, no. 12, pp. 1517–1528.
<https://doi.org/10.1007/s11258-013-0272-0>
- Larcher, W., *Ökologie der Pflanzen*, Stuttgart: Eugen Ulmer, 1976. Translated under the title *Ekologiya rastenii*, Moscow: Mir, 1978.
- Maron, J.L. and Marler, M., Effects of native species diversity and resource additions on invader impact, *Am. Nat.*, 2008, vol. 172, no. 1, pp. 18–33.
<https://doi.org/10.1086/588303>
- Nilsson, C., Engelmark, O., Cory, J., Forsslund, A., and Carlborg, E., Differences in litter cover and understory flora between stands of introduced lodgepole pine and native scots pine in Sweden, *For. Ecol. Manag.*, 2008, vol. 255, nos. 5–6, pp. 1900–1905.
<https://doi.org/10.1016/j.foreco.2007.12.012>
- Porte, A.J., Lamarque, L.J., Lortie, C.J., Michalet, R., and Delzon, S., Invasive *Acer negundo* outperforms native species in non-limiting resource environments due to its higher phenotypic plasticity, *BMC Ecol.*, 2011, vol. 11, p. 28.
<https://doi.org/10.1186/1472-6785-11-28>
- Pyšek, P., Lambdon, P.W., Arianoutsou, M., Kühn, I., Pino, J., and Winter, M., Alien vascular plants of Europe,

- in *DAISIE Handbook of Alien Species in Europe*, Dordrecht: Springer Netherlands, 2009, pp. 43–61.
https://doi.org/10.1007/978-1-4020-8280-1_4.
- Reinhart, K.O., Gurnee, J., Tirado, R., and Callaway, R.M., Invasion through quantitative effects: Intense shade drives native decline and invasive success, *Ecol. Appl.*, 2006, vol. 16, no. 5, pp. 1821–1831.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D., and West, C.J., Naturalization and invasion of alien plants: Concepts and definitions, *Divers. Distrib.*, 2000, vol. 6, no. 2, pp. 93–107.
<https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Rosario, L.C., *Acer negundo*. Fire Effects Information System (FEIS). USDA Forest Service, Rocky Mountain Research Station, Fire Sciences laboratory. 1988.
<https://www.feis-crs.org/feis/faces/index.xhtml?jsessionid=643C2E17A6A3897DE7A5164F7B70016B>. Accessed April 25, 2021.
- Saccone, P., Pagès, J.P., Girel, J., Brun, J.J., and Michalet, R., *Acer negundo* invasion along a successional gradient: early direct facilitation by native pioneers and late indirect facilitation by conspecifics, *New Phytol.*, 2010, vol. 187, pp. 831–842.
<https://doi.org/10.1111/j.1469-8137.2010.03289.x>
- Shavnin, S.A., Veselkin, D.V., Vorobeichik, E.L., et al., Factors of pine-stand transformation in the city of Yekaterinburg, *Contemp. Probl. Ecol.*, 2016, no. 7, pp. 844–852.
<https://doi.org/10.1134/S199542551607009X>
- Sitte, P., Weiler, E.W., Kadereit, J.W., Bresinsky, A., and Körner, C., *Lehrbuch der Botanik für Hochschulen*. Translated under the title *Botanika*, vol. 4: *Ekologiya* (Ecology), Elenevskii, A.G. and Pavlov, V.N., Eds., Moscow: Akademiya, 2007.
- Tomaszewski, D., *Sorbaria* species cultivated in Poland, *Dendrobiology*, 2001, vol. 46, pp. 59–64.
- Tret'yakova, A.S., Specific features of the distribution of alien plants in natural habitats in urbanized areas of Sverdlovsk Region, *Vestn. Udmurt. Univ., Ser. Biol.*, 2016, vol. 26, no. 1, pp. 85–93.
- Vallet, J., Beaujouan, V., Pithon, J., et al., The effects of urban or rural landscape context and distance from the edge on native woodland plant communities, *Biodivers. Conserv.*, 2010, vol. 19, no. 12, pp. 3375–3392.
<https://doi.org/10.1007/s10531-010-9901-2>
- Veselkin, D.V. and Dubrovin, D.I., Diversity of the grass layer of urbanized communities dominated by invasive *Acer negundo*, *Russ. J. Ecol.*, 2019, vol. 50, no. 5, pp. 413–421.
<https://doi.org/10.1134/S1067413619050114>
- Veselkin, D.V., Galako, V.A., Vlasenko, V.E., Shavnin, S.A., and Vorobeichik, E.L., Relationship between the characteristics of the state of Scots pine trees and tree stands in a large industrial city, *Contemp. Probl. Ecol.*, 2015, vol. 8, no. 2, pp. 243–249.
<https://doi.org/10.1134/S1995425515020158>
- Veselkin, D.V., Kiseleva, O.A., Ekshibarov, E.D., Rafikova, O.S., and Korzhinevskaya, A.A., Abundance and diversity of seedlings of the soil seed bank in the thickets of the invasive species *Acer negundo* L., *Russ. J. Biol. Invasions*, 2018, vol. 9, no. 2, pp. 108–113.
<https://doi.org/10.1134/S2075111718020133>
- Veselkin, D.V., Kuyantseva, N.B., Chashchina, O.E., Mumber, A.G., Zamshina, G.A., and Molchanova, D.A., Levels of leaf damage by phyllophages in invasive *Acer negundo* and native *Betula pendula* and *Salix caprea*, *Russ. J. Ecol.*, 2019, vol. 50, pp. 511–516.
<https://doi.org/10.1134/S1067413619060134>
- Veselkin, D.V., Zolotareva, N.V., Lipikhina, Y.A., et al., Diversity of plants in thickets of invasive *Sorbaria sorbifolia*: differences in the effect on aboveground vegetation and seed bank, *Russ. J. Ecol.*, 2020, vol. 51, pp. 518–527.
<https://doi.org/10.1134/S1067413620060090>
- Vinogradova, Yu.K., Maiorov, S.R., and Khorun, L.V., *Chernaya kniga flory Srednei Rossii* (The Black Data Book of the Flora of Central Russia), Moscow: GEOS, 2009.
- Weathers, K.C., Cadenasso, M.L., and Pickett, S.T., Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere, *Conserv. Biol.*, 2001, vol. 15, no. 6, pp. 1506–1514.
- World Flora Online. <http://www.worldfloraonline.org>. Accessed March 30, 2021.

Translated by M. Shulskaya