

Article

Resprouting Control of *Ailanthus altissima* by Means of Cut and Stump Covering: Experimental Evidence for a Promising Technique

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Abstract: *Ailanthus altissima* is an invasive tree threatening the biodiversity in natural and disturbed habitats of temperate regions, primarily because of its high resprouting vigor. To test the effect of light exclusion on stem and root sprouting, black covers were applied on the cut stumps of 3-year-old saplings grown in pots. The treatments were as follows: SL, stumps exposed to light; SH, only stumps covered; SPH, the entire pot covered; C, intact control plants. The covers were removed when the root sprouts appeared. The emergence of stem and root sprouts was checked weekly, and their number and biomass were determined at the growth peak (cut I and III) and the end (cut II and IV) of two seasons after cutting. Stem sprouts were produced only in the first growth season in SL and SH and never in SPH and the controls. The number and biomass of the root sprouts were the highest in SH at cut I and in SL in the following cuts. In SH, the sprouting ceased completely after cut I, suggesting a rapid consumption of root reserves, while in SL and SPH, repeated cutting progressively reduced the sprouting vigor. We concluded that covering the stems after cutting is a promising technique to control ailanthus resprouting without the use of herbicides.

Keywords: apical dominance; bud competition; invasive alien species; phenology; root sprouts; stem sprouts; tree of heaven



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1. Introduction

Ailanthus altissima (Mill.) Swingle, which is a deciduous and dioecious tree native to East China and North Vietnam, is widely diffused in the temperate regions of both hemispheres and is recognized as a dangerous invasive in the United States, temperate and Mediterranean Europe, Australia, and South Africa [1–3]. According to Walker et al. [3], ailanthus has become invasive in almost half of the countries where it was introduced, and this proportion rises to 70% in European countries. In Italy, ailanthus grows in all regions and its diffusion is typically anthropogenic, appearing limited only in undisturbed, well-established vegetation systems and at high altitudes, with a limit around 800–1000 m asl in the Mediterranean regions [4,5]. The preferred habitats are frequently disturbed areas, such as road margins, urban gardens, and degraded sites, but it can also damage open archaeological sites and colonize forest edges and open gaps in natural vegetation [6–9]. The diffusion of ailanthus poses recognized threats to the conservation of native biodiversity. In forests, it was found to reduce the presence of native trees and understory species, and to affect the associated animals and microorganisms [10], whereas in grasslands, it reduced the species richness and increased the presence of ruderal and wide distributed taxa [11]. Moreover, ailanthus was found to be a preferential host of alien pests, such as *Metcalfa pruinosa* and *Hyphantria cunea*, for egg deposition and as a food source [12]. Many traits contribute to the success of ailanthus as an invader, with the most important being clonal reproduction through root suckering, a short juvenile phase, the abundant production of winged fruits, the production of allelochemicals, a high adaptability to nutrient-poor

and droughty soils, and a scarcity of specific pathogens in the invaded regions [4,8,13]. In 2019, Europe included *Ailanthus* on the list of species of Union concern because of its strong negative impact on the native biodiversity [4,14]. Species of EU concern cannot be transported, traded, cultivated, and released into the environment, and Member States should adopt eradication or control measures to reduce their adverse impact on biodiversity and the related ecosystem services. Although the complete eradication of *Ailanthus* is not feasible [3], control measures should be urgently adopted to contain the further spread beyond the current altitudinal/latitudinal limit fostered by climate change, and to protect the natural vegetation, monumental sites, and urban gardens [15,16]. Intervening at early invasion stages is crucial to increase the success of control measures and reduce the impact on the native vegetation [10,11].

Several physical, chemical, and biological techniques have been applied, alone or in combination, but none was completely successful or did not present any drawback [9,17,18]. Physical control by means of cutting was generally unsuccessful, unless it was followed by repeated cutting or hand pulling of sprouts at short intervals, and, in many cases, it led to increased populations, as cutting stimulates resprouting from injured stems, root collars, or lateral roots [15,17,19]. The findings of Constán-Nava et al. [18] demonstrated that repeatedly cutting three-year old *Ailanthus* sprouts in mid-summer for five years reduced the plant biomass but increased the plant density by 64%. Biological control methods are under study, and while damage from insects was rarely observed in *Ailanthus*, the fungus *Verticillium nonalfalfae* and other *Verticillium* species that cause wilting diseases, were found to attack all plant parts [20–22].

Up to now, the best control of *Ailanthus* was obtained with herbicides, in combination or not with cutting [8,17,18]. However, the use of herbicides is limited by law [23], as it may be harmful for human health and the environment. Its use needs the development of appropriate techniques and should be avoided or carefully managed in natural reserves and urban areas [9,15]. Moreover, the success of control techniques was also found to change depending on the plant age and on the timing and sequence of operations. The effectiveness of herbicides is generally higher when applied late in the growth season, as the active compounds are translocated to belowground organs, including the root buds, along with the flux of carbohydrates [8,9,17]. Oppositely, Hoshovsky [24] hypothesized that to reduce resprouting without the use of chemicals, stems should be cut at the beginning of flowering, as the root reserves for leaf and flower development are almost exhausted at this stage and are therefore insufficient to support shoot development. Survival after cutting was higher in young plants than in old plants, while the opposite occurred for the number of sprouts produced per plant [15].

Unfortunately, most research focused on stem sprouts, while the difficulty of eradicating *Ailanthus*, and other invasive trees like *Robinia pseudoacacia* L. and *Populus* sp., is mostly determined by their resprouting vigor from roots, which largely relies on the non-structural carbohydrates stored in the xylem parenchyma of woody roots [25]. Both the below-ground starch concentration and resprouting vigor were found to vary during the year in *Eucalyptus* and to decrease in aging plants [26], which may explain the variable effectiveness of control measures reported for *Ailanthus*. Thus, relating phenological events with the production of stem and root sprouts in both cut and intact plants could be pivotal for giving insight into the sink–source relations driving the activation of resprouting buds. At the juvenile growth phase, the proceeding of the vegetative season could be traced following leaf unfolding in the absence of flowering.

The factors involved in regulating bud dormancy and apical dominance, such as light, were not studied in *Ailanthus* [27] but in *Rosa hybrida*, which is another resprouting woody species, where light stimulated the synthesis of the hormone gibberellin necessary for bud burst, and the bud outgrowth was totally inhibited when decapitated plants were placed in darkness [28,29]. As far as we know, the technique of covering cut stumps has never been tested on *Ailanthus*, but it was found able to kill woody stems of other resprouting species, like poplar and willow, within six months [30]. In *Ailanthus*, black covers were

applied by Badalamenti et al. [15] to limit the diffusion of glyphosate into the environment, which may explain the higher effectiveness reported in comparison with other studies [9]. In addition, in a Swiss technical report, Knüsel et al. [31] suggested applying herbicides on the cut surface of stems and then sealing them with a plastic film as the most effective technique for the control of resprouting.

In the present study, we investigated the role of light on the resprouting vigor from the stumps and roots of cut saplings by arranging a pot experiment in which either stumps or the entire pot surface were covered with a black mulch film. A model of the timing and patterns of sprout emergence from the stem and roots in relation to the phenology of intact control plants was presented to give insight into the sink–source relations between plant parts, which may be determinants and drivers of resprouting vigor. We hypothesized that combining mechanical (cutting) and physical (light exclusion) control operations could minimize *Ailanthus* resprouting without the use of chemicals and could, therefore, be applied without risks for human health and natural biodiversity.

2. Materials and Methods

2.1. Experiment Setup

The experiment was carried out in 2021–2024 at the Department of Agriculture, Food and Environment of the University of Pisa (43°42'40" N, 10°24'43" E) with 3-year-old saplings of *Ailanthus altissima* (Mill.) Swingle obtained from a nursery. The plants were grown in pots, and though this may have restricted the sprouting potential compared with field conditions, pots allowed for assigning sprouts to mother plants without any doubt. The climate was typical Mediterranean with a hot arid summer (Csa) [32] and the mean temperatures were above 5 °C in the coldest month and above 22 °C in the hottest month. The photoperiod ranged from 8 h 46' to 15 h 14'. For the entire period of the research, the minimum and maximum daily temperatures and daily rainfall were obtained from a weather station located at the experimental site (Figure 1). Over the period 2021–2023, the mean annual maximum and minimum daily air temperatures were 21.3 °C and 12.1 °C, respectively, and the mean annual rainfall measured 857 mm.

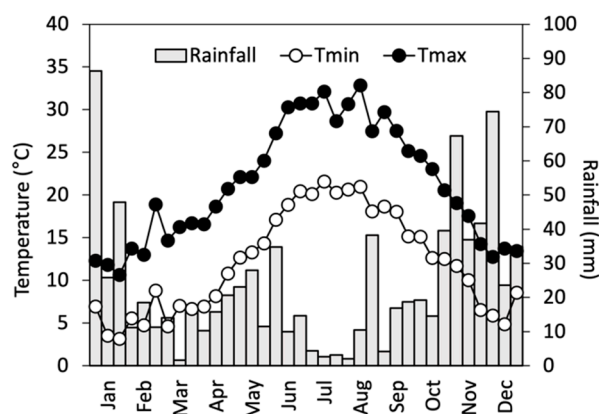


Figure 1. Air minimum and maximum temperatures and rainfall recorded at the experimental site over the years 2021, 2022, and 2023. Temperature values are 10-day averages. Rainfall bars represent 10-day sums.

Cylindric pots that were 50 L in volume (40 cm diameter and height) were filled with agricultural soil collected at a depth between 0 and 15 cm from a field previously cultivated with rapeseed. The soil was classified as sandy Typic Xerorthent [33]. The main soil properties were determined following standard methods and were as follows: 86.3% sand, 7.9% silt, 5.8% clay, 48% water-holding capacity (WHC), 8.2 pH, 5.8% CaCO₃, 0.91% organic C, 0.15 g kg⁻¹ DOC, 1.01 g kg⁻¹ total N, 10.4 mg kg⁻¹ available P, 78.6 mg kg⁻¹ exchangeable K, and 4.93 cmol⁽⁺⁾ kg⁻¹ cation exchange capacity. The pots were placed outdoors and were regularly irrigated by means of drip irrigation. In the SPH treatment,

the irrigation tubes were inserted in a small hole made in the mulch film, which was then sealed to avoid light penetration. Weeds were manually removed. No fertilizers were applied during the experiment.

The experimental design comprised four treatments with six replicates, with each consisting of one pot containing one sapling. Pots were randomly assigned to treatments, which were as follows: not-cut control plants (C); stems cut and stumps left exposed to the light (SL); stems cut and stumps tightly covered with a black biodegradable mulch film (SH); and stems cut and the entire pot covered with a black biodegradable mulch film (SPH). Commercial films based on cornstarch and compliant with EN13432 European standards were used.

Treatments were imposed on winter dormant plants (10 November 2021) by cutting the stems at approximately 15 cm from the soil surface with a hacksaw. The covers were removed from the stumps (SH) and pots (SPH) at the stage when the leaves of the control plants were fully unfolded and the first root sprouts were visible (1 June 2022), which was 203 days after covering. The timing of the principal phenological stages and of successive sprout cuts are reported in Table 1.

Table 1. Timing of phenological events in control plants and sprouts, and the timing of sprout cuts.

Plant Stage	Date		
Winter dormancy of shoots (control tree leaves completely dropped)	1 November 2021	12 October 2022	25 October 2023
Break of winter dormancy (leaf buds swollen in C; in the first season also, stem buds swollen on cut stumps)	16 March 2022	12 March 2023	18 March 2024
First emergence of root sprouts in cut stems	1 June 2022	17 April 2023	22 April 2024
Full vegetative growth (1st leaves of C plants unfolded)	1 June 2022	6 June 2023	31 May 2024
Full vegetative growth of sprouts (1st leaves unfolded)	25 July 2022, cut I	21 July 2023, cut III	-
Leaves of control trees started yellowing	12 September 2022	25 September 2023	-
Leaves of sprouts started yellowing	3 October 2022, cut II	23 October 2023, cut IV	-

2.2. Measurements

The numbers of stem and root sprouts were checked weekly throughout the growth seasons of 2022 and 2023. Stem sprouts comprised both those that emerged from the cut surface and those that emerged from the bark laterally and at the base of the stem [18]. As the imposed treatments did not completely prevent resprouting, we cut the root sprouts for two successive growth seasons. In both years, two cuts were performed: first, when the oldest sprout leaves were fully unfolded (cut I and cut III), presuming this was the stage at which the root resources were depleted by the growth pulse and not replenished yet [18]; second, when the leaves of the control plants were yellow or dropped but sprouts were still green (cut II and cut IV). At all cuts, the sprouts were cut at the stem and soil surface and were counted and weighed. The dry weight was determined after oven drying at 65 °C to constant weight.

2.3. Statistical Analysis

Data were analyzed by means of ANOVA using the software package JMP PRO version 17.0.0. (SAS Institute, Inc., Cary, NC, USA). The number and biomass of the sprouts were analyzed separately for each cut as a factorial design with four factors (C, SL, SH, and SPH) and six replicates. Data were square root transformed when necessary to fulfill the assumptions of normality and homogeneity of variance. Whenever ANOVA reported a significant F value, Tukey's post hoc test was used to separate significantly different means

at $p \leq 0.05$. When the ANOVA was not significant, orthogonal contrasts were used to check for differences between the groups of treatments.

3. Results

3.1. Plant Phenology

In the control plants (C), the leaf buds appeared in approximately mid-March in both years (Table 1). At the same time, swollen buds became visible on the stumps left to the light (SL) in the first growth season, whereas no stem sprouts were produced in the second growth season. The root sprouts appeared later when the first leaves of the control plants were fully unfolded, which we considered to be the stage at which the canopy did not rely on root reserves anymore. At the time all the leaves of the control plants and the first leaves of the stem sprouts were fully unfolded (25 July 2022 and 21 July 2023), we considered that ailanthus reached the peak of the growth season, after which the plants started accumulating new reserves into the roots. The end of the growth season was set in correspondence with the complete leaf yellowing of the control plants (3 October 2022 and 23 October 2023). At this stage, the sprout leaves were still green or red.

3.2. Sprout Number

The covers were removed when root sprouts became visible (1 June 2022), which was 203 days after the treatment imposition. At this time, all the stems left to the light (SL) had sprouts emerging either from the cut surface or laterally from the bark, with an average of five sprouts per plant, whereas the control plants (C) did not present stem sprouts (Table 2). Four out of the six hulled stumps (SH) showed swollen buds, with 1.3 per plant on average, whereas none were detected on the stumps in which the entire pot had been covered (SPH). On the same date, root sprouts had emerged in only half of the control and the SH plants, and with one and two root sprouts per plant on average (Table 2).

Table 2. Percentage of sprouting plants from either the stem or roots and the number of stems, roots, and total sprouts recorded at the time of the cover removal (1 June 2022) and at the four sprout cuts. C, not-cut controls; SL, stems cut and exposed to the light; SH, stems cut and covered; SPH, stems cut, and the entire pot covered. Data are expressed as the mean \pm standard error of six replicates. For each date and parameter, different letters indicate a statistical difference at $p \leq 0.05$ using Tukey’s test.

Treatments	Sprouting Plants (%)		N° of Sprouts per Plant		
	Stem	Roots	Stem	Root	Total
Cover removal (1 June 2022)					
C	0	50	--	1.0 \pm 0.41 a	1.0 \pm 0.41 b
SL	100	0	5.0 \pm 0.58 a	--	5.0 \pm 0.58 a
SH	67	50	1.3 \pm 0.39 b	2.0 \pm 0.94 a	3.3 \pm 1.22 ab
SPH	0	0	--	--	--
Cut I (25 July 2022)					
C	0	67	--	2.5 \pm 0.97 b	2.5 \pm 0.97 b
SL	100	67	4.7 \pm 0.77 a	1.0 \pm 0.33 b	5.7 \pm 0.84 ab
SH	50	100	1.3 \pm 0.77 b	9.2 \pm 1.62 a	10.5 \pm 2.34 a
SPH	0	67	--	4.7 \pm 1.45 ab	4.7 \pm 1.45 ab
Cut II (3 October 2022)					
C	0	50	--	0.5 \pm 0.20 b	0.5 \pm 0.20 b
SL	50	50	1.0 \pm 0.47	8.0 \pm 3.30 a	9.0 \pm 3.70 a
SH	0	0	--	--	--
SPH	0	67	--	1.3 \pm 0.45 b	1.3 \pm 0.45 b
Cut III (21 July 2023)					
C	0	100	--	8.5 \pm 1.87 ab	8.5 \pm 1.87 ab
SL	0	50	--	10.5 \pm 4.78 a	10.5 \pm 4.78 a
SH	0	0	--	--	--
SPH	0	33	--	2.5 \pm 1.45 b	2.5 \pm 1.45 b
Cut IV (23 October 2023)					
C	0	0	--	--	--
SL	0	50	--	7.0 \pm 3.19 a	7.0 \pm 3.19 a
SH	0	0	--	--	--
SPH	0	33	--	0.83 \pm 0.50 b	0.83 \pm 0.50 b

In the following two months, we did not observe any significant initiation of new stem sprouts (Figure 2a), and at each week count, their number was significantly higher in SL than in the other treatments, and did not differ between SH, SPH, and C. Conversely, root sprouts emerged progressively in all treatments, with the highest rate recorded in SH (Figure 2b). The number of root sprouts did not differ between the treatments up to 6 June, while from the 15-June count on, it was always significantly higher in SH than in SL and did not differ between the SPH, C, and SL treatments. Moreover, the number of root sprouts recorded in SH and SPH did not differ statistically, except on 22 June and 13 July. All SH plants produced root sprouts, while one third remained inactive in the other treatments (Table 2). At the peak of the first growth season (25 July), the number of stem sprouts was the same as that recorded on 1st June, whereas the number of root sprouts per plant comprised between one and nine per plant (Table 2). Summarizing, at the peak of the first growth season after cutting, the cut stems left to light (SL) displayed the highest stem sprouting and the cut-and-covered stems (SH) displayed the highest root and total sprouting in terms of both the active plants and sprouts per plant (Table 2).

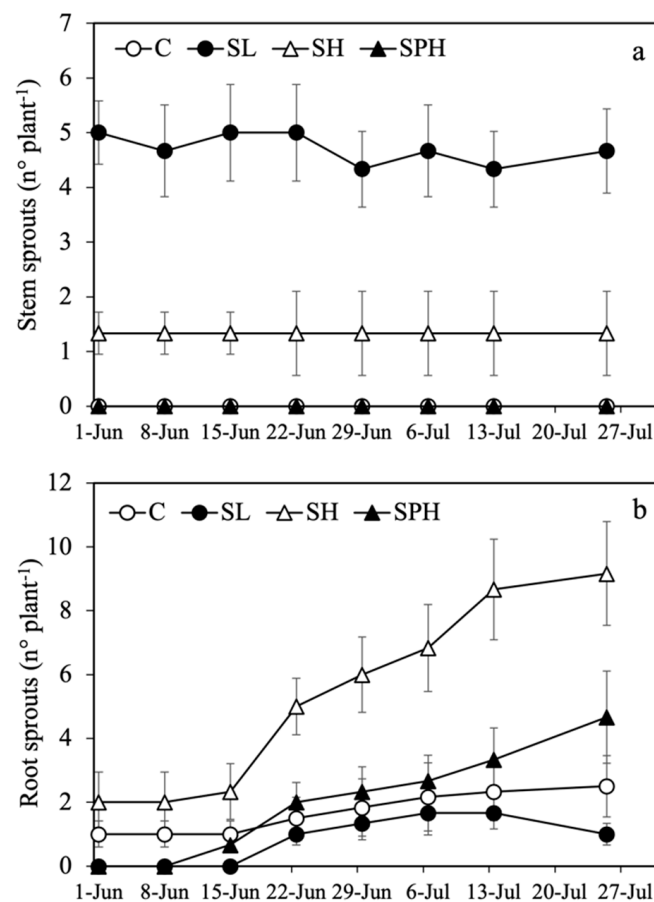


Figure 2. Number of stem (a) and root (b) sprouts produced from the removal of the covers (1 June 2022) up to the peak of the first growth season (25 July 2022), as affected by the treatments. C, not-cut controls; SL, stems cut and exposed to the light; SH, stems cut and covered; SPH, stems cut and the entire pot covered. Error bars denote the SEs ($n = 6$).

New stem sprouts developed only in the SL treatment after cut I, while they did not develop in any treatment after cut II. Conversely, root sprouts emerged in all treatments also during the second growth season, except in SH, in which resprouting stopped completely after cut I (Table 2). It is worth noting that the controls never produced stem sprouts, and in both years, sprouting from roots occurred only in the first part of the growth season. The cumulative number of root sprouts produced by ailanthus plants over the two growth

seasons was 27 per plant in SL, 12 in C, 9 in SH, and 10 in SPH, whereas stem sprouts were produced only in the SL and SH treatments, with six and one per plant, respectively (Figure 3a).

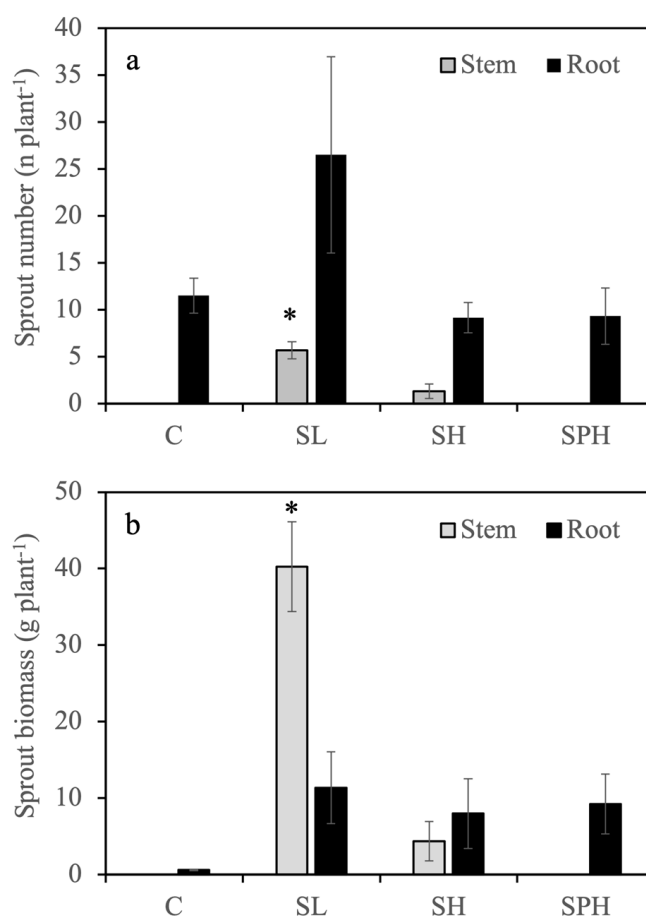


Figure 3. Cumulative number (a) and biomass (b) of stem and root sprouts recorded in the four sprout cuts, as affected by the treatments. C, not-cut controls; SL, stems cut and exposed to the light; SH, stems cut and covered; SPH, stems cut and the entire pot covered. Error bars denote the SEs ($n = 6$). * denotes the statistical difference for the marked treatment at $p \leq 0.05$ using Tukey's test.

3.3. Sprout Biomass

The sprout biomass was affected by treatments differently than the sprout number and, when present, the unit biomass of stem sprouts was higher than that of the root sprouts because of their earlier emergence and generally lower number (Tables 2 and 3). At cut I, the unit biomass of the stem sprouts was more than double in SL than SH, which could be explained by both the longer period of development in SL, which was 131 days compared with 54 in SH, and the lower competition with root sprouts in SL. The biomass of root sprouts showed great variability between the replicate plants but, on average, both the total and unitary biomasses were higher in SH (Table 3). Accordingly, the analysis of contrasts showed that the biomass of the root sprouts was higher in the SH treatment compared with C+SL+SPH at cut I (Table 4).

At cut II, the stem sprouts were present only in SL and their total and unitary biomass were greatly reduced compared with cut I, while the root sprouts were produced only in SL and SPH, with approximately 3 g plant⁻¹ in both (Table 3). Thus, at the end of the first growth season, the cumulative biomass of the sprouts was significantly higher in the cut stems exposed to the light (43.8 g plant⁻¹) than in the other treatments, in which it was 12.4 g plant⁻¹ in SH, 4.2 g plant⁻¹ in SPH, and only 0.06 g plant⁻¹ in the control plants. The treatments also differed in the partitioning of the biomass within the stem and root

sprouts, as over 90% of the biomass was allocated in the stem sprouts in SL and 35% in SH, while SPH and C produced root sprouts only.

Table 3. Biomass of the stem and root sprouts at the four sprout cuts, as affected by the treatments. C, not-cut controls; SL, stems cut and exposed to the light; SH, stems cut and covered; SPH, stems cut and the entire pot covered. Data are expressed as the mean \pm standard error of six replicates. For each cut and parameter, different letters indicate statistical difference at $p \leq 0.05$ using Tukey's test.

Treatments	Stem	Root	Stem	Root	Total
	g dw Sprout ⁻¹		g dw Plant ⁻¹		
			Cut I (25 July 2022)		
C	--	0.02 \pm 0.002 a	--	0.06 \pm 0.024 a	0.06 \pm 0.024 b
SL	8.5 \pm 0.41 a	0.09 \pm 0.026 a	39.5 \pm 5.95 a	0.09 \pm 0.051 a	39.5 \pm 5.96 a
SH	3.3 \pm 0.63 b	0.87 \pm 0.328 a	4.4 \pm 2.56 b	8.0 \pm 4.54 a	12.4 \pm 6.98 b
SPH	--	0.24 \pm 0.102 a	--	1.1 \pm 0.75 a	1.1 \pm 0.75 b
			Cut II (3 October 2022)		
C	--	--	--	--	--
SL	0.82 \pm 0.373	0.40 \pm 0.093 b	0.82 \pm 0.373	3.2 \pm 1.37 a	4.0 \pm 1.74 a
SH	--	--	--	--	--
SPH	--	2.3 \pm 0.54 a	--	3.1 \pm 1.41 a	3.1 \pm 1.41 a
			Cut III (21 July 2023)		
C	--	0.07 \pm 0.005 a	--	0.6 \pm 0.10 a	0.6 \pm 0.10 a
SL	--	0.67 \pm 0.143 a	--	7.0 \pm 3.09 a	7.0 \pm 3.09 a
SH	--	--	--	--	--
SPH	--	1.5 \pm 0.30 a	--	3.9 \pm 2.23 a	3.9 \pm 2.23 a
			Cut IV (23 October 2023)		
C	--	--	--	--	--
SL	--	0.15 \pm 0.032 b	--	1.0 \pm 0.46 a	1.1 \pm 0.46 a
SH	--	--	--	--	--
SPH	--	1.4 \pm 0.26 a	--	1.2 \pm 0.69 a	1.2 \pm 0.69 a

Table 4. Significance (p -value) of orthogonal contrasts for the biomass of root sprouts at the peak of the first (cut I, 25 July 2022) and the second growth season (cut III, 21 July 2023). C, not-cut controls; SL, stems cut and exposed to the light; SH, stems cut and covered; SPH, stems cut and the entire pot covered. ns, not significant.

Contrasts		p -Value	
		Root Sprouts (g Plant ⁻¹)	
		Cut I	Cut III
C	SL + SH + SPH	ns	ns
SL	C + SH + SPH	ns	0.0314
SH	C + SL + SPH	0.0173	ns
SPH	C + SL + SH	ns	ns
SH + SPH	C + SL	ns	ns

At cut III, the biomass of the root sprouts did not differ significantly between the treatments, but the analysis of contrasts highlighted that it was higher in SL compared with the other treatments (Table 4). At cut IV, only SL and SPH produced root sprouts, with approximately 1 g plant⁻¹ in both (Table 3). As in the first growth season, also in the second, the cumulative biomass of the sprouts was significantly higher in the cut stems exposed to the light (8.1 g plant⁻¹), followed by SPH, with 5.1 g plant⁻¹, and by the controls, with 0.6 g plant⁻¹, while the SH plants did not produce any sprout over the entire growth season. However, differently from the first growth season, in the second, sprouting occurred only from the roots, and the achieved biomass was approximately fivefold smaller.

The cumulative biomass of stem sprouts produced by *ailanthus* saplings over the two growth seasons after cutting was approximately ninefold greater when the stumps

were left to light (SL) compared with those that were covered (SH) (Figure 3b). Conversely, the cumulative biomass of the root sprouts did not differ significantly between the cut treatments, which comprised between 8 (SH) and 11.4 g plant⁻¹ (SL) and was negligible in the control plants. It is worth noting that while in SH, 100% of the root sprout biomass was produced before cut I, in SL and SPH, 71% and 54%, respectively, of their cumulative biomass was produced during the second growth season (Figure 4).

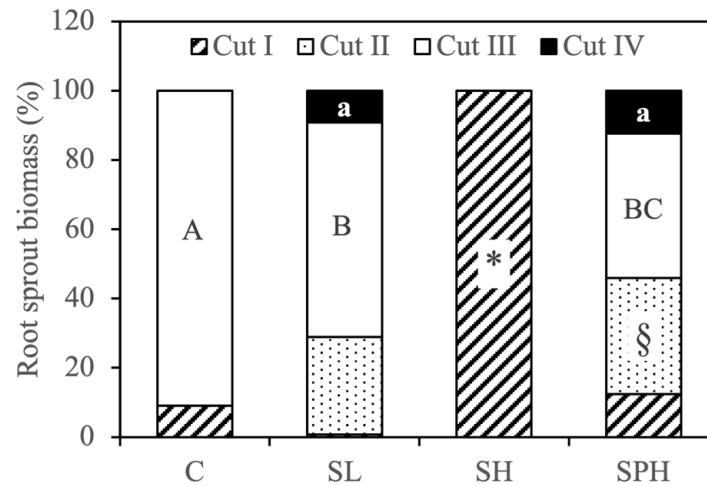


Figure 4. Percent partitioning of the cumulative biomass of root sprouts within the four sprout cuts, as affected by the treatments. C, not-cut controls; SL, stems cut and exposed to the light; SH, stems cut and covered; SPH, stems cut and the entire pot covered. Within each cut, different fonts or symbols indicate the statistical difference between the treatments at $p \leq 0.05$ using Tukey's test. Missing fonts or symbols are different from those reported.

3.4. Sprouting Model

In the first growth season, the patterns of leaf phenology in intact plants and the correspondence with the emergence of stem and root sprouts suggest that the leaf emission inhibited stem sprouting and exerted a strong competition on the emergence of root sprouts (Figure 5 C). Cutting greatly stimulated the sprouting from stems when stumps were left exposed to the light and, like canopy leaves, stem sprouts also seemed to exert a strong competition on the emergence of root sprouts (Figure 5 SL). In SL, indeed, sprouting from roots showed a marked increase only after the removal of stem sprouts with cut I. The application of black covers greatly reduced the production of stem sprouts in SH (Figure 5 SH) and permanently inhibited it in SPH, in which the entire pot was covered (Figure 5 SPH). Conversely, the emergence of root sprouts appeared stimulated in these treatments, probably because of the lower (SH) and no (SPH) competition with stem sprouts. In SH, no resprouting occurred after the sprout cutting at the peak of the first growth season (cut I) (Figure 5 SH), and in the control plants, the new root sprouts died before cut II (Figure 5 C). In SL and SPH, indeed, sprouting also proceeded after cutting at the end of the first growth season (cut II), from both stems and roots in the former and only from roots in the latter (Figure 5 SL and SPH). However, these late-produced sprouts did not survive the winter. In the following growth seasons, the timing of phenological events in the control plants and the patterns of root sprouting were similar the first season, with the exception that sprouting started earlier, around mid-April, probably because they developed from the bases of the sprouts cut in the preceding season (Table 1).

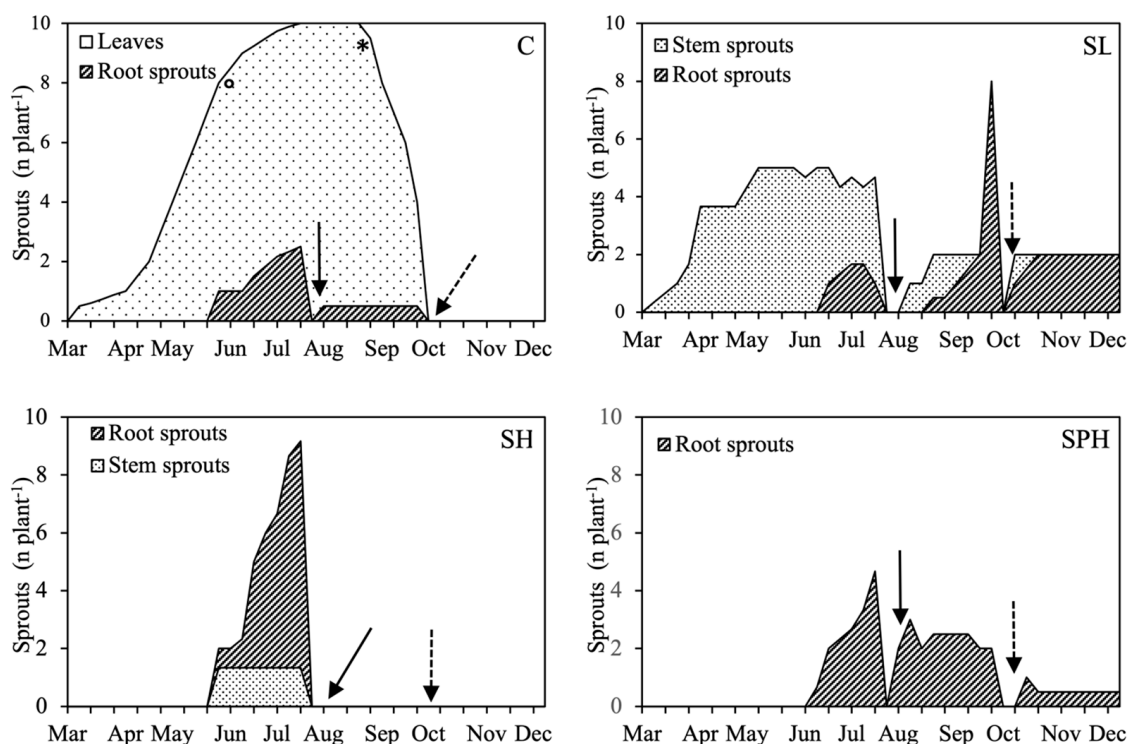


Figure 5. Timing of the stem and root sprout emergence in the different treatments and correspondence with the leaf phenology of control plants during the first growth season after the stem cutting. C, not-cut controls; SL, stems cut and exposed to the light; SH, stems cut and covered; SPH, stems cut and the entire pot covered. Arrows indicate sprout cuttings: solid line, cut I (25 July); dashed line, cut II (3 October). In C, ° indicates the stage the first leaves were completely unfolded (1 June), while * indicates the time the leaf started yellowing (12 September).

4. Discussion

Like most research that addressed the eradication of *Ailanthus*, we found that leaving the stems exposed to the light after cutting (SL) greatly stimulated the stem and root sprouting, with the latter emerging later and to a lesser extent [9,17–19]. These patterns are consistent with the hypothesis of Schneider et al. [27], where both apical dominance and competition for resources concurred in regulating the bud outgrowth. The release of apical dominance caused by cutting activated stem sprouts, where growth exerted a strong sink for root reserves and new assimilates, thus hindering the development of root sprouts. In contrast, cutting the *Ailanthus* saplings at winter dormancy and immediately covering the stumps with a black hull (i.e., SH) reduced the percentage of active individuals and the average number of stem sprouts per plant during the following vegetative season. Stem sprouting was permanently prevented when the soil around the stumps was covered too (i.e., SPH). Conversely, covering did not inhibit the root sprouting, which was higher in SH and SPH than in SL during the first part of the growth season after cutting, which was probably driven by the small or even no competition with stem sprouts for root resources.

The successive interventions of sprout cutting performed during the two growth seasons after the treatment imposition were differently effective. Neither the stem nor root sprouts emerged in SH after cut I, whereas four cuts failed in stopping resprouting from roots in 50% of the SL individuals, and 33% of the SPH individuals. The prolonged resprouting vigor of *Ailanthus* stumps exposed to light was probably because of the ability of the cut stems to photosynthesize and exchange gases with the atmosphere, thus supporting sprout growth also in the absence of leaves. *Ailanthus* is not mentioned by Berry et al. [34] among the species that present permeable stem tissues that support photosynthesis, but we observed a green ring just beneath the cork in the cut stumps, which demonstrated that woody stem chlorophyll is also present in this species. The application of covers

inhibits stem photosynthesis and greatly reduces gas exchanges and water fluxes, which are essential for the demolition of reserves and the transport of non-structural carbohydrates and hormones [27,35]. According to Sun et al. [36], the vascular tissue of woody plants can also conduct light along the stem and into the roots, and more light is absorbed by cut surfaces. Successively, by leaking out of the vascular system, light reaches the surface tissues, thus inducing bud proliferation in both the stem and roots [36]. Light perception directly by roots placed near the soil surface may explain why stem sprout primordia developed under the covers in the SH treatment but not in SPH, in which the roots were in darkness too.

In general, the success of control techniques relies on the depletion of root resources, while the exhaustion of buds may hardly limit resprouting, as their number is very high, especially in juvenile phases [4,26]. Studies on *Ailanthus* demonstrated, however, that the technique of successive cuttings alone failed in depleting root resources in a few years, independently of the season the plants were cut and the number of successive sprout cuttings [18,19]. In small areas or when manual labor is available, it was also demonstrated that hand pulling was more effective than cutting, as it avoided resprouting from residual sprout stumps [4]. According to our results, covering stems just after winter cutting (SH) induced a flush of sprouts at the beginning of the following growth season, which probably exhausted the root and stump reserves [37] and stopped any further resprouting after their removal (cut I). It may be that cutting at the peak of the growth season and not later also played a role in preventing the storage of new assimilates. Otherwise, residual root resources seemed to still be available for resprouting when the soil surface was also covered (SPH), which was probably because of the lower cumulative sprout biomass produced during the first growth season compared with SH.

The patterns of sprout emergence and growth in response to treatments provided evidence of competitive relationships between the buds located at different positions on the plant, with the competitive strength of buds decreasing in the order of canopy > stem > roots. The uncut 3-year-old saplings of *Ailanthus* never produced stem sprouts, which confirmed the findings of Constán-Nava et al. [18] and the hypothesis that apical dominance permanently inhibits stem and collar buds [27]. Conversely, intact plants also produced root sprouts, which, however, dried out before the end of the growth season, which suggests that the mother-plant roots exerted a strong sink for resources. Though our findings may be biased by the pot conditions, and Kowarik [38] reported that undisturbed populations also produced root sprouts, understanding the success of root sprouts in established *Ailanthus* stands could be of concern for controlling the diffusion of existing populations.

The later emergence of root sprouts, which was approximately when the leaf unfolding and stem sprouting approached a plateau, could be explained only in part by the decreased competition with stem buds for root reserves, as it also started later in the treatments with scarce stem sprouting. Moreover, resprouting in October, despite the control leaves being yellow, suggests that the growth season of roots did not coincide with that of shoots, which probably started and ended later. These observations allowed us to infer that, in *Ailanthus*, both internal and external factors regulate bud outgrowth differently in stems and roots. In stems, light seems to be the driving factor for both canopy and stem buds, with the former exerting apical dominance on the latter, whereas in roots, the development of sprouts seems to rely primarily on the amounts of reserves stored in the root tissues and on the soil temperature [4,27,35]. Though *Ailanthus* displays a broad latitudinal range, at present, it colonizes a wide range of habitats in the temperate regions of north America, while in Europe, its occurrence is progressively confined to urban areas with the increase in latitude [1,4]. This difference, which was imputed to the higher winter survival of sprouts because of warmer summers in the American region [4], may disappear in the close future due to climate change and it is to expect that in northern Europe, *Ailanthus* will show sprouting patterns like in the Mediterranean region in the next decades. In any case, we can presume that the length of the sprouting period and the rate of sprout growth will be related to the length of the vegetative season and the rate of biomass accumulation of intact plants

in all colonized environments. Thus, by relating the timing of sprout development with the phenology of intact plants, our model may overcome the variability due to pedoclimatic conditions and can, therefore, also be applied in other regions.

Our results demonstrate that control operations consisting of either covering the cut stems or repeatedly cutting the sprouts during two years after cutting failed in eliminating the resprouting of *Ailanthus* when applied separately, while their combination (SH) completely inhibited resprouting after cutting the sprouts only once at the peak of the first growth season after the stem cut (end of July).

5. Conclusions

In conclusion, the results of this preliminary study show that cutting plants and immediately covering the stumps with a black biodegradable mulch film is a promising technique for controlling *Ailanthus*, as it inhibited resprouting after cutting once the first flush of sprouts had been produced. This technique, which does not use herbicides, is not harmful to humans and allows for a prompt restoration of pre-invasion biodiversity. Therefore, it is best suited for urban areas, along roads, in archaeological sites, and to stop invasion within and at the edges of nature reserves. By providing insight into the correspondence between canopy phenology and sprout development, as well as into the competitive relationships among plant parts, our study adds valuable knowledge for selecting the most effective timing of stem cutting and cover removal. Further research should test the effectiveness of the cover technique in field conditions and should also focus on developing the most appropriate cover materials in terms of the ease of application, durability for the intended period, and rapid degradability in the soil after use.

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