

Soil Moisture in Urbanized Habitats Invaded by Alien *Acer negundo*

D. I. Dubrovin^a*, O. S. Rafikova^a, and D. V. Veselkin^a

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

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

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Abstract—We assessed the soil moisture in urbanized habitats dominated by alien (invasive) for Eurasia tree species *Acer negundo*. We supposed that the soil water content under the dense canopy of *A. negundo* is increased compared with the soil water content under other tree species. Sample plots in urbanized habitats in the city of Yekaterinburg (Middle Urals, Russia) were combined into paired blocks: with the dominance of *A. negundo* or the dominance of other tree species. The conditions in each block were as similar as possible, except for the dominant tree species. In 2019–2021, 170 records of the soil water content of the upper 5 cm of soil, 85 records each in habitats dominated by *A. negundo* or other tree species, were performed. The average soil water content in habitats invaded by *A. negundo* ($20.0 \pm 0.9\%$) was slightly but significantly higher than in habitats dominated by other tree species ($18.1 \pm 0.8\%$). The differences were close during the three growing seasons. Also, the differences in soil moisture between habitats dominated by *A. negundo* and other tree species were stable when taking into account the peculiarities of weather conditions and the sample plots altitude. Thus, *A. negundo* is a transforming species with respect to the moisture regime in target habitats. The mechanisms of the environment-transforming impact of *A. negundo* can be associated with the features of both aboveground organ structures and the accumulation and decomposition of leaves and litter, as well as other soil processes.

Keywords: alien plants, biological invasions, ecohydrology, environmental impacts, invasive transforming plants, canopy structure, disturbed habitats

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INTRODUCTION

Alien plants can have an environmentally transforming effect on native ecosystems, showing properties of an edicator species [1]. Such plants, if they expand the range and type of habitats, are classified as transforming species; their distribution causes a high concern [1]. Environmental transforming impacts that change the conditions or the amount of resources in communities are taken into account as leading explanations in several hypotheses on the success of alien species: Global Competition Hypothesis, Sampling Hypothesis, and Ideal Weed Hypothesis [2]. Environmental transforming impacts of alien plants can be realized by influencing the light regime of ecosystems [3, 4], the features of nutrient cycling [4], and different components of biota [5–9].

The idea of a direct causal relationship prevails in plant ecology studying moisture as an environmental factor. At the same time, the moisture regime (soil moisture and precipitation) is considered as a factor that affects both the species composition of communities and the state of individuals [10]. The inverse problem—the effect of plants on soil moisture, is considered less often. For example, it discusses in studying

the post-cutting transformation of forest habitats [11], studying the phenomenon of hydraulic lift [12], or creating drought-resistant varieties.

Alien plants may need more, less, or the same amount of water as native plants [13, 14]. Some of them are able to use soil moisture more efficiently, which allows them to be more competitive compared to native plants in lack of moisture [15, 16]. Both a decrease [13, 17] and an increase [13, 18, 19] in available soil moisture compared to native plant communities were observed in habitats occupied by alien plants. Sometimes there was no transformation of the moisture regime under the dominance of alien species [13, 20, 21]. Indirect arguments also indicate the possibility of multidirectional changes in soil moisture in thickets of alien plants. For example, it has been confirmed that alien plants create a denser canopy of leaves than native ones [3, 22–24]. The resulting shading may contribute to an increase in moisture under the canopy of alien species [25]. At the same time, a large mass of leaves actively transpires, which can lead to soil desiccation [14, 26].

Such heterogeneity of the results is apparently caused by the functional diversity of invasive plants

and it emphasized the need to test the hypothesis about the soil moisture regime for each species. The purpose of this study is to test the hypothesis regarding the features of soil moisture in habitats dominated by the invasive *Acer negundo*. We do not know any special studies of the moisture regime in the communities invaded by *A. negundo*. It has been repeatedly shown [27–29] that it creates more shading than native trees. *A. negundo* is known to be attracted to lowland and floodplain habitats, although this species can also grow in dry upland habitats in the primary [30] and secondary [31, 32] ranges. Based on the ability to have a high shading effect, we tested the hypothesis that under similar conditions the soil moisture in the habitats with dominance of *A. negundo* is higher than in habitats with dominance of other tree species.

MATERIAL AND METHODS

Area. The study was carried out in 2019–2021 within and around the city of Yekaterinburg, its population is 1.5 million people. It is the administrative center of the Sverdlovsk oblast, located in the southern taiga subzone of the boreal-forest zone. The vegetation cover is dominated by pine (*Pinus sylvestris* L.) forests on soddy-podzolic soils and burozems [33]. The climate is temperate continental; winters are long and cold with stable snow cover; summer is short. The average annual temperature is +3.0°C, the average temperature is –12.6°C in January and +19.0°C in July. The average annual precipitation is 550–650 mm. Maximum precipitation occurs in the warm season (May–August), during which about 60–70% of the annual amount falls. The solar altitude at solar noon in June–July is 52°–56°.

Acer negundo is a tree that grows up to 20(25) m high and up to 90(100) cm in diameter. The native range covers North America from the Rocky Mountains to the Atlantic coast and from Canada to Florida [30]. It was introduced into Europe in the 17th century. In Russia the tree has been known since the second half of the 18th century. *A. negundo* is included in the list of the most dangerous invasive species in Europe [34], Belarus [35], and Russia [36, 37] (including Sverdlovsk oblast [38]). In its native range, it grows in floodplain mesotrophic deciduous and coniferous forests, oak woodlands, prairies, fields, and swamps [30]. In the secondary range, it inhabits coastal phytocenoses, mesophytic oak forests, pine forests, disturbed and semi-natural habitats, and it is considered as a transforming species [35, 36]. In the Middle Urals, it is widespread in ruderal and other anthropogenically transformed habitats; it propagates in urban forest parks [39]. In the thickets of *A. negundo*, the α - and γ -diversity of herbs decreases [40, 41], and its high canopy cover is one of the mechanisms of influence on the ground cover [42].

Sample plots. The design of the study is a randomized block observation or a passive experiment. Paired

sample plots (SPs) were selected to measure soil moisture. A block (Fig. 1) was considered to be a site, i.e., a territory that includes a pair of SPs: one SP invaded by *Acer negundo* (An+) and one control SP dominated by another tree species (An–). The species with a total number of trunks on the SP greater than the number of trunks of any other species was considered to be dominant. In one block, the An+ and An– SPs were of the same size, 10 × 10 or 20 × 20 m, and in similar conditions: they were (a) similar in altitude and landscape type; (b) located at a distance of no more than 0.4 km from each other; and (c) close in the degree of anthropogenic transformation. Close values of tree canopy cover were another important criterion for combining the An+ and An– SPs in the same block. Thus, the conditions at the An+ and An– SPs in the same block were similar and differed only in the dominant tree species. An– SPs were dominated by *Malus baccata* (L.) Borkh., *Prunus padus* L., *Pinus sylvestris* L., *Quercus robur* L., *Salix alba* L., *Sorbus aucuparia* L., *Tilia cordata* Mill., and *Ulmus laevis* Pall.

The position of the SP in the relief was characterized by its altitude above sea level (m), which was measured using the SASPlanet program. Altitudes varied from 226 to 309 m a.s.l.

Measurements of the soil water content (SWC) of the upper 5 cm of soil. The SWC measurements of the top 5 cm of the mineral part of the soil were carried out with an HH2 Moisturemeter (UK; Delta-T Devices). The leaves and litter were removed, the sensor was put into the upper layer of the mineral part of the soil vertically downwards, and SWC (in %) was recorded. SWC measurements were performed during 1–3 tours each growing season (Table 1). In one block, SWC measurements were always performed on the same day, so that no precipitation occurred between measurements at the An+ and An– SPs. SWC measurements were carried out according to two designs:

Design I: SWC was measured at 25 points randomly placed within a 10 × 10 m SP or 20 × 20 m SP with leaves and litter removed just before the measurement. Design I was implemented in 2019–2021.

Design II: SWC was measured at 18–24 points on 10 × 10 m SP, confined to fixed areas 0.5 × 0.5 m in size, on which leaves and litter were removed (once at the beginning of the growing season) and the upper 3–5 cm of soil. Design II was implemented in 2019 and 2021.

Canopy cover. We took the color photos of the leaf canopy at each SP in mid-July at 10 random points vertically upwards (from a height of 0.8–1.2 m). In total, 680 canopy photos were taken in 2019 and 2020 using a Lumix DMC-FP2 digital camera (CCD sensor: 1/2.5"/10.3 million pixels/primary color filter; photo resolution: 3648 × 2736 pixels). The images were converted to binary using Adobe Photoshop 11.0 (Adobe System Inc., 2008) in such a way that black pixels corresponded to natural sunlight barriers, and white pixels corresponded to the open sky. Canopy

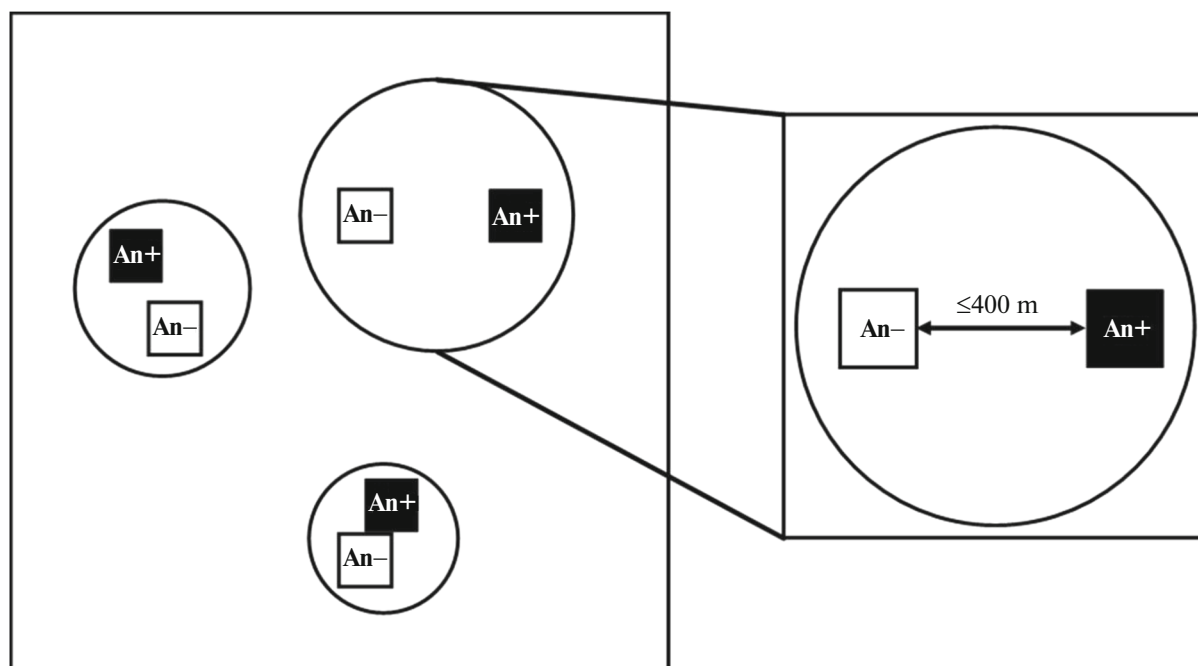


Fig. 1. Layout of sample plots (squares) within blocks or sites (circles); An+ – plots in the thickets of *A. negundo*, An– – plots in the thickets of other tree species.

cover was analyzed using the Matlab R2018b program (9.5.0.944444, The MathWorks Inc., 2018) [42], which estimated the ratio of black pixels to the total number of pixels in the image and the average value of this parameter for the SP, which was analyzed as Canopy cover.

Weather conditions of the growing seasons. Average daily air temperatures and total precipitation from May 1 to August 31, 2019–2021 were extracted from the resource <http://www.pogodaiklimat.ru> [43]. The growing season of 2019 was cool and wet (Table 2), the 2020 season was average in terms of temperature con-

Table 1. Dates and number of SWC measurements

| Date | Number of areas | | Total measurements |
|--|-----------------|-----|--------------------|
| | An– | An+ | |
| Design I: litter removal just before SWC measurement | | | |
| July 22–August 5, 2019 | 11 | 11 | 550 |
| August 20–22, 2019 | 11 | 11 | 550 |
| June 22–26, 2020 | 9 | 9 | 450 |
| July 24–August 3, 2020 | 19 | 19 | 950 |
| July 25–August 4, 2021 | 11 | 11 | 550 |
| Design II: removal of litter, loosening of the top 3–5 cm of soil before the first tour of SWC measurement in the growing season | | | |
| July 10, 2019 | 5 | 5 | 240 |
| July 18, 2019 | 5 | 5 | 240 |
| August 22, 2019 | 5 | 5 | 240 |
| July 15, 2021 | 3 | 3 | 108 |
| July 25, 2021 | 3 | 3 | 108 |
| August 3, 2021 | 3 | 3 | 108 |
| Total | 85 | 85 | 4094 |

Table 2. Average daily air temperatures and total precipitation in the growing seasons of 2019–2021

| Month | Average daily air temperature, °C | | | Total precipitation, mm | | |
|--------|-----------------------------------|------|------|-------------------------|-------|------|
| | 2019 | 2020 | 2021 | 2019 | 2020 | 2021 |
| May | 7.6 | 9.0 | 11.8 | 39.0 | 13.3 | 15.5 |
| June | 11.1 | 9.9 | 13.1 | 49.0 | 72.9 | 51.9 |
| July | 14.8 | 16.8 | 14.5 | 126.1 | 20.7 | 84.5 |
| August | 12.2 | 12.9 | 14.8 | 94.3 | 156.5 | 79.4 |

ditions with a rather wet June and dry July, and the 2021 season was the warmest with an average precipitation.

The characteristics of the current weather conditions in the period immediately preceding the measurement of soil moisture included the amount of precipitation (mm) that fell within 10 days before the measurement of soil moisture. The period of 10 days was chosen on the basis of a preliminary analysis, when the total precipitation was calculated for the period from 1 to 30 days before the measurement of soil moisture. The total precipitation for 10 days showed the strongest regression relationship with SWC.

Data analysis. The average value of SWC (or other parameter) at one SP in a particular tour of measurements, i.e., $n = 2 \times 85 = 170$, was the unit for statistical analysis. Student's *t*-test for pairwise related variables was used to compare the SWC values for the An+ and An– SP pairs with the variability due to all other factors eliminated. The relationship of weather conditions and habitat features with SWC was assessed using general (GLM) and mixed (LMM) linear models. In LMM, the random factor was a block or site. The values expressed in fractions (SWC and canopy cover) were analyzed after preliminary arcsine transformation. Values of total precipitation for 10 days are after a preliminary logarithm. However, untransformed values are used in the text, tables, and figures. The standard error is given through the symbol \pm . The calculations were performed using the JMP 10.0.0 packages (SAS Institute Inc., USA, 2012) and STATISTICA 10.0 (StatSoft, USA).

RESULTS

The arithmetic mean in the entire array of 170 SWC values obtained over three growing seasons was $19.1 \pm 0.6\%$, the median was 17.9%, and the coefficient of variation was 40.2%.

Soil moisture in the An– and An+ habitats. Soil moisture depends on a large number of environmental factors: habitat conditions and growing season conditions, such as rainfall patterns. At the first stage, we performed an analysis of SWC using Student's *t*-test for related variables in order to establish the features of SWC depending on the main factor of interest to us: the tree dominant. This approach made it possible to

estimate the differences in SWC values in the An– and An+ habitats, with the variability associated with other factors, the influence of which we assumed or did not assume. The average SWC in habitats dominated by *A. negundo* was significantly higher than in thickets of other tree species (Fig. 2a): $18.1 \pm 0.8\%$ in the An– plot type and $20.0 \pm 0.9\%$ in the An+ plot type ($t = -1.87$, $dF = 85$, $P = 0.0001$).

The main factors affecting soil moisture. In order to estimate the contribution of the dominant tree species to the overall SWC variation, we calculated the GLM model, which includes discrete and continual predictors: (1) plot type: *A. negundo* or another species dominates tree layer; (2) year of measurement: meaning that this predictor summarizes the weather and phenological features of the growing season; (3) SWC measurement design: with litter removal immediately before each measurement or with litter removal once a season before the first tour of measurements; (4) the SP altitude above sea level; and (5) the sum of precipitation for 10 days preceding the SWC measurement. All two-factor interactions were evaluated, except for the year \times measurement design interaction (Table 3).

The overall quality of the GLM model was high, with the combination of predictors used explaining about 73% of the total SWC variability. All main effects were statistically significant. Consequently, the SWC varied in different years, also depending on the observation option, the measurement design, the altitude, and the amount of recent precipitation. Only one factor out of nine was statistically significant. With additional consideration of the area on which the pair of areas An– and An+ was located as a random factor in the LMM model, the quality of explanation of SWC variability improved. Moreover, all effects that are significant in the GLM are also significant in the LMM.

The average SWC values were $24.4 \pm 0.8\%$ in 2019; $14.0 \pm 0.6\%$ in 2020; and $16.3 \pm 0.9\%$ in 2021. When litter was removed from the site once a season before the first measurement (design II), the SWC values were on average lower ($17.2 \pm 0.9\%$), and when litter was removed immediately before each measurement (design I), they were higher ($19.8 \pm 0.7\%$).

Although the interaction of the factors “year \times measurement design” could not be assessed, higher SWC values when removing the litter immediately before measuring the SWC were clearly visible both in

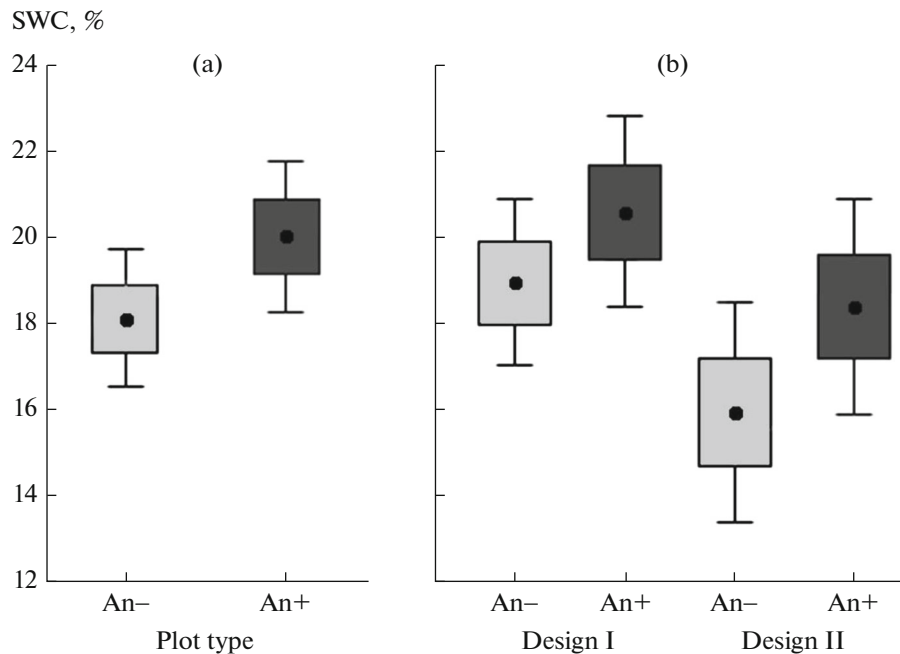


Fig. 2. Soil water content (SWC; mean, \pm SE, \pm 95% confidence interval) of the combined sample (a) and for different measurement designs (b) in the thickets of different tree species (An-; light gray figures) and in the thickets of *Acer negundo* (An+; dark gray figures).

2019 and 2021: in 2019, $SWC = 27.9 \pm 0.9\%$ with design I and $19.3 \pm 1.1\%$ with design II; in 2021, $SWC = 18.4 \pm 1.2\%$ with design I and $13.7 \pm 1.0\%$ with design II. The regularity of higher SWC values during the removal of litter immediately before the moisture measurement was also seen when comparing the An- and An+ plots (Fig. 2b).

The SWC values naturally decreased with an increase in the altitude regardless of the dominant tree (Fig. 3a). Differences in the slopes of the regression lines of the dependences “Altitude – SWC” in the An- and An+ plots were insignificant (Table 3). For every 10 m of altitude, SWC decreased on average by $1.1 \pm 0.3\%$ in plots of *A. negundo* and by $0.9 \pm 0.3\%$ in plots of other tree species.

The SWC values naturally increased with an increase of precipitation that fell 10 days before the measurement regardless of the dominant tree (Fig. 3b). Differences in the slopes of the regression lines of the 10-day precipitation–SWC dependences in the An- and An+ plots were insignificant (Table 3). For every 10 mm of precipitation, SWC increased on average by $2.0 \pm 0.3\%$ in plots of *A. negundo* and by $1.6 \pm 0.3\%$ in plots of other tree species.

Canopy cover as a soil moisture factor. High canopy cover and the resulting high shading on the soil surface or at the level of the grass layer is one of the mechanisms of the environment-transforming influence of *A. negundo* [29, 42]. Therefore, we used the example of SWC measurements in the seasons of 2019 and 2021 to find out which group of factors is more likely to be

associated with SWC variability: characteristics of canopy cover or the presence/absence of litter. We calculated a GLM model including the following predictors: (1) year; (2) SWC measurement design; (3) canopy cover of woody plants; (4) altitude; and (4) the total precipitation for 10 days preceding the SWC measurement (Table 4).

The combination of used predictors explained about 74% of the total variability in SWC values during the 2019 and 2021 growing seasons. Effects related to the characteristics of the conditions in the plots, i.e., with predictors “year,” “altitude,” and “precipitation in 10 days,” were reproduced as statistically significant. Of the two factors of interest to us (measurement design), a weak effect was observed only for the first predictor. In other words, soil moisture in urbanized habitats depended on the litter removal but did not depend on the canopy cover.

DISCUSSION

The soil moisture in urbanized woody habitats varied greatly in different years, depending also on the altitude and the precipitation regime. The influence of the measurement design on SWC was less pronounced; the size of the effect was associated with the litter removal. Differences related to the taxonomic position of the dominant tree were small and they explained only a small part of the overall variability in SWC estimates. However, the differences associated

Table 3. The significance of the influence of five predictors, including the “plot type” factor, and their interactions in the GLM and LMM (with the random factor of “plot”), explaining the variability of SWC in urbanized habitats during the growing seasons of 2019–2021

| No. | Combination of predictors | <i>dF</i> | GLM | | LMM | |
|-----|--|-----------|----------|----------|----------|----------|
| | | | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> |
| 1 | Plot type | 1 | 6.08 | 0.0148 | 8.55 | 0.0040 |
| 2 | Year | 2 | 83.99 | <0.0001 | 84.52 | <0.0001 |
| 3 | Measurement design | 1 | 47.91 | <0.0001 | 20.29 | <0.0001 |
| 4 | Altitude | 1 | 43.60 | <0.0001 | 11.81 | 0.0026 |
| 5 | Precipitation for 10 days | 1 | 48.33 | <0.0001 | 62.60 | <0.0001 |
| 6 | Plot type × year | 2 | 0.79 | 0.4579 | 1.03 | 0.3581 |
| 7 | Plot type × measurement desing | 1 | 0.04 | 0.8457 | 0.02 | 0.8912 |
| 8 | Plot type × altitude | 1 | 0.35 | 0.5550 | 0.55 | 0.4602 |
| 9 | Plot type × precipitation for 10 days | 1 | 0.14 | 0.7066 | 0.18 | 0.6694 |
| 10 | Year × altitude | 2 | 1.20 | 0.3028 | 0.43 | 0.6514 |
| 11 | Year × precipitation for 10 days | 2 | 2.82 | 0.0626 | 2.17 | 0.1176 |
| 12 | Measurement desing × altitude | 1 | 0.52 | 0.4706 | 0.54 | 0.4667 |
| 13 | Measurement desing × precipitation for 10 days | 1 | 7.54 | 0.0068 | 10.67 | 0.0014 |
| 14 | Precipitation for 10 days × altitude | 1 | 0.93 | 0.3376 | 1.98 | 0.1618 |
| | R^2 | | 0.732 | | 0.809 | |
| | R^2_{Adj} | | 0.700 | | 0.786 | |

with the dominant tree were identified for different methods of analysis.

Our working hypothesis was confirmed: a higher soil moisture was observed in habitats invaded by *A. negundo* than in habitats dominated by other tree species under similar conditions. This conclusion is reliable because the data were obtained from a large number of SPs in a series of repeated moisture recordings over a period of 3 years. In some areas, repeated SWC measurements were made 5 times. This conclusion is also realistic, since other patterns of SWC variability associated with altitude, precipitation, and interannual variability are expected and explainable. In particular, the following are well understood: (1) the dependence of SWC estimates on the amount of precipitation for the previous period: the more abundant the precipitation, the higher the soil moisture; (2) the dependence of SWC on the altitude: the higher the altitude of the measurement, the lower the soil moisture; and (3) a higher SWC during the wet and cool season of 2019 compared to the warmer and less humid seasons of 2020 and 2021. Therefore, we can assume that other patterns established on our SWC estimates are plausible.

The results of other studies of soil moisture in thickets of alien species has been very diverse. Evidences have been published of both a decrease [13, 14, 17], an invariance [13, 14, 20, 21], and an increase [13, 14, 18, 19] of soil moisture under alien plants compared to com-

munities of native species. One of the reasons for such diversity was associated with the life form of species [14]. On average, it was drier under alien herbs than under native ones, but it was somewhat wetter under alien trees than under native ones [14]. Therefore, our results agree rather than contradict the body of published information.

The explanation of the probable reasons for the features of soil moisture in *A. negundo* thickets is possible from two positions.

The first one means that *A. negundo* often occupies wetter habitats than other tree species. In order to minimize the probability of such differences, we used a block design with the selection of pairs of habitats invaded by *A. negundo* and controls. The weather conditions and precipitation regime during the growing season for the An– and An+ habitats were the same on the scale of our study. The An– and An+ habitats could differ primarily in their altitude. However, the SPs in pairs in one block were homogeneous according to this condition: the average altitude of An– SP was 261 ± 23 m a.s.l., the average altitude of An+ SP was also 261 ± 23 m a.s.l. (test for dependent samples: $t = -0.04$; $dF = 17$; $P = 0.9648$). Consequently, our data did not allow us to assume that the increased soil moisture in the thickets of *A. negundo* was explained by its initial selectivity to the conditions of moistening of habitats. In general, it seemed unlikely that there could be causes that would explain the increased initial soil

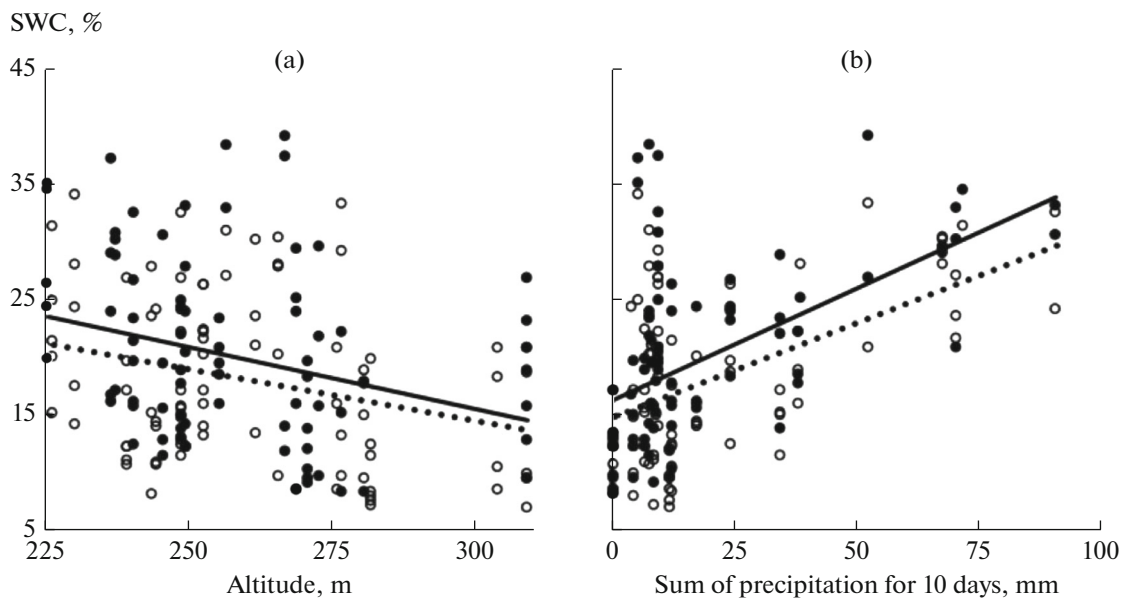


Fig. 3. Relationship of soil water content (SWC) with altitude (a) and total precipitation during 10 days before measurements (b) in habitats dominated by *Acer negundo* (●, solid line) and other tree species (○, dotted line).

moisture in habitats with *A. negundo* and that would be in urbanized ecosystems where natural processes and patterns were subject to strong and unpredictable anthropogenic transformations.

The second position was the assumption that the difference in SWC values between the An– and An+ habitats was related to the ecophysiological or ecological features of *Acer negundo* itself. In other words, it is possible that the increased soil moisture in habitats dominated by *A. negundo* was created by itself. Trees can reduce soil moisture by intercepting precipitation by canopies [44, 45] and transpiration [14, 26], and increase it by shading the soil [25] and creating a layer of litter, which slows down evaporation from the soil surface [46]. It was known that woody plants, both native and invasive, consume more moisture than herbaceous plants [13, 14, 47–49]. Since transpiration is closely related to the intensity of photosynthesis in mesophilic plants with C3 photosynthesis, intensive photosynthesis and transpiration can be assumed in *A. negundo*, as in a fast-growing species [14, 50, 51]. However, these properties would lead to the drying up of the soil, not to an increase in its moisture content.

The increased soil moisture in the thickets of *A. negundo* can be explained by its ability to create high shading or thick litter. Despite our efforts to select similar SPs, canopy cover in the An+ plots was slightly higher ($90.0 \pm 0.5\%$) than in the An– plots ($88.5 \pm 0.7\%$), and these differences were significant (test for linked populations: $t = 2.22$; $dF = 65$; $P = 0.0303$). It was also expectedly higher shading under the canopies of *A. negundo* ($13 \pm 2 \text{ lux} \times 10^2$) than under the canopies of other trees ($25 \pm 4 \text{ lux} \times 10^2$) [29]. Increased shading in thickets of *A. negundo* has also been

observed by other researchers [27, 28, 52]. Therefore, the increased soil moisture in the thickets of *A. negundo* can be explained by its ability to form a dense leaf canopy. But when we compared the SWC values with the habitat conditions (Table 4), this assumption was not confirmed. According to our estimates, soil moisture did not depend on the canopy cover, but it depended on the litter removal. The areas where the litter was removed prior to the start of the measurement period were drier than the areas where the litter was removed just before the SWC measurement. This phenomenon is understandable. It is known that the litter has a significant moisture capacity [53] and prevents the evaporation of water from the mineral part of the soil [46]. The observed difference in SWC between the An– and An+ habitats could be explained, for example, by assuming that the litter is more developed in An+ than in An–. However, the characteristics of the litter, the rate of their accumulation and decomposition in *A. negundo* thickets are not known. At the same time, a high rate of *A. negundo* litter decomposition is known [54], which does not support the assumption that the litter layer is the cause of increased moisture in habitats with its dominance.

Thus, comparison of our results with published data did not allow us to easily explain the causes of increased soil moisture in *A. negundo* thickets. There are arguments both for and against that increased moisture may be associated with structural features of the leaf apparatus and canopies or with the accumulation and decomposition of *A. negundo* litter, but there is not enough information to reliably resolve this issue.

Table 4. The significance of the influence of five predictors, including the “canopy cover” factor, and their interactions in the GLM and LMM models (with a “SP” random factor), explaining the variability of SWC in urbanized habitats during the growing seasons of 2019 and 2021

| No. | Combination of predictors | <i>dF</i> | GLM | | LMM | |
|-----|--|-----------|----------|----------|----------|----------|
| | | | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> |
| 1 | Year | 1 | 86.78 | <0.0001 | 91.50 | <0.0001 |
| 2 | Measurement design | 1 | 5.28 | 0.0233 | 4.80 | 0.0305 |
| 3 | Canopy cover | 1 | 0.95 | 0.3323 | 0.57 | 0.4506 |
| 4 | Altitude | 1 | 19.84 | <0.0001 | 9.73 | 0.0048 |
| 5 | Precipitation for 10 days | 1 | 26.92 | <0.0001 | 35.17 | <0.0001 |
| 6 | Year × canopy cover | 1 | 0.03 | 0.8744 | 0.01 | 0.9074 |
| 7 | Year × altitude | 1 | 0.32 | 0.5698 | 0.30 | 0.5882 |
| 8 | Year × precipitation for 10 days | 1 | 1.36 | 0.2455 | 2.63 | 0.1075 |
| 9 | Measurement design × canopy cover | 1 | 0.06 | 0.8157 | 0.11 | 0.7398 |
| 10 | Measurement design × altitude | 1 | 0.22 | 0.6432 | 0.46 | 0.5016 |
| 11 | Measurement design × precipitation for 10 days | 1 | 9.95 | 0.0020 | 10.88 | 0.0013 |
| 12 | Canopy cover × altitude | 1 | 2.86 | 0.0936 | 1.60 | 0.2105 |
| 13 | Canopy cover × precipitation for 10 days | 1 | 0.59 | 0.4422 | 0.49 | 0.4844 |
| 14 | Altitude × precipitation for 10 days | 1 | 0.50 | 0.4813 | 1.20 | 0.2760 |
| | R^2 | | 0.735 | | 0.799 | |
| | R^2_{Adj} | | 0.703 | | 0.774 | |

CONCLUSIONS

The results can be summarized in the form of three statements.

The soil moisture is higher in habitats invaded by the alien tree *Acer negundo* compared to habitats with other dominant trees. The difference in soil moisture between habitats invaded by *A. negundo* and other species is small, but this difference is established reliably and it steadily manifests in different growing seasons against the background of other habitat features and against the background of the influence of weather conditions. Thus, the main part of the working hypothesis related to the direction of expected differences in soil moisture between habitats with and without *A. negundo* dominance was confirmed.

It is more likely that the reason for the increased soil moisture in *A. negundo* thickets is not the initial differences between habitats, but the environment-transforming effect of *A. negundo* itself. This conclusion is less reliable than the first one, but it confirms that *A. negundo* is not only an alien tree and an invasive species with an expanding range and range of habitats, but also a transforming species that can change not only the light regime in invaded communities [29, 42], but also the moisture regime.

The working hypothesis of a significant relationship between canopy cover and soil moisture in urbanized habitats was not confirmed. Therefore, special studies are needed to understand the mechanisms of

the environment-transforming effect of *A. negundo*. In this case, one should take into account the effects associated both with aboveground structures and processes, and with the accumulation and decomposition of litter, as well as other soil processes.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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