Article

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Possible Factors of Poplar Susceptibility to Large Poplar Borer Infestation

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Abstract: Poplars (*Populus* spp.) are of significant ecological and economic importance. Long-term breeding efforts were aimed mainly at obtaining fast-growing and productive plants and less considered resistance to pests. This study aimed to identify the patterns of susceptibility to *Saperda carcharias* (Linnaeus, 1758) (Coleoptera: Cerambycidae) among *Populus* hybrids and pure species, considering crossing combinations and some other traits. In our research, 35 clones of poplar species and hybrids of the Ukrainian and foreign selection from the *Aigeiros*, *Tacamahaca*, and *Leucoides* sections were tested in 2021 and 2023 in the plantation created in 2014 in Eastern Ukraine. *S. carcharias* preferred infesting clones with earlier foliage development, larger diameters, and height increments. Specifically, hybrids with American maternal lineage showed the highest susceptibility, whereas those with European maternal lineage or Asian origin displayed lower infestation levels or resistance, respectively. This variability suggests a complex relationship between genetic background and pest resistance, underlining the need for a deeper understanding of the factors influencing susceptibility to *S. carcharias*. Selecting native species clones or creating mixed clone plantations could enhance the resilience of poplar plantations to pest threats.

Keywords: *Populus* spp.; hybrids; clones; *Saperda carcharias*; phenology; height increment

1. Introduction

Poplar trees (*Populus* spp.) play a crucial role ecologically and economically due to their rapid growth and versatility in various applications, including timber production, bioenergy, and environmental remediation [1–5]. However, the Short Rotation Woody Crops (SRWC) yields are often reduced by a range of interacting environmental stressors, including frost [6], drought [27], salinity [8], pathogens [9], and phytophagous insects [10]. With climate change and increasing ecological pressures, understanding the complex interplay between insect herbivory resistance and the tolerance mechanisms to these abiotic stressors has become paramount. Dozens of species of phytophagous insects feed and develop in all organs of poplar causing various effects on tree viability, growth rate, and wood quality [9,11,12]. It depends on insect biological traits, population density, plant susceptibility, and environmental conditions [13–17].

Breeding efforts have historically focused on obtaining fast-growing and productive plants [18–24]. However, these plants had various responses to stress induced by abiotic factors of the environment and activities of living organisms within the environment. Particularly, as susceptibility to insect damage varies widely among clones, the limited genetic diversity of poplar in large SRWC areas may heighten the risk of pest-related losses or abiotic disasters [10].

Most studies of insect resistance in poplar hybrids and clones have focused on defoliators [27] because the foliage damage is visible and easy to quantify, and these insects can be controlled by spraying with an insecticide [9,11,28]. At the same time, phloem-boring or xylophagous insects at SRWC can, at high population densities, weaken trees by maturation feeding on leaves, gnaw the galleries of different diameters and at different depths in trunks, branches, and roots, actively or passively vector the pathogens, or create conditions for the penetration of pathogens through entrance holes and promote their development by weakening the trees [14,15,29–32]. Some insects of this group have relatively low prevalence and harmfulness in forests but increase the population density at a single-species plantation, particularly *Cryptorhynchus lapathi* (Linnaeus, 1758) (Coleoptera: Curculionidae: Cryptorhynchinae), *Saperda carcharias* (Linnaeus, 1758) (Coleoptera: Cerambycidae), *Cossus cossus* (Linnaeus, 1758) (Lepidoptera: Cossidae), *Paranthrene tabaniformis* (Rottemburg, 1775) (Lepidoptera: Sesiidae) [9,11,12], and *Anoplophora glabripennis* Motschulsky, 1853 [32]. In eastern Ukraine, ten of 72 investigated xylophagous poplar species, were rated as the most dangerous. However, most of them are highly harmful in the case of inhabiting over 60 % of trees [14,15].

Large poplar longhorn beetle *S. carcharias* is one of them because it inhabits only living, healthy trees regardless of age [33,34], damages foliage and the bark of new growth at maturation feeding [35,36], and promotes the pathogen invasion [37] causing physiological harm [14]. The larva excavates a long and wide gallery deep into the wood [33,38] causing technical harm. The timber of damaged trees may be used for paper, pulp, or match production but not for saw timber, furniture, and veneering [39]. The life cycle of *S. carcharias* lasts 2 to 4 years, according to climatic conditions [40–42]. Even within the same tree, larvae develop in the upper part of the trunk for 2 years, and in the base of the trunk for 3–4 years [35,36]. The larvae pupate starting in May, depending on the instars of the hibernating individuals, and due to the heterogeneous temperature regime both within the plantation and in one tree, the emergence of adults and the colonization of new trees continues until September [40–42].

Since detecting the xylophagous insects in the early stages of tree colonization requires more effort than in the case of defoliators, and control is expensive and little effective [11], the best way to reduce negative consequences for plantation production is to increase the diversity of clones and hybrids [9].

Fritz et al. [43] have suggested that clone resistance against herbivores is affected by hybridization in four different ways: the same resistance of hybrids and parents, intermediate resistance of hybrids compared to the parents, hybrid susceptibility, and hybrid resistance is close to either more susceptible or more resistance parent. Responses of different insect species may vary widely to the same hybrid host. This indicates diverse genetic effects of interspecific hybridization on resistance.

The resistance of parental forms as a result of long-term coevolution may be one of the important factors of resistance to pests. For example, Manchurian ash (*Fraxinus mandshurica* Rupr.) coevolved with emerald ash borer, *Agrilus planipennis* Fairmaire, 1888 (Coleoptera: Buprestidae) and is more resistant than North American or European ash species [44]. Usually, clones with the same parents have similar resistance. However, the progeny of *P. trichocarpa* is generally more resistant to caterpillar-like damage [17]. Research has shown that cultivar 'Robusta' (*Populus deltoides* × *P. nigra*), obtained about 1910, is more susceptible to some insects than other *P. deltoides* × *P. nigra* crosses of more recent origin. At the same time, *P. deltoides* × *P. nigra* hybrids were damaged more intensively than *P. trichocarpa* (Torr. & Gray) clones [17].

In Ukraine, numerous studies have been carried out with hybrids *P. deltoides*, *P.* × *euramericana, P. trichocarpa, P. laurifolia, P. lasiocarpa* primarily focusing on growth [1,20,45–51] and biology [21,52]. However, modern studies on the resistance of poplar hybrids to insects are only starting in eastern Ukraine.

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This article aims to identify patterns of susceptibility or resistance to *Saperda carcharias* (Linnaeus, 1758) (Coleoptera: Cerambycidae) infestation among *Populus* hybrids and pure species, focusing on the influence of their seasonal development, stem diameter, height increment, and crossing combinations.

2. Materials and Methods

2.1. Study Region and Tested Poplar Clones

The experimental site is located on the territory of the State Enterprise "Kharkiv Forest Research Station", 15 km from Kharkiv, in the Kharkiv region, Ukraine (50°05′01″ N, 36°18′25″ W, 156 m a.s.l.) (Figure 1). This area falls under the Forest-Steppe zone as per comprehensive forestry zoning [53]. Climate data obtained from ClimateCharts.net (Zepner et al., 2020) indicates an average annual temperature of +8.8°C and an average annual rainfall of 535.2 mm for the period 2001-2020 [54]. The climate is classified as temperate continental (Dfb) according to the Köppen classification system [55].

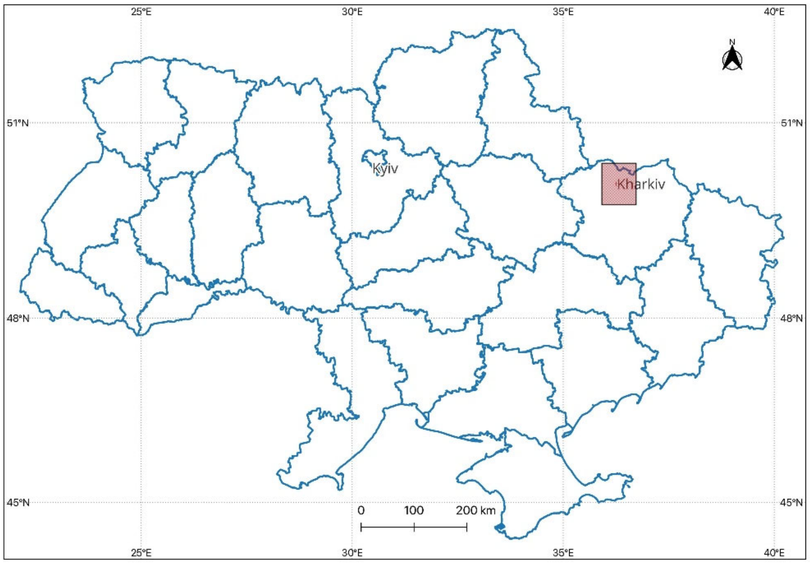

Figure 1. Location of study plot in the map of Kharkiv region (Ukraine).

Researches were carried out in the collection of poplar (*Populus* sp.) and willow (*Salix* sp.) clones. The plot is flat, with a slight slope to the north. On the northern and western sides, it is bordered by deciduous forests, which include mainly *Quercus robur* L., *Acer platanoides* L., *Tilia cordata* Mill., and *Ulmus laevis* Pall. The rows of plants on the plantation are arranged from south to north. The distance between rows is 2 m and between plants in a row 2 m.

The cuttings, rooted the previous summer in an open field nursery and dormant for the winter, were planted in the spring of 2014. The plot encompasses 35 clones of poplar, representing species and hybrids selected from the *Aigeiros*, *Tacamahaca*, and *Leucoides* sections (Table 1).

Table 1. Tested poplar clones.

Section abbr.	Hybrids / Crossing combination	Clone name	Ref.
A	*P.* × *canadensis* (Pc)	'Bachelieri' (Bh), 'Sakrau79' (Sk79), 'Robusta' (Rob), 'Tronco' (Tr), 'Constanta' (Cn), 'Veryla' (Ve), 'Sakrau45-51' (Sk45), 'Brabantika' (Br)	[39,45,48]
A	*P. deltoides* (Pd)	'Gulliver' (Gu), 'Deltopodibna' (De), 'Karolinska 162' (Ka),	[45,48]

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A	*P. deltoides* × *P. nigra* cv. 'Italica' (Pd × PnIt)	'Strilopodibna' (St),	[46]
A	*P. nigra* × *P. deltoides* (Pn × Pd)	'Gradizka' (Gr), 'Keliberdynska' (Ke), 'Robusta 16' (Rob16)	[39,45]
A	*P. nigra* × *P. nigra* cv. 'Italica' (Pn × PnIt)	'Rosijska' (Ro), 'Pioner' (Pi), 'Addita' (Ad)	[39,48]
A	*P. nigra* cv. 'Pyramidalis' (PnPrm)	'Slava Ukrayiny' (Sl)	[45]
T	*P. trichocarpa* (Pt)	'Volosystoplidna' (Vo), 'Lada' (La)	[48]
T	*P. trichocarpa* × *P. laurifolia* (Pt × Plrf)	'Druzhba' (Dr)	[48]
T	*P. simonii* f. fastigiata (PsimF)	'Rohanska' (Rh)	[48]
A × L	*P.* × *canadensis* cv. 'Regenerata' × *P. lasiocarpa* (PcRg × Pls)	'Perspektyvna' (Pe)	[45]
A × L	*P. deltoides* × *P. lasiocarpa* (Pd × Pls)	'Udyvytelnaya' (Udv)	[45]
A × T	*P.* × *canadensis* × *P. trichocarpa* (Pc ×Pt)	'Lvivska' (Lv), 'Mobilna' (Mo)	[45]
A × T	*P. deltoides* × *P. balsamifera* (Pd × Pbls)	'Kanadska×balsamichna' (KB)	[48]
A × T	*P. nigra* cv. 'Italica' × *P. laurifolia* (PnIt × Plrf)	'Novoberlinska-7' (N7), 'Novoberlinska-3' (N3)	[45,48]
A × T	*P. nigra* cv. 'Italica' × *P. trichocarpa* (PnIt × Pt)	'Lubenska' (Lu)	[45]
A × T	(*P. nigra* cv. 'Italica' x *P. nigra*) × *P. balsamifera* (PnIt × Pn × Pbls)	'Versia' (Vr)	[45]
A × T	*P. suaveolens* ×*P.* × *berolinensis* (Psv × Pbrl)	'Ivantiivska' (Iv)	[46,48]
A × T	*P. simonii* × *P. nigra* cv. 'Italica' (Psim × PnIt)	'Kytaiska × pyramidalna' (Kp)	[46]
T × L	*P. trichocarpa* × *P. lasiocarpa* (Pt × Pls)	'Nocturne' (No)	[46,48]

Note: A—Aigeiros, T—Tacamahaca, L—Leucoides.

In 2021, part of the trees on the plantation were cut to assess the biomass obtained from individual clones. In 2022, access to the plantation was impossible due to military operations. In 2023, it was discovered that the crowns of the pruned plants had been restored.

2.2. Weather Data Analysis

To compare the weather conditions of individual years, the following indicators were evaluated: average air temperature for a year and vegetation period (period with air temperature over 10 °C); the sum of precipitation for a year, and vegetation period; the dates of stable transition of temperature over 5 and 10 °C, and Hydrothermal index (HTI).

The dates of stable transition of temperature over 5 and 10 °C were evaluated according to a method by V. Meshkova [56]. G. T. Selyaninov hydrothermal index (HTI) was calculated as

$$HTI = 10 \times \frac{\sum P}{\sum t}\ , \tag{1}$$

where ΣP is precipitation for a period with mean monthly air temperature over 10 °C, mm; Σt is the sum of daily air temperature for the same period, °C [57].

2.3. Field Data

Surveys of the distribution of phytophagous insects on plantations and assessment of the condition of clones were carried out in 2019–2021 and 2023. When examining each plant, the stem

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diameter at the lower part was measured with a caliper. Plant condition (healthy, dead) and the presence of pest infestation were recorded (Figure 2, Table S1).

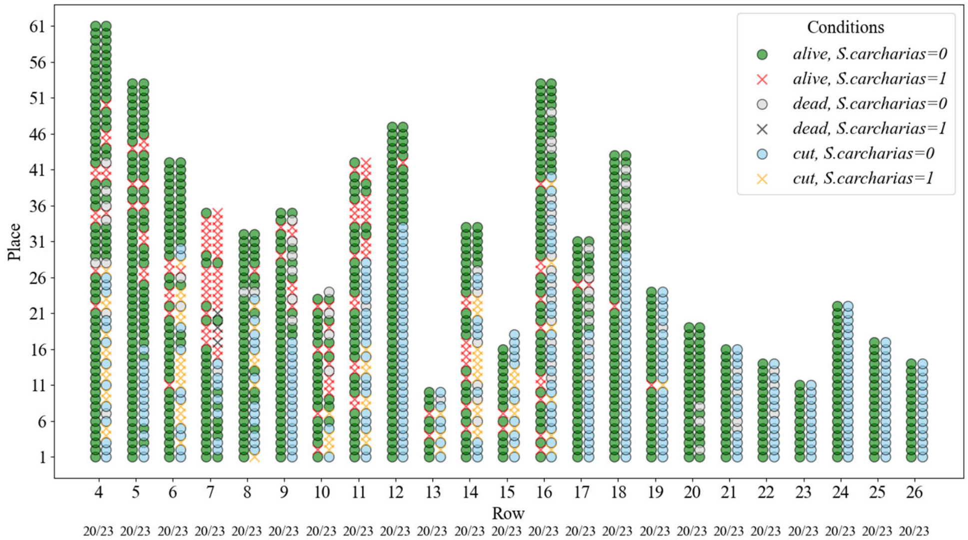

Figure 2. Location of alive, dead, cut, and infested by *S. carcharias* plants at the experimental plot in 2020 (before cutting) and in 2023 (after cutting).

Particular attention was paid to identifying *S. carcharias*. Its presence at the site was evidenced by characteristic frass, and foliage damage as a result of maturation feeding of the adults (Figure 3a,b).

(**a**) (**b**)

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(c) (d)

Figure 3. Signs of *S. carcharias* in plantation: (a) frass at the base of the trunk, chips, and streaks are visible; (b) maturation feeding of an adult; (c) a gallery inside the stem; (d) cross-section in the lower part of infested poplar stem.

Galleries of this longhorn beetle inside the stem could be seen after cutting the plant (Figure 3cd).

Poplar infestation by *S. carcharias* was calculated as the ratio of infested and all plants of each clone expressed as a percentage. The error of this indicator was calculated considering the number of plants in a given clone, and the comparison of infestation for different clones was assessed using the criterion Z [58]. Mean monthly air temperature and precipitation for 1990–2020 for Kharkiv were taken from the ClimateCharts.net web platform [54], and respective weather indicators for the years of field research were taken from the website [59].

The rate of poplar foliage development was assessed on 10 plants of each clone by the scoring scheme: 1—dormant buds completely enveloped by the scales; 2—bud swelling with scales slightly diverging showing a narrow yellow margin; the presence of one or more droplets of balsam; 3—bud sprouting, with tips of the small leaves emerging out of the scales; 4—buds completely opened with leaves still clustered together; scales still present; 5—leaves diverging with their blades still rolled up; scales may be present or absent; 6—leaves completely unfolded (but smaller in size than mature ones); lengthening of the axis of the shoot evident; scales absent [60].

The average score on the day of recording was calculated. Considering the preliminary assessment of the seasonal development of the clones, the arithmetic mean score of each clone, obtained from the assessment on April 20, was used for comparison. The clones with foliage in phase ≤ 3 were considered as late, 3.1–4—medial, and 4.1–5 early.

The date of completing the growing season was assessed on 10 plants of each clone on October 15 by the proportion of fallen leaves. The clones with a percentage of foliage fall ≤ 60% were considered as late, 61–90 %—medial, and >90 %—early.

The stem diameter and height increment of these trees was also measured on October 15. The clones with stem diameter ≤ 6 cm were considered as small, 6.1–7 cm—medial, and >7 cm—large. The clones with height increment ≤ 60% were considered as low, 61–90 %—medial and >90 %—high.

All data were organized using the software Excel 2019. Software Open-source Python libraries (Pandas, NumPy, and Matplotlib (Python 3.13.0) [61] and PAST: Paleontological Statistics Software Package for Education and Data Analysis [62] were used for data analysis and visualization.

To evaluate the relationship between the intensity of infesting poplar clones by *S. carcharias*, and clones' seasonal development, diameter, and height growth, these indicators were ranked and analyzed using a χ^2-text comparing observed χ^2 values with χ^2 values at $p = 0.05$ or $p = 0.01$ [58,62].

3. Results

3.1. Weather Conditions

In all years of the study, the annual air temperature in the plantation area exceeded long-term data: from 2.1°C (by 23.7%) in 2019 to 0.4°C (by 4.6%) in 2021 (Table 2). However, the temperature of the growing season exceeded long-term data to a lesser extent: from 1.8°C (by 10.1%) in 2019 to 0.3°C (by 1.9%) in 2021. The date of stable temperature transition over 5°C was earlier by 10 days in 2019, 20 days in 2020, and 13 days in 2023. In 2021, this date was 4 days later than long-term data. However, the date of stable temperature transition over 10°C was earlier than long-term data only in 2019 and 2023 (by 7 and 6 days, respectively), and in 2020 and 2021 it occurred 8 and 7 days later, respectively.

Table 2. Climatic indicators for 1990–2020 and the years of field research for Kharkiv meteorological station.

Climatic indicators *	1990–2020	2019	2020	2021	2023
Air temperature, T°C					
– for year	8.8	10.8	10.4	9.2	10.3
– for vegetative period	17.4	19.2	17.9	17.8	18.2
Date of stable transition of temperature					
– over 5°C	29/03	19/03	9/03	2/04	16/03
– over 10°C	16/04	9/04	24/04	23/04	10/04
Precipitation, mm					
– for year	535.2	342.3	494.6	399.0	694.1
– for the vegetative period	287.2	159.4	285.1	217.8	354.2
Hydrothermal index**	0.90	0.45	0.87	0.67	1.06

*Note: data for 2022 are not full because of military actions; **HTI=10*R/Σt where R is precipitation in millimeters for the period with temperatures above 10°, Σt is the sum of temperatures (°C) for the same time [57].

The annual precipitation in 2019–2021 was lower than long-term data (in 2019—by 180.1 mm, or by 34.5%). However, in 2023 it exceeded long-term data by 171.7 mm (32.9%). Precipitation for the growing season was almost twice less than the long-term values. In 2020, it was almost the same as the long-term values, and in 2023 it exceeded them by 23.3%. The hydrothermal index in 2019 was almost 2 times less than the long-term value, in 2020 it was almost equal to the long-term value, and in 2023 it even exceeded it (Table 2).

3.2. Prevalence of S. carcharias Depending on Clone Phenology, Size, and Management

A survey in 2020 showed that out of 696 trees inspected, 72 (10.3%) were infested by *S. carcharias*, 2 (0.3%) by *Saperda populnea* (Linnaeus, 1758), 4 (0.58%) by *Sesia apiformis* (Clerck, 1759) (Lepidoptera: Sesiidae), and 4 (0.58%) died of unknown causes. In 2021, *S. carcharias* has already infested 12 % of trees. After cutting in 2021 and restoring the crowns, in the survey of 2023, uncut trees amounted to 32.5%, trees after cutting with restored crowns—57.6%, and dead trees—10%. At the same time, *S. carcharias* was found in all three dead trees, and among cut and uncut trees—18.8% and 26.3%, respectively (Figure 4).

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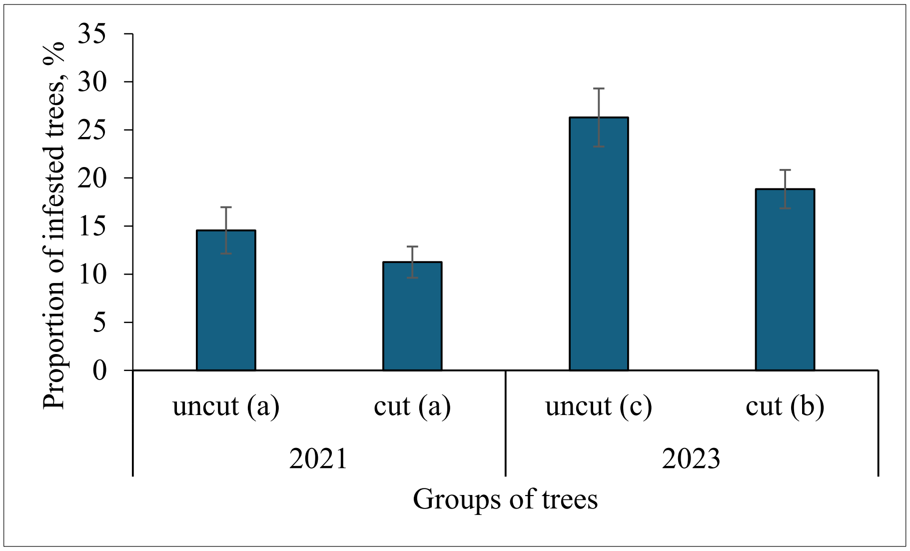


Figure 4. Proportion of poplar trees, infested by *S. carcharias* in 2021 (before cutting) and 2023 (after cutting). The infestation of groups of trees with the same letters in parentheses has no significant difference at p=0.05.

Infestation of uncut and cut groups of trees by *S. carcharias* was higher in 2023 compared with 2020, however, it was significantly greater in uncut trees (see Figure 4).

Infestation by *S. carcharias* was higher in 2023 compared with 2020 for most clones (Figure 5). In both years of assessment, the clone 'Ivantiivska' was the most infested by *S. carcharias*. In three more clones ('Kytaiska × pyramidalna', 'Karolinska 162', and 'Volosystoplidna') over 50 % of trees were infested.

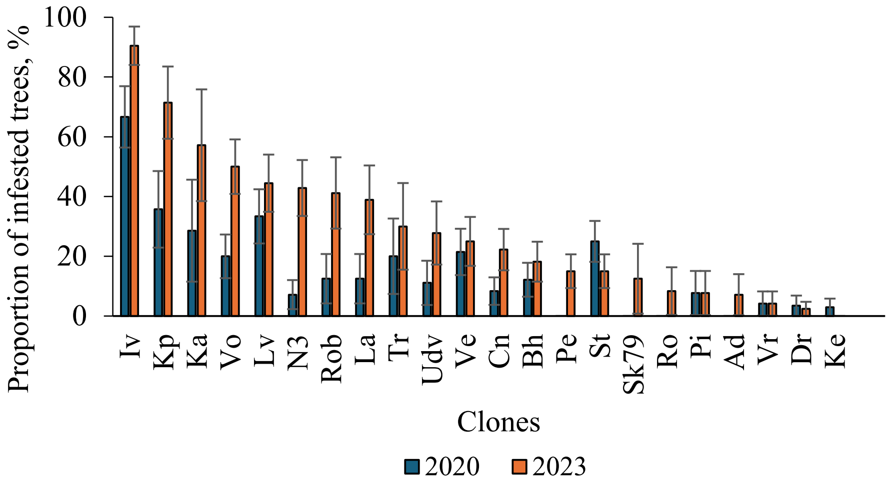
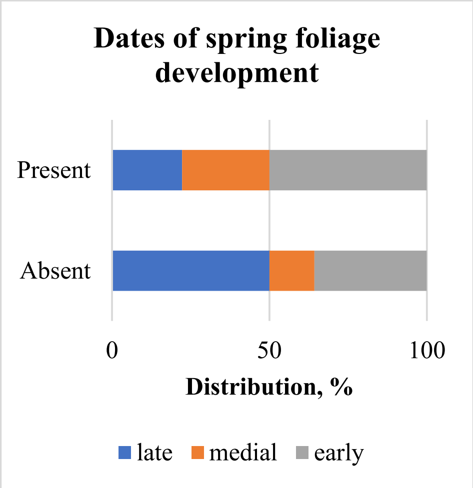


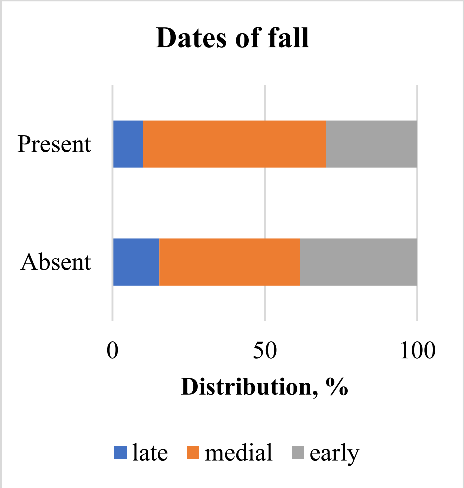
Figure 5. The proportion of trees infested by *S. carcharias* in poplar clones in 2020 and 2023 (non-infested clones are not shown). Full clone names are presented in Table 1.

Four clones ('Perspektyvna', 'Sakrau79', 'Rosijska', and 'Addita') were infested only in 2023. 12 clones were not infested in both years, particularly, 'Deltopodibna', Gradizka', 'Gulliver', 'Kanadska×balsamichna', 'Lubenska', 'Mobilna', 'Nocturne', 'Novoberlinska-7', 'Robusta 16', 'Rohanska', 'Sakrau45-51', 'Slava Ukrayiny'. To reveal the possible causes of various infestation levels of clones, some of their traits were analyzed.

Distribution by the dates of spring foliage development for poplar clones with *S. carcharias* presence and absence differed significantly ($\chi^2 = 17.4$; $\chi^2_{0.05} = 6.0$; $\chi^2_{0.01} = 9.2$). The clones with earlier foliage development were more susceptible to infestation (Figure 6a). At the same time, the dates of the fall have no significant impact on *S. carcharias* presence
($\chi^2 = 4.0$; $\chi^2_{0.05} = 6.0$) (Figure 6b).



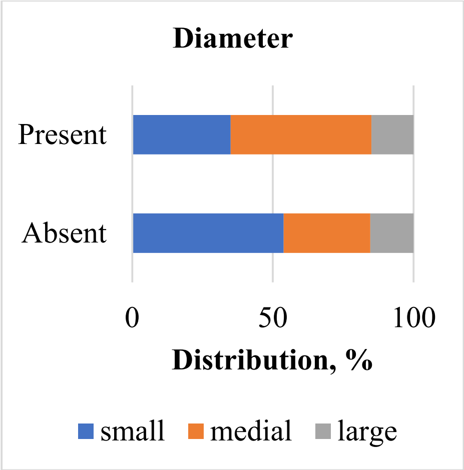
(**a**)



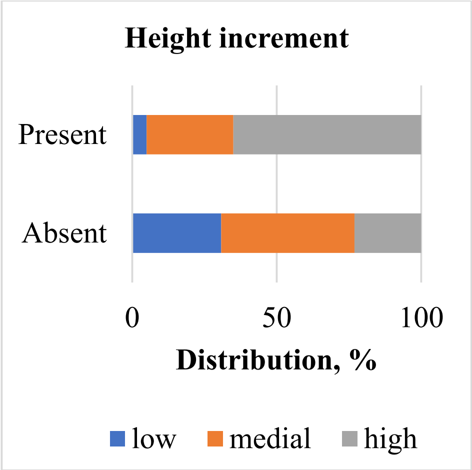
(**b**)

Figure 6. Distribution of poplar clones, infested by *S. carcharias* (present) and non-infested (absent) (**a**) depending on the score of foliage development on April 20: phase ≤ 3—late; 3.1–4—medial; 4.1–5 early; (phase 3—bud sprouting, with tips of the small leaves emerging out of the scales; phase 4—buds completely opened with leaves still clustered together; scales still present; phase 5—leaves diverging with their blades still rolled up; scales may be present or absent;) (**b**) depending on the percentage of foliage fall on October 15: fall ≤ 60%—late; 61–90 %—medial; >90 %—early.

The average diameter of non-infested trees was 5.9 ± 0.06 cm, and of trees infested with *S. carcharias* 6.6 ± 0.19 cm, but in both groups of trees, there were the plants with a diameter of 1 to 12 cm. *S. carcharias* preferred colonizing clones with larger diameters ($\chi^2 = 8.6$; $\chi^2_{0.05} = 6.0$) (Figure 7a) and height increment ($\chi^2 = 41.9$; $\chi^2_{0.05} = 6.0$; $\chi^2_{0.01} = 9.2$) (Figure 7b).



(**a**)



(**b**)

Figure 7. Distribution of poplar clones, infested by *S. carcharias* (present) and non-infested (absent) (**a**) depending on poplar stem diameter: small ≤ 6 cm; medial—6.1–7 cm; large—>7 cm; (**b**) depending on height increment: low ≤ 60%; 61–90 %—medial; >90 %—high.

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3.3. *Prevalence of S. carcharias Depending on Clone Origin and Crossing Combination*

S. carcharias infested clones of all tested poplar sections and their combinations, except T × L (Figure 8).

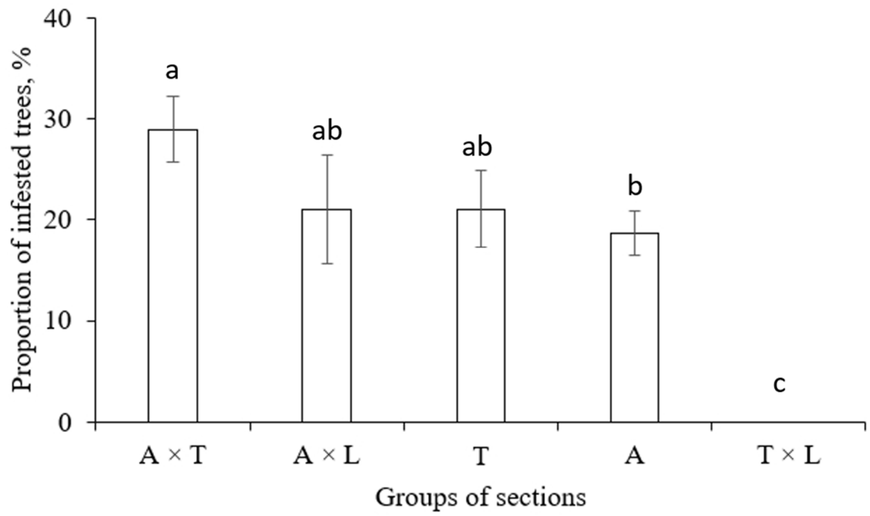
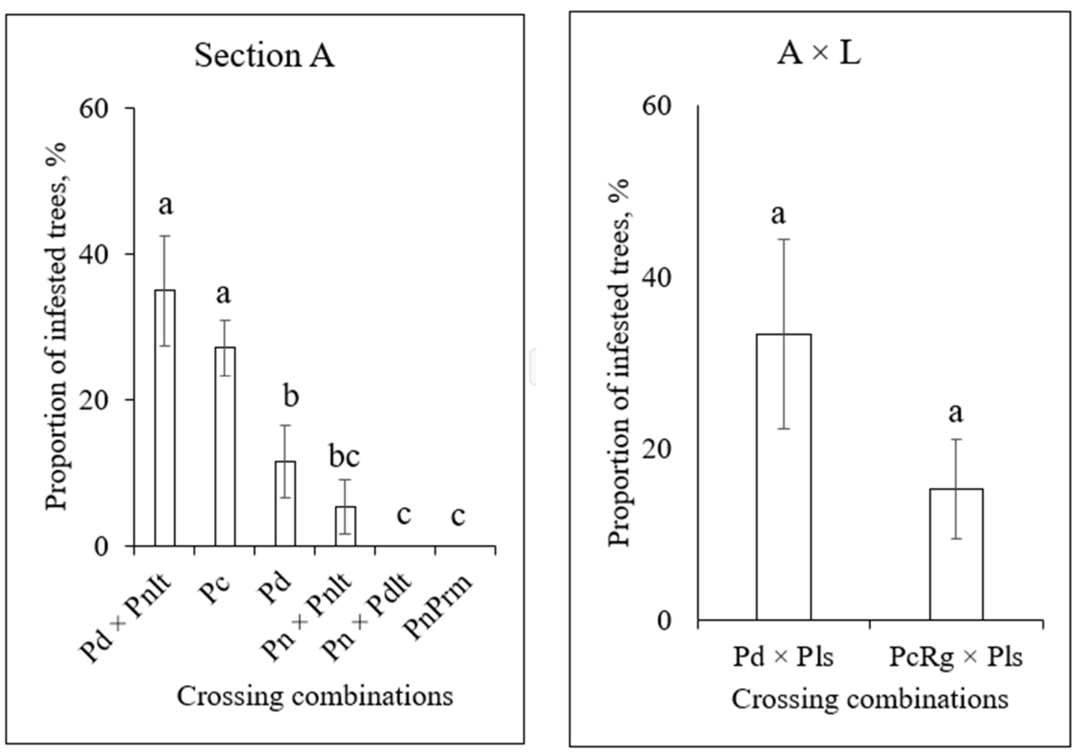


Figure 8. Proportion of poplar clones, infested by *S. carcharias*, depending on the group of sections. The columns with the same letters have no significant difference at p=0.05. Sections: A—*Aigeiros*, T—*Tacamahaca*, L—*Leucoides*.

However, within each of the four susceptible combinations of sections, there were hybrids with high or low resistance to infestation by this pest (Figure 9). Among the hybrids from section *Aigeiros*, those with a maternal plant of American origin (*P. deltoides*) exhibited significantly higher susceptibility to infestation by *S. carcharias* compared with hybrids with a maternal plant of European origin (*P. nigra*) (Figure 9a).



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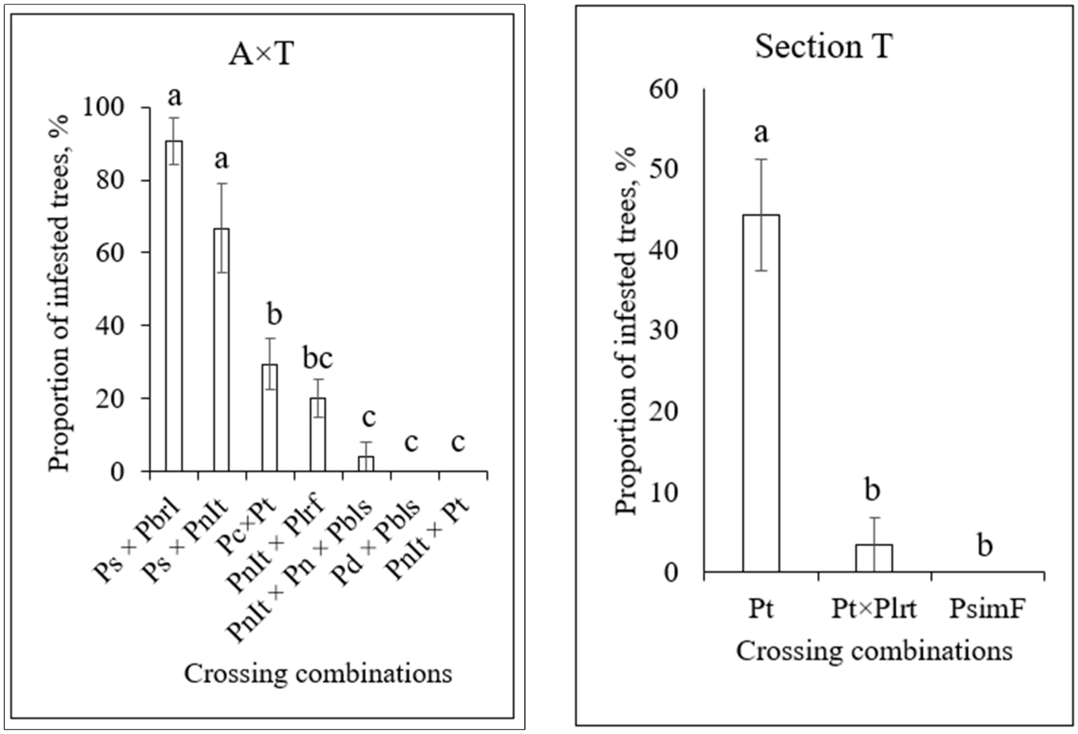
(**a**) (**b**)



(c) **(d)**

Figure 9. The **p**roportion of poplar clones, infested by *S. carcharias*, depending on crossing combinations in the groups of sections: (**a**)—Section A; (b)—A × L; (c)—A × T; (d)—Section T. The columns with the same letters in parentheses have no significant difference at p=0.05. The abbreviations of crossing combinations are mentioned in Table 1.

Maternal plants of crossing combination A × L were also of American origin, and paternal (*P. lasiocarpa*) were of Asian origin. Although the *S. carcharias* infestation of the presented hybrids differed almost twice, the differences were not statistically confirmed (Figure 9b). In the A × L hybrid group, the clones with a maternal plant of Asian origin (*P. suaveolens*, *P. simonii*) were considerably more heavily infested compared with clones of European maternal lineage. However, the hybrid *P. deltoides* × *P. balsamifera*, descending from two American parents, showed no infestation (Figure 9c). *P. trichocarpa* plants were the most infested (44.2 %) in the Tacamahaca section. Only 3.4% of plants having an American maternal and Asian paternal (*P. trichocarpa* × *P. laurifolia*) lineage were infested by *S. carcharias*, and the third member of this group having Asian origin (*P. simonii* f. *fastigiata*) was not infested at all (Figure 9d).

4. Discussion

In our research, 35 clones of poplar species and hybrids of the Ukrainian and foreign selection from the *Aigeiros*, *Tacamahaca*, and *Leucoides* sections were tested in 2021 and 2023 for sustainability or resistance to infestation by *S. carcharias* in the plantation created in 2014 in Eastern Ukraine.

Infestation by *S. carcharias* was higher in 2023 compared with 2020 for most clones (Figure 5). In both years of assessment, the clone 'Ivantiivska' was the most infested by *S. carcharias*. Three more clones ('Kytaiska × pyramidalna', 'Karolinska 162', and 'Volosystoplidna') had over 50 % infestation.

12 clones were not infested in both years, particularly, 'Deltopodibna', Gradizka', 'Gulliver', 'Kanadska × balsamichna', 'Lubenska', 'Mobilna', 'Nocturne', 'Novoberlinska-7', 'Robusta 16', 'Rohanska', 'Sakrau45-51', 'Slava Ukrayiny'. To reveal the possible causes of various infestation levels of clones, some of their traits were analyzed.

In all years of the study, the annual air temperature in the plantation area exceeded long-term data, but the dates of the stable temperature transition over 10°C occurred earlier than long-term data in 2019 and 2023 by 7 and 6 days, respectively, and occurred 8 and 7 days later it in 2020 and 2021 (see Table 2). Such variations could affect the attractiveness, suitability, and susceptibility of poplars to *S. carcharias* and larvae development inside the trunk. This warrants further investigation into their role in pest infestation dynamics.

In our research, the precipitation and hydrothermal index in 2019–2021 were inferior to long-term data, and in 2023 exceeded them (see Table 2). Lack of precipitation usually promotes phytophagous insect development while its increase promotes tree resistance [56]. Since the development length of *S. carcharias* larvae in the poplar trunk varies depending on locality and year, this aspect is also advisable for further study in different clones.

Infestation of uncut and cut trees by *S. carcharias* was higher in 2023 compared with 2020, however, it was significantly greater in uncut trees (see Figure 4). This may be because after cutting a part of the trunk was left with insufficient height for the galleries of *S. carcharias*. However, the plants were cut at a height of about 40 cm, and the length of the galleries in the dissected plants from which the adults emerged did not exceed 17 cm (our unpublished data). It is possible also that wood moisture decreased after cutting, which was unfavorable for larvae development.

In our research, the clones with earlier foliage development were more susceptible to infestation (see Figure 6a), while the dates of the fall had no significant impact on *S. carcharias* presence (Figure 6b). However, in Canada, resistant to *Cryptorhynchus lapathi* (L.) (Coleoptera: Curculionidae) poplar clones were flushed approximately three weeks earlier than the susceptible clones [63]. The conflicting findings may be because *C. lapathi* larvae mine in the bark while developing through three instars, and then move into the xylem, while *S. carcharias* larva immediately gnaws a gallery to the sapwood. The choice of plants with earlier leaf development may be explained by the availability of foliage for *S. carcharias* maturation feeding, which then becomes able to mate and lay eggs on nearby trees.

The dates of the fall have no significant impact on clone infestation by *S. carcharias* because it needs foliage only for maturation feeding after adult emergence, which goes on from May to August [35,36].

In our research, *S. carcharias* preferred colonizing clones with larger diameters (Figure 7a) and height increments (Figure 7b). The first may be because the larva cannot complete its development in young plants with insufficient wood volume. The second phenomenon may be because the plants with greater height increments usually have greater radial increments [53] and sufficient wood volume for larvae development [39].

S. carcharias showed a wide capacity to infest clones across all presented poplar sections and their crossing combinations, except the *Tacamahaca* and *Leucoides* cross. Within each crossing combination, there was a discernible variation in susceptibility levels. This variation underscores the complex nature of hybrid resistance, suggesting that neither clone origin nor crossing combination alone can predict susceptibility to *S. carcharias*.

The studies have provided mixed results regarding the susceptibility of *Populus* hybrids compared to pure species in the face of pest infestations. In Sweden, Christersson [18] has studied that hybrids *P. trichocarpa* and *P. deltoides* were more prone to pest attacks, unlike their pure *P. trichocarpa* counterparts which were largely spared. In Canada, Kalischuk et al. [64] reported that poplar hybrids suffered severe infestations by poplar bud gall mites, and no trees were severely infested in areas where pure poplars grew.

Contrary to these findings, in Latvia, the study by Zeps et al. [37], no significant differences in susceptibility of rot and poplar borer were found between hybrid and European aspen. In Finland, Välimäki and Heliövaara's [38] research indicates no significant difference in poplar borer larval galleries between aspens and hybrid aspens. A study by Moore and Wilson [65] in Michigan found no discernible preference by *S. inornata* for hybrid over pure *Populus* species, despite attacking a substantial proportion of the population. This lack of preference challenges the notion that Populus hybrids are inherently more vulnerable to pests.

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Among the hybrids from section *Aigeiros*, those with a maternal plant of American origin (*P. deltoides*) exhibited higher susceptibility to infestation. Conversely, hybrids with a maternal plant of European origin (*P. nigra*) showed significantly lower infestation levels. This pattern suggests a pivotal role of maternal lineage in determining hybrid susceptibility to pest attacks.

For the crossing combinations of *Aigeiros* and *Leucoides*, *P. deltoides* × *P. lasiocarpa* showed a significantly high infestation rate, while *P.* × *canadensis* cv. 'Regenerata' × *P. lasiocarpa* had a lower infestation rate, suggesting variability in pest resistance even within specific crossing combinations.

In the *Aigeiros* and *Tacamahaca* hybrid group, clones with a maternal plant of Asian origin (*P. suaveolens*, *P. simonii*) were more heavily infested, while those with European maternal lineage were less affected. Interestingly, the hybrid *P. deltoides* × *P. balsamifera*, descending from two American parents, showed no infestation, highlighting the complexity of genetic influences on pest resistance. The experience of Hannon et al. [29] suggests that hybrids with *P. deltoides* × *P. nigra* parentage are more resistant to stem borers than *P. trichocarpa* × *P. deltoides* or *P. trichocarpa* × *P. nigra* parentage.

Among the representatives of section *Tacamahaca*, *P. trichocarpa* was significantly more susceptible to *S. carcharias* infestation. However, a genome-wide association study (GWAS) conducted by Sepúlveda et al. [31] on *P. trichocarpa* provenances revealed three SNP markers significantly associated with resistance to *S. calcarata*. This discovery indicates that *P. trichocarpa* employs a sophisticated machinery of genetic expression and metabolite production to fend off *S. calcarata* attacks in different conditions. Another representative with an American maternal and Asian paternal (*P. trichocarpa* × *P. laurifolia*) lineage exhibited low infestation rates. The third representative, of Asian origin (*P. simonii* f. *fastigiata*), was not infested, suggesting a potential genetic basis for resistance.

When sorting non-infested clones by parent origin, it was observed that European and American species were more prevalent by plant count, whereas European-American and European-Asian hybrids dominated by clone count. This distribution suggests a nuanced relationship between genetic background and pest resistance, warranting further exploration into the specific genetic or environmental factors that confer resilience against *S. carcharias* infestation. Hybrids with European maternal lineage generally exhibited lower susceptibility to pest infestations, suggesting a robust genetic basis for resistance within these lines. Hybrids derived from American maternal lineage tend to be more vulnerable to pests, necessitating careful consideration in breeding programs aiming for pest-resistant poplar cultivars. The presence of Asian maternal lineage or complex crossing combinations involving Asian lineage can result in higher susceptibility.

The findings underscore the importance of considering maternal lineage and specific hybrid genetic makeup when developing poplar breeding strategies to enhance resistance to pest infestations. Further research into the genetic and environmental interactions influencing these susceptibility patterns is crucial for advancing pest-resistant poplar cultivation.

The exploration of alternative strategies, such as the utilization of selected clones of native species or the creation of mixed clone plantations, emerges as a viable path toward the sustainable development of poplar plantations resilient to the dynamic threats of pests and pathogens. Our results corroborate the alternative strategy proposed by Biselli et al. [9] about creating mixed clone plantations, which emerge as viable paths toward the sustainable development of poplar plantations resilient to the dynamic threats of pests and pathogens.

Insect herbivory resistance, a key trait in poplar trees, influences their ability to withstand and recover from damage caused by herbivorous insects. This resistance trait is critical for maintaining tree health and productivity. On the other hand, the ability of hybrid poplars to tolerate environmental stresses like frost, drought, and salinity can significantly affect their survival and growth in diverse ecosystems. These abiotic stressors are becoming more pronounced due to changing climate patterns and land-use practices, making it imperative to investigate how insect herbivory resistance may interact with the trees' abilities to tolerate such stressors. Further research into the genetic and environmental interactions influencing these susceptibility patterns is crucial for advancing pest-resistant poplar cultivation.

5. Conclusions

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Among 35 clones of poplar species and hybrids of the Ukrainian and foreign selection from the *Aigeiros*, *Tacamahaca*, and *Leucoides* sections in the plantation created in 2014 in Eastern Ukraine, *S. carcharias* preferred infesting clones with earlier foliage development, larger diameters, and height increments. Infestation by *S. carcharias* was greater in 2023 compared with 2020 for most clones, however, 12 clones from 35 tested were not infested in both years. *S. carcharias* preferred colonizing clones with earlier foliage development, larger diameters, and height increments. American origin showing higher susceptibility, European origin demonstrating lower susceptibility, and Asian origin or mixed lineages presenting variable resistance to *S. carcharias* infestation. The findings underscore the importance of considering maternal lineage and specific hybrid genetic makeup when developing poplar breeding strategies to enhance resistance to pest infestations. Further research into the genetic and environmental interactions influencing these susceptibility patterns is crucial for advancing pest-resistant poplar cultivation. The utilization of selected clones of native species or the creation of mixed clone plantations emerges as a viable path toward the sustainable development of poplar plantations resilient to the dynamic threats of pests.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org, Table S1: Database of tested clones' health condition.

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