

Regeneration and spread patterns of *Acer negundo* L. in habitats with different levels of anthropogenic disturbance

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ABSTRACT

This study investigates the regeneration and spread of the invasive alien tree species *Acer negundo* L. in forest and roadside habitats subjected to different levels of anthropogenic disturbance in Lithuania. *A. negundo* is considered one of the most aggressive non-native woody species in riparian and disturbed forest ecosystems, posing ecological and management challenges due to its high regenerative capacity. Field investigations were conducted in 2024–2025 in the Dubrava and Jonava regional divisions of the state forest enterprise (VMU). Regeneration patterns were assessed in forest sample plots and roadside transects representing recently cut stands, forest edges, and open roadside habitats subjected to repeated mechanical disturbance. Naturally regenerated individuals were classified by height and origin, distinguishing vegetative regeneration associated with stumps and underground woody structures from seed-origin saplings. Additional laboratory experiments were carried out to assess seed germination following cold stratification. The results showed that regeneration was strongly concentrated in disturbed habitats. After cutting, vegetative regeneration clearly dominated: stump-origin shoots accounted for approximately 60% of all regenerants, while other vegetatively regenerated individuals comprised about 30%. Total densities exceeded 38,000 saplings per hectare in roadside transects. Seed-origin individuals represented only about 10% of regeneration in forest stands, indicating limited natural establishment despite the species' high reproductive potential. Laboratory germination reached 82% after cold stratification, and individual female trees produced on average about 21,000 samaras (42,000 seeds) per season. These findings demonstrate that the persistence and spread of *Acer negundo* are primarily driven by vegetative regeneration following mechanical disturbance, while seed-based reproduction facilitates longer-distance dispersal and population expansion. The study provides quantitative evidence of the species' high phenotypic plasticity and explains its invasive success in disturbed forest-edge and roadside habitats of the temperate zone.

Keywords: *Acer negundo*, vegetative regeneration, seed regeneration, anthropogenic disturbance, forest edges, invasive species.

INTRODUCTION

Acer negundo L. is a non-native invasive tree species in Europe that has become widespread in riparian zones, forest edges, urban environments, and other anthropogenically disturbed habitats (Sikorska et al., 2019; Campagnaro et al., 2018). Owing to its high ecological plasticity, rapid growth, and tolerance to repeated disturbance, the species is increasingly recognized as a major driver of habitat homogenization and biodiversity loss in temperate ecosystems (Saccone et al., 2013). Native to central and northern North America, *A.*

negundo naturally occurs in river floodplains and riparian forests, where it often forms extensive stands under dynamic disturbance regimes (DeWine and Cooper 2007). The species was introduced to Europe in the 17th century and widely planted as an ornamental and utility tree due to its fast growth and adaptability to variable environmental conditions (Straigytė et al., 2015).

In Lithuania, *A. negundo* was introduced in the early 19th century and extensively used in urban green spaces, roadside plantings, and later in forest plantations (Straigytė et al., 2015). Although initially valued for its tolerance to soil moisture

fluctuations and low maintenance requirements, the species gradually escaped cultivation and spread into semi-natural and natural habitats. Its expansion accelerated during the second half of the 20th century, particularly in riparian zones, forest edges, and other disturbed environments (Sikorska et al., 2019).

By the 1960s, *A. negundo* was already recognized as problematic in forestry due to its ability to outcompete native riparian species, particularly willows (*Salix* spp.), and to alter stand structure. However, formal recognition of the species as invasive and its inclusion in national eradication regulations occurred much later, in 2004, reflecting the long lag phase typical of woody plant invasions in Europe (Straigytė et al., 2015; Ministry of Environment of the Republic of Lithuania, 2004). At the European Union level, *A. negundo* is currently listed among priority invasive alien species under Regulation (EU) No. 1143/2014.

The invasion success of *A. negundo* is closely linked to its biological traits. The species demonstrates high tolerance to environmental stressors such as flooding, shading, pollution, and repeated mechanical disturbance (Porté et al., 2011). It reproduces both vegetatively and generatively, producing abundant stump-origin shoots after cutting and large quantities of wind- and water-dispersed samaras (Burns and Honkala, 1990; Sikorska et al., 2019).

According to the Silvics of North America, *A. negundo* exhibits strong vegetative regeneration from stumps and underground structures and produces large quantities of wind-dispersed seeds with physiological dormancy requiring cold stratification (Overton, n.d.).

Previous studies have shown that logging can alter the trade-off between seed-based and vegetative regeneration in woody species, with species-specific shifts in regeneration strategy shaping post-disturbance population structure (Li et al., 2020).

Vegetative regeneration allows rapid local persistence following disturbance, while seed-based regeneration facilitates spatial expansion beyond existing stands, particularly along river corridors and disturbed forest edges (Saccone et al. 2013). Experimental studies have shown that *A. negundo* outperforms native tree species under conditions of high light availability and non-limiting resource supply, whereas its competitive advantage declines under shaded or resource-limited environments (Porté et al., 2011).

In addition to these effects on regeneration and competitive interactions, invasive *A. negundo* has been shown to influence ecosystem processes through leaf litter inputs, affecting microbial abundance and activity in riparian environments (Krevš and Kučinskienė, 2017).

Although the ecological impacts of *A. negundo* in riparian and urban habitats are well documented, quantitative information on the relative contribution of vegetative versus seed-based regeneration under different types and intensities of anthropogenic disturbance remains limited, particularly in temperate forest and forest-edge ecosystems. Understanding this balance is essential for interpreting population dynamics after disturbance and for predicting invasion trajectories.

The aim of this study was to evaluate the regeneration intensity and spread of *A. negundo* in forest habitats subjected to different forms of anthropogenic disturbance. Specifically, we assessed the relative importance of vegetative and seed-based regeneration in shaping population structure following logging and roadside management, combining field inventories with seed production and germination experiments.

MATERIALS AND METHODS

Regeneration and spread of *Acer negundo*

Studies on the regeneration and spread of box elder (*Acer negundo* L.) were conducted in 2024–2025 in the Dubrava and Jonava regional divisions of the State Forest Enterprise of Lithuania. The investigations were carried out in mature forest stands in which *A. negundo* formed part of the stand composition. The study plots differed in whether forest harvesting operations had been conducted or not. The study sites were located in central Lithuania (approximately 54.9–55.1° N, 23.9–24.2° E).

Regeneration of *A. negundo* in forest stands was assessed in eight study plots established in the Dubrava and Jonava regional divisions. Six plots were located in mature stands where harvesting had been carried out and where *A. negundo* stumps and belowground woody structures were present, while two plots were established in mature stands where no harvesting had been conducted. Each study plot was treated as an independent sampling unit. Within each plot, eight systematically distributed sample plots of 0.01

ha (10 × 10 m) were established. In these plots, the abundance of *A. negundo* regeneration, its distribution among height classes, origin (where possible), and vitality and damage status were recorded. Basic stand characteristics of each study plot are presented in Table 1.

All naturally regenerated individuals were classified into height groups following the standard methodology used in the National Forest Inventory of Lithuania (Kuliešis and Kulbokas 2009): group I – saplings up to 0.5 m in height; group II – saplings of 0.5–1.5 m high; group III – saplings of 1.5–3 m high and group IV – saplings height exceeding 3 m.

According to origin, regeneration was classified as vegetative or generative. Vegetative regeneration included stump sprouts and vegetative shoots originating from belowground or superficial woody structures. Stump sprouts were recorded when regeneration was directly connected to a remaining *Acer negundo* stump or its fragments. Vegetative shoots occurring away from visible stumps were attributed to vegetative regeneration from belowground structures; however, their exact anatomical origin could not be determined unequivocally under field conditions. Generative regeneration was identified based on the presence of a pronounced taproot formed from seed germination; therefore, seed origin could be reliably determined only for individuals up to 1.5 m in height. Identification of origin in taller individuals was limited due to the subsequent development of horizontal root systems.

Additional investigations of *A. negundo* regrowth were conducted in roadside habitats that differed in the type and timing of anthropogenic

disturbance. In total, six transects were established, each 60 m in length and 3 m in width. Three transects were located in regularly mown roadside grasslands, where mowing is performed annually and regeneration was assessed in spring of the same year. The remaining three transects were established along forest edges adjacent to roads, where clearing operations had been carried out two years prior to the survey, allowing assessment of *Acer negundo* regrowth after a longer period following mechanical disturbance.

Seed germination tests

Seeds of *A. negundo* were collected in autumn 2024 from eight forest stands. After drying, samaras were manually cleaned and wings were removed. Seeds were mixed thoroughly, and germination tests were conducted using three replicates of 100 seeds; in total, germination was assessed for 1200 seeds. Germination tests were conducted under controlled laboratory conditions at a forestry research laboratory in Lithuania.

Seeds were subjected to moist-cold stratification for 60–90 days at 3 ± 1 °C. Germination was carried out on moist filter paper in Petri dishes at 15 ± 1 °C under an 8–12 h photoperiod for 21 days.

Seedling development was assessed on days 7 and 21. Seeds were evaluated individually and classified as normal seedlings, abnormal seedlings, empty seeds, dead (rotten) seeds, or mechanically damaged seeds according to ISTA criteria. Classification was based on visual assessment of seed and seedling morphology during germination; empty seeds were identified by the absence of endosperm or embryo, dead (rotten)

Table 1. Stand characteristics of the studied sites

Sample plot number	Species composition of stand*	Forest site	Age	Stocking level	Remarks
1	4Q4Qr2B+Rb, Ku	Nc	43	0.7	<i>A. negundo</i> was removed in 2021
2	7B1Q1D+Ku, Rb	Nb	40	0.7	<i>A. negundo</i> was removed in 2021
3	5M4Q1B+Rb, Ku, D	Nb	40	0.7	<i>A. negundo</i> was removed in 2021
4	8B2Q+Ku	Nb	43	0.7	
5	8B1Q1D+Ku	Nb	43	0.7	
6	9Q1B+Ku	Nc	50	0.6	<i>A. negundo</i> was removed in 2023
7	9Q1B+Ku	Nc	50	0.6	<i>A. negundo</i> was removed in 2022
8	9B1Q+Ku	Lc	40	0.6	<i>A. negundo</i> was removed in 2023

Note: * Species composition is expressed according to the Lithuanian forest typology system, where numbers indicate the proportion of tree species in tenths of stand composition. Abbreviations denote tree species as follows: Ku – box elder (*Acer negundo*), Q – oak (*Quercus robur*), Qr – red oak (*Quercus rubra*), B – birch (*Betula pendula*), D – aspen (*Populus tremula*), M – larch (*Larix decidua*), Rb – black locust (*Robinia pseudoacacia*).

seeds by tissue discoloration and decay, and mechanically damaged seeds by visible physical injuries to the seed coat or embryo. Empty and dead seeds were recorded as non-germinated seeds. When seed viability was uncertain, a tetrazolium test was applied. Germination results were expressed as absolute numbers and percentages. Mean values and standard deviations were calculated based on three replicates.

Fruiting assessment

Fruiting intensity of *A. negundo* was assessed on ten fruiting trees selected within the study area. Only trees bearing samaras were included in the analysis. Fruiting was evaluated at the individual-tree level. For each sampled tree, all accessible fruiting branches meeting the selection criteria were included in the assessment. A fruiting branch was defined as a second- to fourth-order twig at least 0.5 m in length bearing at least one cluster of samaras. Only branches of the same hierarchical order were considered to avoid double counting.

For each tree, the total number of fruiting branches was recorded. The length of fruiting branches was measured, and the number of samaras per branch was counted. The number of seeds per branch was estimated by multiplying the number of samaras by two. Total numbers of samaras and seeds per tree were calculated by summing values across all fruiting branches. In addition, mean samara density was calculated as the number of samaras per meter of branch length.

Data were analyzed using descriptive statistics. Mean values, standard deviations, and ranges were calculated for regeneration, fruiting, and seed germination characteristics. Regeneration data were summarized separately for forest plots and roadside transects representing different disturbance regimes. Seed germination results were expressed as percentages and absolute values. All data processing and analyses were performed using Microsoft Excel.

RESULTS AND DISCUSSION

The regeneration dynamics of *Acer negundo* saplings was assessed in areas where ornamental stands were clear-cut

In transects established along roadside belts within the Jonava Forest Division, an average of 45

A. negundo stumps (range 43–46) with a diameter greater than 3 cm (range 3–17 cm) were recorded, corresponding to approximately 2500 stumps ha⁻¹. Across all transects, the total density of *A. negundo* saplings exceeded 38,000 individuals per hectare, indicating a very intensive vegetative regeneration following mechanical disturbance. On average, more than 15 vegetatively regenerated shoots were recorded per stump, demonstrating the strong resprouting capacity of the species.

Analysis of the contribution of stump-origin shoots across height classes showed that their proportion increased with sapling height, indicating a higher growth potential of stump-origin regeneration compared to other vegetatively regenerated shoots. Similar regeneration patterns, where stump-origin shoots dominate higher height classes after disturbance, have been reported for other invasive woody species (Williams-Linera et al., 2023).

Height class distribution revealed that the majority of regenerating individuals were between 0.5 and 3.0 m tall, whereas saplings shorter than 0.5 m accounted for approximately one-fifth of the total population (Figure 1). This pattern indicates rapid post-disturbance shoot growth and the formation of a dense regeneration layer dominated by vigorous vegetative sprouts.

Similar regeneration patterns have been reported in the USDA *Silvics of North America*, where *Acer negundo* is described as a species with strong vegetative vigor and the ability to regenerate from stumps and underground vegetative structures even under suboptimal environmental conditions (Burns and Honkala, 1990). This capacity allows the species to rapidly recover after mechanical disturbance and contributes to its persistence in anthropogenic habitats. As emphasized by Kenefick et al. (2024), invasive tree species with high resprouting ability can maintain population stability despite repeated disturbance, which is consistent with the regeneration dynamics observed in the studied transects.

A moderate positive correlation was found between stump diameter (3–17 cm) and the total number of sprouts ($R^2 = 0.47$; $p < 0.001$) (Figure 2a), indicating that thicker stumps produce a higher number of vegetative shoots. This relationship is commonly attributed to larger carbohydrate reserves and a higher density of dormant buds in larger stems (Bond and Midgley, 2001) and has been reported for other invasive woody species with strong resprouting capacity (Kurokuchi et al., 2010).

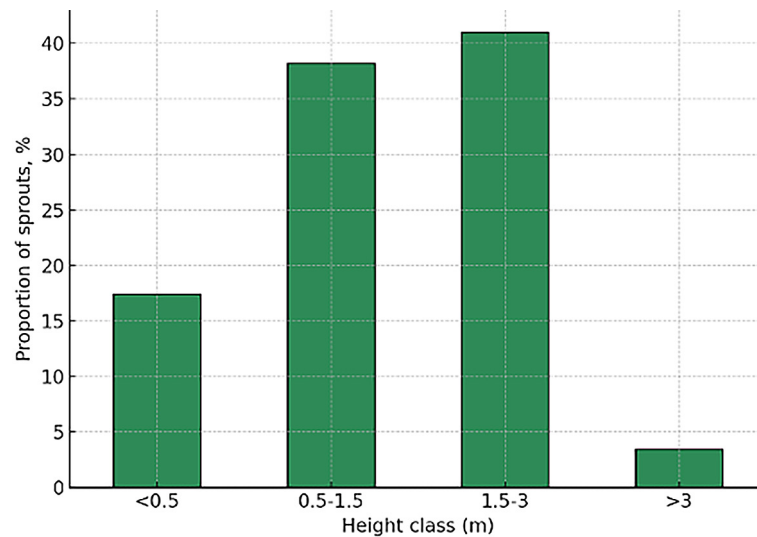


Figure 1. Height class distribution of *A. negundo* saplings (%)

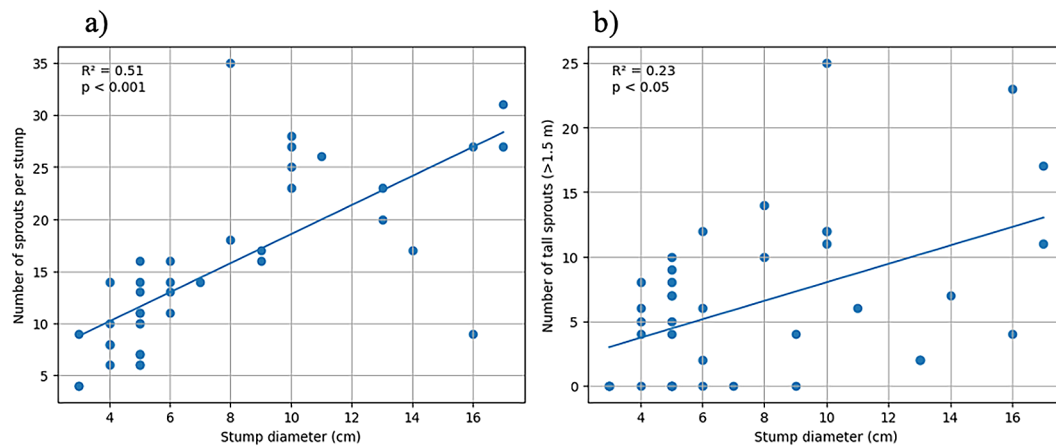


Figure 2. Relationships between stump diameter and sprouting intensity of *A. negundo*. (a) Relationship between stump diameter and total number of sprouts per stump. (b) Relationship between stump diameter and number of tall sprouts (>1.5 m)

A weaker but still significant relationship was observed between stump diameter and the number of tall sprouts (>1.5 m) ($R^2 \approx 0.25$; $p < 0.05$) (Figure 2b), suggesting that stump size influences not only the quantity of shoots but also the likelihood that some individuals reach higher height classes.

This indicates that mechanical removal alone is not an effective control method. Similar conclusions have been reported from protected areas, where repeated mechanical control of *A. negundo* often fails due to strong resprouting capacity and rapid vegetative recovery (Nikolaeva et al., 2020). As noted by Saccone et al. (2013) and Sikorska et al. (2019), the management of *A. negundo* populations should be based on an integrated approach that includes enhancing ecological resistance,

restoring habitats, and incorporating socio-ecological factors.

According to Del Tredici (2001), thicker stems possess greater reserves of photosynthetic resources in roots and stems, enabling faster growth and providing a competitive advantage.

In annually mown meadow transects, *Acer negundo* regeneration was dominated by sprouts 0.5–1.5 m in height, which accounted for approximately two-thirds of all individuals per hectare (Figure 3). Sprouts shorter than 0.5 m represented about one-third of the population, whereas individuals taller than 1.5 m were rare (<2 %).

In contrast, transects located along forest-adjacent roadsides and surveyed two years after mechanical clearing showed a different height

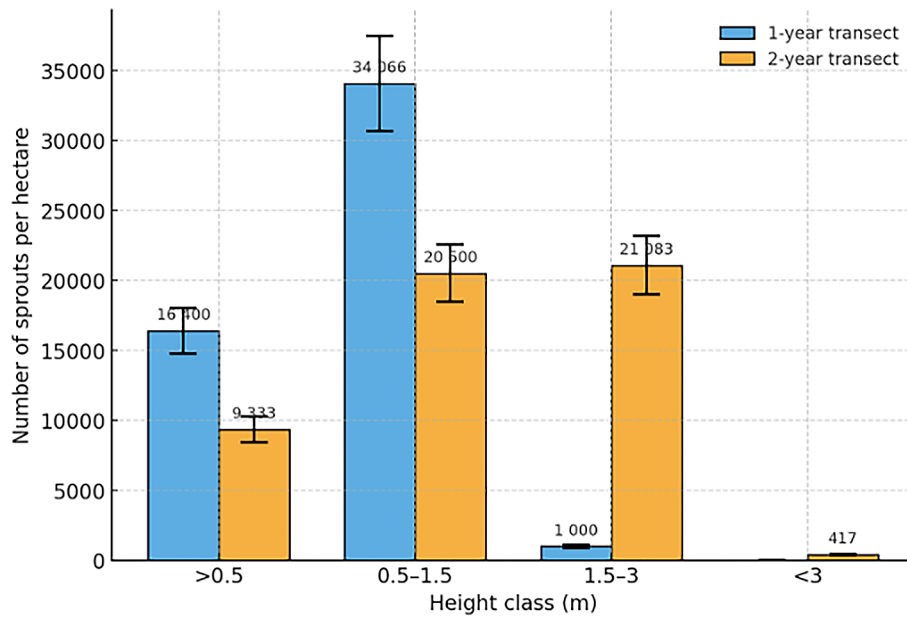


Figure 3. Height class distribution of *A. negundo* sprouts in 1- and 2-year transects (individuals per hectare)

structure, with a lower proportion of short sprouts and a higher proportion of individuals in the 1.5–3 m height class.

Thus, differences in height structure primarily reflect mowing frequency and time since mechanical disturbance rather than differences in regenerative capacity.

Despite annual mowing, *A. negundo* maintained a strong vegetative resprouting capacity in meadow transects, forming a dense but low regeneration layer. Regular cutting limited vertical growth but did not prevent clonal persistence, allowing the species to survive under continuous disturbance.

Similar patterns of resilience to repeated mechanical disturbance have been reported for invasive plant species in various ecosystems (Dostál

et al., 2013; Chytrý et al., 2012). These studies indicate that mowing and roadside maintenance may reduce biomass and height growth but often fail to eliminate invasive species, instead maintaining open and well-lit conditions that support continued regeneration.

Regeneration of *A. negundo* in forest stands

In forest sample plots located in the VMU Jovana and Dubrava regional divisions, the average density of naturally regenerated *A. negundo* individuals, including stump-origin shoots and other vegetatively regenerated individuals spatially associated with parent trees, reached approximately 2660 saplings per hectare, although regeneration

Table 2. Density of *A. negundo* saplings (ha⁻¹) in sample plots

Sample plot number	Number of trees ha ⁻¹	Number of stumps ha ⁻¹	Number of saplings ha ⁻¹	Saplings height class				Part of Stump sprouts, %
				<0.5 m	0.5–1.5 m	1.5–3 m	>3 m	
1	0	60	855	142	122	204	387	74.3
2	0	102	959	1	0	367	591	95.3
3	0	30	368	4	22	101	241	89.2
4	112	0	90	50	30	10	0	0
5	89	0	60	50	10	0	0	0
6	28	130	4790	3370	590	730	100	73.9
7	16	160	5400	200	1000	2000	2200	52
8	67	220	8760	1500	3000	2860	1400	92
Mean ±SE	37.75 ± 16.0	87.75 ± 28.1	2660.25 ± 1149.7	664.62 ± 425.5	596.75 ± 366.3	784.00 ± 377.5	614.88 ± 278.5	59.59 ± 13.9

intensity varied markedly among plots (Table 2). Recently logged plots (plots 6–8) exhibited the highest regeneration densities, while uncut stands (plots 4–5) supported only sparse regeneration. Previously logged plots lacking overstory trees (plots 1–3) showed intermediate sapling densities dominated by tall, stump-origin shoots.

Across all forest plots, the majority of regenerated individuals belonged to the 1.5–3 m height class, with an average of 784 individuals per hectare. Vegetative regeneration clearly dominated: stump-origin shoots accounted for approximately 60% of all saplings, while an additional ~30% consisted of vegetative shoots emerging independently of visible stump structures. These vegetative shoots were mainly observed in areas where woody underground or near-surface structures occurred close to the soil surface, with adequate aeration and soil moisture, often forming linear or clustered spatial patterns around parent trees.

Seed-origin saplings constituted approximately 10% of the regenerated population and were typically found several metres away from mature trees in more open and well-lit microsites. Although generative regeneration played a secondary role compared to vegetative reproduction, it contributed to spatial expansion beyond the immediate vicinity of parent trees. Previous studies indicate that natural germination of *A. negundo* seeds is generally low without prolonged cold stratification (Burns and Honkala, 1990), which is consistent with the limited proportion of seed-origin individuals observed in this study.

Comparison with roadside transects showed that the average number of vegetatively regenerated shoots per stump was higher in forest stands (approximately 30 saplings per stump) than in open, regularly mown habitats (about 15 saplings per stump). This difference likely reflects contrasting microclimatic and disturbance conditions. In forest environments, higher soil moisture and reduced temperature fluctuations may enhance stump vitality and support intensive resprouting, whereas repeated mowing in open habitats limits shoot development.

The height structure of stump-origin regeneration was closely related to the time elapsed since cutting. In plots where logging had occurred in 2018–2019 (plots 1–3), tall individuals (>3 m) predominated, accounting for approximately 40–60% of all vegetatively regenerated shoots. In contrast, in plots subjected to more recent cutting (plots 6–8), low shoots (<0.5 m) dominated,

comprising 65–70% of all individuals. These patterns indicate a typical post-disturbance regeneration trajectory, in which short shoots prevail shortly after cutting, followed by gradual differentiation into higher height classes over time (Matula et al., 2020; Li et al., 2022).

Regeneration intensity in the Dubrava plots was strongly influenced by light availability and microclimatic conditions. Uncut stands with closed canopies supported only sparse regeneration, primarily composed of low-height individuals. In contrast, open areas created by recent logging supported dense populations of vigorous vegetative shoots. This confirms that *A. negundo* regenerates most effectively under increased light availability, whereas establishment and growth are restricted under shaded conditions (Porté et al., 2011). Similar patterns have been observed in other forest ecosystems, where canopy gaps created by disturbance significantly facilitate the establishment of invasive plant species by increasing light availability (Subedi et al., 2024).

Overall, the results demonstrate that vegetative regeneration is the principal mechanism driving *A. negundo* persistence in forest habitats following disturbance, while seed-based regeneration contributes to longer-distance spread and spatial expansion.

Seed germination of *A. negundo*

Seed germination tests showed high viability of *Acer negundo* seeds. Normal seedlings accounted for 82% of all tested seeds (984 out of 1200) (Figure 4). Abnormal seedlings comprised 9% (108), mechanically damaged seeds 3% (36), dead (rotten) seeds 2% (24), and empty seeds 4% (48).

Overall, non-viable seed categories represented approximately 18% of the total sample. The high proportion of normal seedlings indicates a strong generative regeneration potential of *A. negundo* following cold stratification.

The high proportion of normally developed seedlings indicates that *A. negundo* possesses a substantial generative regeneration capacity, despite vegetative reproduction being the dominant local renewal mechanism. Similar germination levels have been reported for this species following sufficient cold stratification (Burns and Honkala, 1990; Kiseleva et al., 2020).

The effectiveness of seed germination under natural conditions depends on winter climatic regimes. In Lithuania, winters typically provide

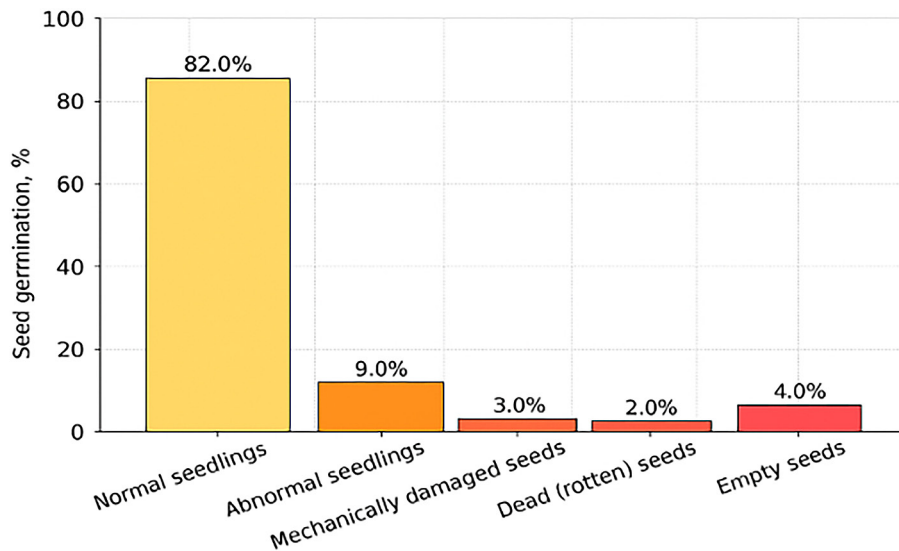


Figure 4. Seed germination structure of *A. negundo* (n = 1200)

prolonged cold periods that are sufficient to break physiological dormancy in *A. negundo* seeds. These conditions are broadly comparable to those within the native range of the species in North America, suggesting that natural winter stratification enables successful germination in spring.

Although seed-origin individuals constituted a smaller proportion of regeneration compared to vegetative shoots, effective seed germination facilitates dispersal beyond existing clonal patches and contributes to spatial expansion into newly disturbed habitats. This combination of strong vegetative persistence and viable seed-based regeneration enhances the invasive potential of *A. negundo*.

Despite the very high seed viability of *Acer negundo* observed under laboratory conditions, seed-based regeneration was limited under natural field conditions, likely due to unfavorable microhabitat availability, competition with intensive vegetative regeneration, and repeated anthropogenic disturbance, highlighting a clear discrepancy between regenerative potential and its realization in natural ecosystems.

Seed production of *A. negundo*

Seed production in *A. negundo* was abundant but showed high variability among individual

Table 3. Quantitative characteristics of *A. negundo* seed production per tree

Tree ID	Number of fruiting branches	Approx. branch length (m)	Number of samaras per branch	Number of seeds per branch	Total samaras per tree	Total seeds per tree
1	115	2.4	389	778	44735	89470
2	81	1.5	123	246	10692	21384
3	93	1.6	277	554	25761	51522
4	72	1.4	103	206	7416	14832
5	102	2.3	282	564	28764	57528
6	86	1.8	221	442	19006	38012
7	79	1.4	172	344	13588	27176
8	97	1.9	233	466	22601	45202
9	83	2.5	307	614	25481	50962
10	76	1.4	172	344	13072	26144
Mean	88.4	1.82	227.9	455.8	21111.6	42223.2
Standart deviation (SD)	13.28	0.44	88.49	176.98	10961.36	21922.72

Note: values are mean ± SD; n = 10 trees. Seed counts assume two seeds per samara.

trees (Table 3). Female trees produced between 7.4 and 44.7 thousand samaras per season (equivalent to 14.8–89.5 thousand seeds), with an average of 21.1 thousand samaras (42.2 thousand seeds) per tree. The yield was largely determined by the number of fertile branchlets and the fruit load per branch - on average, 88 branchlets per tree, about 228 samaras per branch, and approximately 125 samaras per meter of branch length. The maximum recorded value (89.5 thousand seeds) indicates that under favorable conditions, seed production may reach or even exceed the threshold reported in previous studies (Valantinaitė et al., 2011).

The results indicate that *A. negundo* exhibits a high reproductive potential under favorable environmental conditions. Although the variation among individuals was substantial, even the least productive trees produced several thousand seeds per season, ensuring continuous replenishment of the seed bank. Such variability may be associated with tree vitality, age, and light availability. Reproductive effort in female individuals increases with crown exposure and nutrient accessibility, which supports the observed pattern in this study.

Overall, these findings confirm that the species is capable of prolific seed production, which, combined with its strong vegetative regeneration, enhances its invasive success in disturbed habitats.

CONCLUSIONS

The study demonstrates that the regeneration of *Acer negundo* after disturbance is primarily driven by vegetative processes, which enable the species to persist and rapidly re-establish populations following mechanical cutting. Vegetative regeneration ensures local population stability even under repeated disturbance and represents the dominant short-term response in both open and forested habitats.

Regeneration patterns varied across habitats and disturbance regimes, indicating a high degree of ecological plasticity. Differences in height structure were mainly associated with mowing intensity, light availability, and time since disturbance, rather than with intrinsic differences in regenerative capacity. This suggests that observed variation in shoot height reflects post-disturbance dynamics and resilience rather than reproductive success per se.

Seed-based regeneration played a secondary but ecologically important role. Although

generative recruitment contributed less to local stand renewal than vegetative regeneration, it remains essential for spatial expansion and colonization beyond the immediate vicinity of parent trees. High seed production and successful germination following cold stratification indicate that generative reproduction complements vegetative persistence and enhances long-term spread potential.

Taken together, the results highlight a dual regeneration strategy in *A. negundo*, combining rapid vegetative recovery after disturbance with effective seed production and dispersal. This combination allows the species to maintain populations under a wide range of environmental conditions and disturbance intensities, contributing to its invasive success in anthropogenically influenced landscapes.

From a management perspective, the dominance of vegetative (coppicing) regeneration suggests that mechanical removal alone may be insufficient for effective control of *Acer negundo*. Disturbance such as cutting or mowing often triggers intensive resprouting, potentially increasing local regeneration density. Therefore, effective control strategies should combine repeated follow-up treatments with measures that restore canopy closure and enhance competition from native tree species, particularly in forest edges and roadside habitats following disturbance. In a broader ecological context, the findings are consistent with patterns reported for other invasive woody species that rely on strong resprouting ability and flexible regeneration pathways. The dominance of vegetative regeneration following disturbance underscores the importance of disturbance regimes and habitat structure in shaping invasion dynamics, while seed-based regeneration facilitates longer-term expansion across the landscape.

Overall, *A. negundo* exhibits a regeneration strategy characterized by high resilience, rapid recovery, and strong adaptive capacity, which together explain its persistence and spread in disturbed forest edges, riparian zones, and managed open habitats.

REFERENCES

1. Bond, W.J., Midgley, J.J. (2001). Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution*, 16(1), 45–51. [https://doi.org/10.1016/S0169-5347\(00\)02033-4](https://doi.org/10.1016/S0169-5347(00)02033-4)
2. Burns, R.M., Honkala, B.H. (Eds.) (1990). *Silvics*

- of North America: Volume 2. Hardwoods. U.S. Department of Agriculture, Forest Service, Agriculture Handbook 654. Washington, DC: U.S. Government Printing Office. https://www.srs.fs.usda.gov/pubs/misc/ag_654_vol2.pdf?utm
3. Campagnaro, T., Brundu, G., Sitzia, T. (2018). Five major invasive alien tree species in European Union forest habitat types of the Alpine and Continental biogeographical regions, *Journal for Nature Conservation*, 43, <https://doi.org/10.1016/j.jnc.2017.07.007>.
 4. Chytrý, M., Wild, J., Vojtech, J., Dendoncker, N., Reginster, I., Pino, J., Vila, M., Maskell, L., Kuhn, I., Spangenberg, J., Settele, J. (2012). Projecting trends in plant invasions in Europe under different scenarios of future land-use change. *Global Ecology and Biogeography* 26(3), 343–357. <https://nora.nerc.ac.uk/id/eprint/8780>
 5. Del Tredici, P. (2001) Sprouting in temperate trees: a morphological and ecological review. *Botanical Review*, 67(2), 121–140. <https://doi.org/10.1007/BF02858075>
 6. DeWine, J.M., Cooper, D.J. (2007) Effects of river regulation on riparian box elder (*Acer negundo*) forests in canyons of the Upper Colorado River Basin, USA. *Wetlands* 27, 278–289.
 7. Dostál, P., Müllerová, J., Pyšek, P., Pergl, J., Klinerová, T. (2013) The impact of an invasive plant changes over time. *Ecology Letters*, 16, 1277–1284. <https://doi.org/10.1111/ele.12166>
 8. European Parliament and Council (2014). Regulation (EU) No 1143/2014 on the prevention and management of the introduction and spread of invasive alien species. Official Journal of the European Union L 317, 35–55. Retrieved from <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A32014R1143>
 9. Kenefick, C., Livesley, S., Farrell, C. (2024) A systematic review of resprouting in woody plants and potential implications for the management of urban plantings. *Ecol Evol* 14(1), e10839. <https://doi.org/10.1002/ece3.10839>
 10. Kiseleva, O.A., Loretts, O.G., Veselkin, D.V. (2020). Seed size and cold stratification affect *Acer negundo* and *Acer ginnala* seed germination. *Agronomy Research*, 18, 461–471. <https://doi.org/10.15159/AR.20.153>
 11. Krevš, A., Kučinskienė, A. (2017). Influence of invasive *Acer negundo* leaf litter on benthic microbial abundance and activity in the littoral zone of a temperate river in Lithuania. *Knowledge and Management of Aquatic Ecosystems*, 418, 26. <https://doi.org/10.1051/kmae/2017015>
 12. Kuliešis, A., Kulbokas, G. (2009). Lietuvos nacionalinė miškų inventorizacija 2004–2008. Miškų išteklių ir jų kaita [National forest inventory of Lithuania 2004–2007. Forest resources and their changes]. Lietuvos miškų ūkio statistika, II dalis. Kaunas: Valstybinė miškotvarkos tarnyba, 88 p.
 13. Kurokochi, H., Matsushita, K., Yamada, K. (2010). Resprouting ability of *Robinia pseudoacacia* following clearcutting in Japan. *Journal of Forest Research*, 15(4), 249–255. <https://www.jstor.org/stable/40802414>
 14. Li, R., Yan, Q., Xie, J., Wang, J., Zhang, T., Zhu, J. (2020). Effects of logging on the trade-off between seed and sprout regeneration of dominant woody species in secondary forests of the Natural Forest Protection Project of China. *Ecol Process*, 11(16). <https://doi.org/10.1186/s13717-022-00363-3>
 15. Matula, R., Řepka, R., Šebesta, J., Pettit, J.L., Chamagne, J., Šramek, M., Horgan, K., Madera, P. (2020). Resprouting trees drive understory vegetation dynamics following logging in a temperate forest. *Sci Rep* 10, 9231. <https://doi.org/10.1038/s41598-020-65367-5>
 16. Ministry of Environment of the Republic of Lithuania. (2004). Order No. D1-433 on the approval of the list of invasive species in Lithuania (consolidated version D1-810, 2016). Available via e-TAR: <https://www.e-tar.lt/portal/it/legalAct/TAR.7B6390A69C91/iQxXseSvqU>
 17. Nikolaeva, A.A., Golosova, E.V., Shelepova, O.V. (2020). Methods of combating *Acer negundo* L. in specially protected natural areas. *BIO Web Conf* 24, 00063. <https://doi.org/10.1051/bioconf/20202400063>
 18. Overton, R. P. (ed.). (n.d.). *Acer negundo* L. In *Silvics of North America* (USDA Forest Service). Retrieved from <https://dendro.cnre.vt.edu/dendrology/USDAFSSilvics/3.pdf?utm>
 19. Porté, A.J., Lamarque, L.J., Lortie, C.J., Michalet, R., Delzon, S. (2011). Invasive *Acer negundo* outperforms native species in non-limiting resource environments due to its higher phenotypic plasticity. *BMC Ecol* 11, 28. <https://doi.org/10.1186/1472-6785-11-28>
 20. Saccone, P., Girel, J., Pages, J.P., Brun, J.J., Michalet, R. (2013). Ecological resistance to *Acer negundo* invasion in a European riparian forest: Relative importance of environmental and biotic drivers. *Applied Vegetation Science* 16, 184–192. <https://doi.org/10.1111/j.1654-109X.2012.01227.x>
 21. Sikorska, D., Sikorski, P., Archiciński, P., Chormański, J., Hopkins, R.J. (2019). You can't see the woods for the trees: Invasive *Acer negundo* L. in urban Riparian Forest harms biodiversity and limits recreation activity. *Sustainability* 11(20), 5838. <https://doi.org/10.3390/su11205838>
 22. Straigyte, L., Cekstere, G., Laivins, M., Marozas, V. (2015). The spread, intensity and invasiveness of the *Acer negundo* in Riga and

- Kaunas. *Dendrobiology* 74, 157–168. <http://dx.doi.org/10.12657/denbio.074.016>
23. Subedi, A., Adhikari, A., Tiwari, A., Shrestha, B.B. (2024). Canopy gaps facilitate establishment of invasive plants in a subtropical broadleaved forest of central Nepal, *Ecological Frontiers*, 44(4), 781–787. <https://doi.org/10.1016/j.ecofro.2024.02.009>
24. Valantinaitė, A., Straigytė, L., Jurkšienė, G. (2011). Comparative analysis of invasion intensity of box elder (*Acer negundo* L.) and Sosnowskyi hogweed (*Heracleum sosnowskyj* Manden). *Rural Development* 2011, Proceedings 2, 161–166. <https://portalcris.vdu.lt/server/api/core/bitstreams/db7e9741-f763-4140-9ace-1c595bef7a75/content>
25. Williams-Linera, G., Milton, H., Diaz-Toribio, M. (2023). Resprouting and foliar functional traits driving the invasiveness of *Eriobotrya japonica* in a secondary cloud forest, *Trees, Forests and People*, 14, 100455. <https://doi.org/10.1016/j.tfp.2023.100455>