

EFFECT OF REPETITIVE MOWING ON COMMON RAGWEED (*AMBROSIA ARTEMISIIFOLIA* L.) POLLEN AND SEED PRODUCTION

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Abstract: *Ambrosia artemisiifolia* L (common ragweed) is a familiar roadside weed in southern Québec (Canada) that produces large amounts of airborne pollen responsible for multiple rhino-conjunctivitis (hay fever) cases. As roadside weeds are increasingly controlled by mowing alone, the effect of a mowing treatment on pollen production was evaluated. *Ambrosia artemisiifolia* plants were grown in a greenhouse at 4 densities (1, 3, 6 and 12 plants per 314 cm² pot) and either left intact or mowed (10 cm from the ground) when the plants reached 25 cm in height, i.e. twice during the life cycle of this annual plant. Pollen production per male inflorescence was collected in open-top bags and counted. Inflorescence mass, length, location on the plant and date of anthesis onset was noted. Above-ground plant biomass and seed production was also evaluated. Mowed plants produced less pollen per unit of inflorescence length than intact plants. Pollen production per plant was reduced by a factor of 8.84 by the double mowing treatment, while viable seed production per plant was reduced by a factor of 4.66, irrespective of density. Mowing twice has the potential to reduce airborne pollen loads but *Ambrosia artemisiifolia* seed banks are unlikely to be depleted by this management strategy.

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INTRODUCTION

Common ragweed (*Ambrosia artemisiifolia* L., Asteraceae) is an annual weed widespread in eastern Canada [5, 6, 21] and in the US Eastern and North Central states [48]. Native to the New World, its distribution is expanding in Europe [44]. Leaf shape, plant size, allocation to inflorescences and pubescence vary from one plant to another [5]. Its seed production can range from 3,000–62,000 seeds per plant and 4% of these seeds can remain viable in the soil for at least 39 years [16, 47]. *Ambrosia artemisiifolia* is a monoecious species. Male inflorescences are located on upper terminal branches and female flowers are located in lower leaf axils [5].

Ambrosia artemisiifolia flowers are wind pollinated. A single plant can produce billions (10⁹) of pollen grains [20, 40]. In Canada, anthesis generally occurs from August to September [6, 13, 15, 22, 24]. During the flowering period, where *Ambrosia artemisiifolia* plants are common, ragweed pollen is the most abundant airborne pollen [12, 22] and is responsible for most cases of rhino-conjunctivitis (hay fever) and a number of asthma cases [10]. The detrimental health effects caused by pollen from other widespread *Ambrosia* species, principally *A. trifida* L. and *A. psilostachya* DC., are limited or localized due to the relative scarcity of these species in Canada [6]. As little as 5–10 pollen grains m⁻³ of *A. artemisiifolia* can potentially trigger an allergic reaction in sensitive individuals [3].

In the province of Québec, Canada, 9.4–17.5% (in areas where the species is present) of the population now suffer from seasonal hay fever [25, 45]. This number is also likely to increase in the future if global warming increases *A. artemisiifolia* pollen production [40, 50] and/or its flowering period [9]. Therefore, controlling this weed is not only an agricultural issue, as most weeds are, but an increasing public health concern.

Ragweed is an early successional plant that grows in disturbed areas such as fields, roadsides, waste areas and dwellings under construction [7, 31, 39]. In crop fields, it can be abundant in corn, soybean, and some horticultural crops [8]. In crops, ragweed control is mostly obtained by applying herbicides. Along highways and rights-of-way, widescale herbicide use has declined [46]. Environmental and health concerns from citizens has led cities, and eventually 2 Canadian provinces (Québec in 2003 and Ontario in 2009) to ban the cosmetic use of lawn care herbicides such as 2,4-D, MCPA and mecoprop [35, 36]. Therefore, mowing is now one of the prevailing weed control methods in city lawns.

Mowing does not eliminate *Ambrosia artemisiifolia* pollen production as the species will respond to the treatment by producing more secondary branches [49]. There are publications on biomass, flower and seed count reduction from mowing [4, 14, 15, 49]. However, we are unaware of studies that have actually measured pollen production following a mowing treatment. Flowers from mowed plants might not produce the same amount of pollen as those from uncut plants. Late flowering inflorescences are likely to produce less pollen [40] and resource allocation to male flowers could be reduced in response to the mowing treatment. Moreover, since gender allocation is size-dependent in *Ambrosia artemisiifolia* [2], increasing ragweed density, i.e. lowering individual plant size, might modify allocation to pollen production and response to mowing. Our goal was to evaluate the effect of a severe but relatively standard mowing treatment on ragweed pollen and seed production. We hypothesized that pollen production per unit of male inflorescence regrowth would be severely reduced by the mowing treatment, and that this effect would be even more drastic at higher plant density. As female flowers are located on lower leaf axils, we also assumed that seed production would be reduced to a lesser extent than pollen production by the mowing treatment.

MATERIALS AND METHODS

Experimental conditions and design. In September 2007, over 3,000 ragweed seeds were collected from roadside populations (>100 individuals) in the city of Québec (46°49'N, 71°13'W) and stored at 4°C. Forty-five days before the experiment, the seeds were placed in moist sand (5% water content) at 4°C. The seeds were then left at room temperature (20°C) in ambient light for a few days. Germinated seeds were then sown in flats containing standard potting soil until emergence. Seven days after

emergence, seedlings were replanted in pots (20 cm diameter) at desired densities and grown at 14:10 photoperiod, 22°C day, 17°C night, until maturity (Long day conditions ensure that ragweed plants produce predominantly staminate flowers and do not exhibit a dwarf stature [1]; growing conditions were also based on weather data from Saint-Jean-sur-Richelieu, Québec, Canada). Pots were watered as needed and plants were fertilized twice a week during 4 weeks with a nutrient solution (N, P₂O₅, K₂O; 20-20-20 Plant-Prod®, 1 g l⁻¹) to ensure normal growth. Fertilisation was then stopped as roadside plants do not usually grow in nutrient rich conditions. The factorial design was completely randomised (pots were randomly relocated in the greenhouse every week) and included a mowing treatment (mowed and intact), 4 densities (1, 3, 6 and 12 plants per 314 cm² pot) and 5 replicates (+ 10 extra pots for single plants). Densities correspond to ca. 32, 96, 191 and 382 plants m⁻² of soil. Densities along roadsides in 2 rural areas of southern Québec can range from 0–594 plants m⁻² [42]. Others report at least 100 plants m⁻² along some road sections [17, 34]. The mowing treatment consisted of cutting down the plants to 10 cm height when they reached 25 cm in height, i.e. twice during the experiment (41 and 51 days after germination). Average plant height (\pm standard error (STE)) during the first and second mowing treatment, respectively, was 25.75 \pm 1.20 cm and 25.14 \pm 0.94 cm. Dry biomass removed during these first and second cuts corresponded to 0.457 \pm 0.086 g plant⁻¹ and 0.348 \pm 0.049 g plant⁻¹, respectively. Standard cutting height in municipalities is 10 cm, often done using a tractor-mounted blade [15]. Vegetation along roads is often cut when it reaches approximately 25 cm for visibility and aesthetics, and to limit shrub and tree growth [17]. Some authors have suggested optimal mowing dates based on flowering phenology [15], but plant height is easier to assess and ensured all densities would be cut on the same date. Nevertheless, our first mowing corresponded with anthesis onset, as recommended [15]. Some pollen production did occur before the mowing treatments and was evaluated at 0.966 \pm 0.1304 million pollen grains per inflorescence. Average length of all mowed inflorescences (n=63) was 8.25 \pm 0.33 cm. The number of inflorescences per mowed and intact plant at the end of the experiment and their average flowering date is shown in Figure 1. Pollen production was evaluated for 2 plants per experimental unit (located in the centre of the pot). When plants started bolting, open top plastic bags were set on all male inflorescences to collect the pollen.

Data collection on bagged inflorescences. During the experiment, the date at which each bagged inflorescence started to produce pollen (phenological growth stage no. 61 of the BBCH scale) [23] was noted in order to evaluate days to anthesis. When flowering had ceased, these inflorescences were cut at base. Because allocation to the apex and initial branches can be higher than to branches that form later during ontogeny [32], the location of the

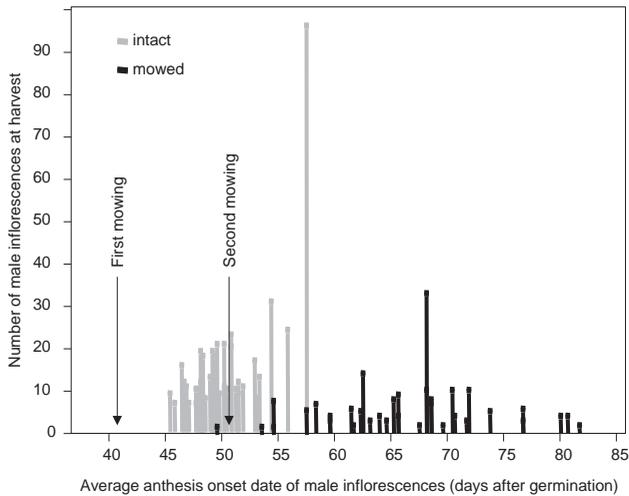


Figure 1. Number of male inflorescences that started flowering on a given day after germination in the greenhouse for intact (gray) and mowed (black) plants. Mowed plants were cut at 10 cm height when they reached 25 cm height (twice). Mowing dates are indicated by arrows.

male inflorescence on the plant and length of the inflorescence was noted. Inflorescence locations were grouped in 7 classes (1=terminal (apex), 2=second branch, 3=third branch, 4=fourth branch, 5=fifth branch, 6=sixth branch, other=branches stemming from these or of higher order). As the initial branching pattern is opposite, 2 branches could be classed in the same order on a single plant. Bags with mould or water accumulation resulting from condensation were discarded from pollen count measures. Pollen production was evaluated using a published methodology [40]. The pollen collected in the bags was rinsed with 15 ml of distilled water and 0.02% of Tween 20 into test tubes. The solution was then vortexed, to break the anthers, and stirred before each pollen sampling [40]. Pollen grains were counted with a haemocytometer (American Optical, Scientific Instrument Division, Buffalo, NY). These inflorescences were then dried at 70°C during 3 days and weighed.

Data collection on whole plants. When plants started to senesce (84 days after emergence), all plants were cut at base and dried at 70°C for 3 days. We did not observe differences in senescence between treatments. Plants had to be harvested before seed dispersal in order to be able to collect the seeds from the plants located in high density pots. Above-ground plant and seed biomass of bagged plants was measured. Total male inflorescence length and seed production was also evaluated. Seed viability was tested using a standard tetrazolium staining technique [26].

Allometric model and statistical analyses. Because many bagged inflorescences were discarded (310 out of 792), the measures taken on the other male inflorescences served to generate an allometric model to estimate the pollen production (p_i) of discarded inflorescences.

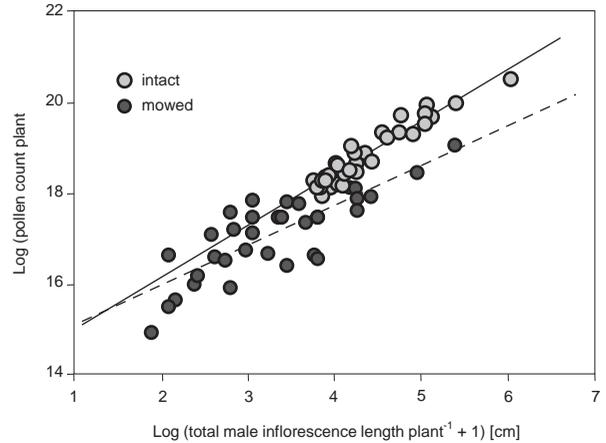


Figure 2. Relationship between log male inflorescence length and log pollen count for intact (grey circles) and mowed (black circles). Mowed plants were cut at 10 cm height when they reached 25 cm height (twice). Regression lines are shown for intact (solid line) and mowed plants (dashed line).

A preliminary analysis revealed that all variables, and a single interaction term were significant. Therefore, the model was based on inflorescence length, inflorescence location, days to anthesis, plant density and mowing treatment, following the equation:

$$\text{Log}(p_i) = \mu + l_i + loc_i + a_i + d + m + (l_i m)$$

where μ is a constant and l_i is inflorescence length, loc_i is inflorescence location, a_i is inflorescence days to anthesis (days from germination to anthesis onset), d is plant density, and m is plant mowing treatment (Tab. 1). The pollen production of all inflorescences (measured and estimated) could then be summed in order to obtain total pollen production per plant. The effect of the mowing treatment and plant density on whole plant pollen, seed and biomass production was evaluated using factorial ANOVA. All data was subjected to natural logarithmic transformation (except seed counts which were subjected to square root transformation) to meet ANOVA assumptions (normality of sampling distribution and homogeneity of variances).

RESULTS

The model estimating pollen production per inflorescence explained 72.6% of the variation in the measured pollen count. Pollen production per inflorescence was positively associated with inflorescence length ($t=12.44$, $p<0.001$) and negatively associated with days to anthesis ($t=-9.26$, $p<0.001$) (Tab. 1). The effect of inflorescence length on pollen production was modulated by the mowing treatment ($t=-6.59$, $p<0.001$) (Tab. 1). This interaction can also be observed at the whole plant level by plotting total pollen production over total inflorescence length. Mowed plants generally produced less pollen per unit of inflorescence length (Fig. 2). Increasing density reduced pollen production per inflorescence ($t=-2.89$ to 2.03 , $p<0.05$ to 0.01)

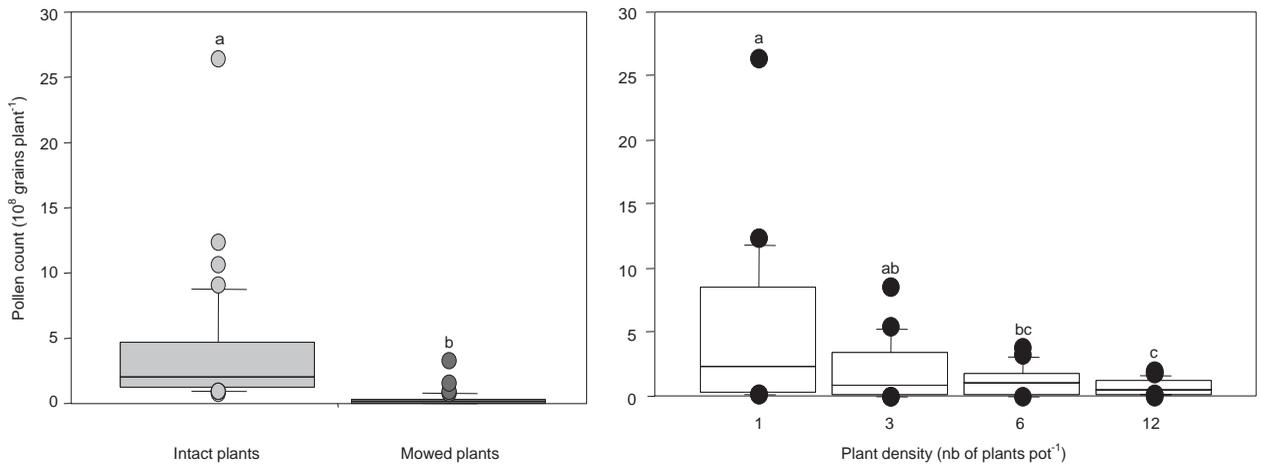


Figure 3. Box plots of pollen production (in number of pollen grains shed per plant) for intact and mowed plants (left) and all plants growing at different densities (right) in the greenhouse. Mowed plants were cut at 10 cm height when they reached 25 cm height (twice). Boxes topped by the same letter are not significantly different ($\alpha=0.05$).

(Tab. 1) to some extent as inflorescences in high density pots produced ca. half as much pollen as single plants. Inflorescence location on the plant and mowing alone were less predictive of pollen production per inflorescence. Only the highest-order inflorescences (“Other” class) produced less pollen than the other branches (Tab. 1).

Table 2 shows the results of the factorial ANOVAs. Mowing plants twice or varying plant density significantly affected most variables. Interaction terms between mowing and plant density were not significant (Tab. 2). Mowing and increased plant density were both associated with reduced pollen production ($p < 0.001$). Mowed plants produced, on

average, 9.16 times less pollen (0.4309×10^8 pollen grains) than intact plants (3.9481×10^8 pollen grains) and pollen production lowered as density increased with high density plants (12 plants per pot) producing 6.95 times less pollen compared to single plants (Fig. 3). Average pollen production of mowed plants before the mowing treatments was 0.0156×10^8 pollen grains plant⁻¹. If this value is added to the total pollen production, the reduction in pollen production by the mowing treatment is by a factor of 8.84. Total inflorescence length was also reduced for mowed and higher density plants, with values 3.36 and 5.04 (at 12 plants per pot) times lower than intact and single plants,

Table 1. Parameter estimates and probability values for the multiple linear regression estimating the pollen production of *Ambrosia artemisiifolia* per inflorescence.

Parameter	Group	Coefficient	SE	<i>t</i> -Value	<i>p</i> -Value
Intercept	μ	18.660	0.425	43.89	<0.0001
Inflorescence length	l_i	0.097	0.008	12.44	<0.0001
Inflorescence location (Reference 1)	loc_i				
	other	-0.282	0.079	-3.58	0.0004
	6	0.142	0.128	1.11	0.2689
	5	0.009	0.108	0.09	0.9267
	4	-0.074	0.094	-0.79	0.4308
	3	-0.052	0.010	-0.52	0.6030
	2	0.213	0.108	1.97	0.0499
Density (reference 1)	d				
	12	-0.229	0.079	-2.89	0.0041
	6	-0.217	0.072	-3.02	0.0027
	3	0.138	0.068	2.03	0.0427
Days to anthesis	a_i	-0.060	0.006	-9.26	<0.0001
Mowing treatment (Reference mowed)	m	-0.148	0.076	1.96	0.0512
Mowing * inflorescence length	$(m * l_i)$	-0,04	0.0069	-6.59	<0.0001

Group – see Materials and Methods for a detailed description of the equation; Coefficient – estimate of the regression coefficient; SE – Standard error of the regression coefficient; *t*-Value – ratio of the regression coefficient to its standard error; *p*-Value – probability of the *t* statistic.

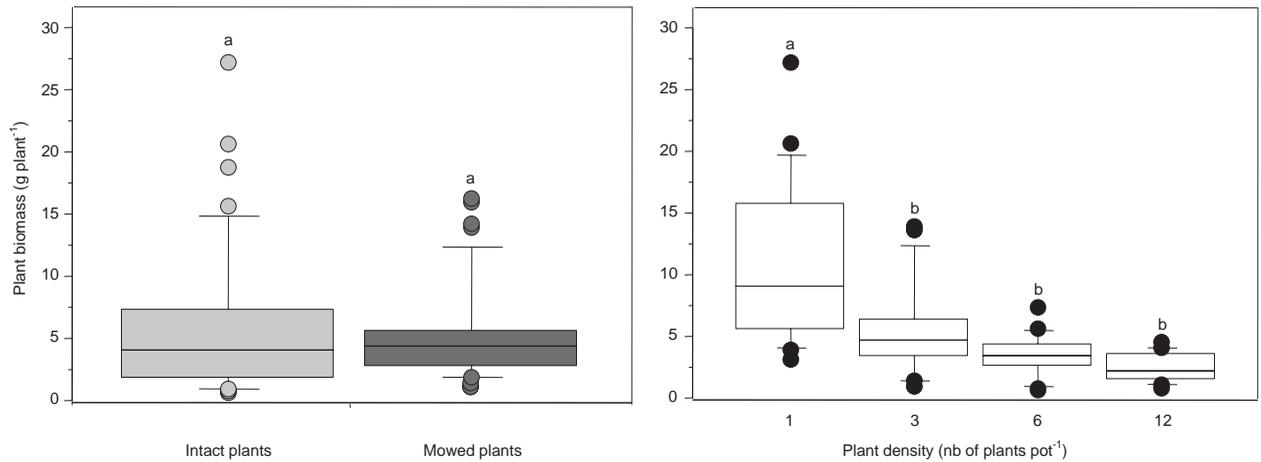


Figure 4. Box plots of biomass per plant for intact and mowed plants (left) and all plants growing at different densities (right) in the greenhouse. Mowed plants were cut at 10 cm height when they reached 25 cm height (twice). Boxes topped by the same letter are not significantly different ($\alpha=0.05$).

Table 2. Factorial ANOVA results for the effect of mowing and plant density on pollen production, inflorescence length, days to anthesis, plant and seed biomass, biomass allocation to seed production and seed production.

Source	DF	Sum of Squares	F Ratio	p-Value
Pollen count (log x + 1)				
Mowing treatment	1	20.734	127	<0.001
Density	3	4.786	9.81	<0.001
Mowing * density	3	0.636	1.30	0.2804
Total inflorescence length (cm) (log x + 1)				
Mowing treatment	1	66.618	53.34	<.0001
Density	3	16.961	4.526	0.0059
Mowing * density	3	4.840	1.292	0.2840
Days to anthesis (days)				
Mowing treatment	1	1.463	176	<.0001
Density	3	0.011	0.468	0.7050
Mowing * density	3	0.030	1.199	0.3171
Plant biomass (g) (log x + 1)				
Mowing treatment	1	0.0501	0.2161	0.6435
Density	3	15.421	22.187	<0.0001
Mowing * density	3	0.8726	1.2555	0.2962
Seed biomass (g) (log x + 1)				
Mowing treatment	1	0.1222	23.068	<0.0001
Density	3	0.0117	0.7374	0.0002
Mowing * density	3	0.989	2.706	0.0516
Seed biomass per plant biomass (g/g) (log x + 1)				
Mowing treatment	1	0.1221	23.068	<0.0001
Density	3	0.0117	0.7364	0.5337
Mowing * density	3	0.0149	0.9431	0.4244
Seed production (nb) (\sqrt{x})				
Mowing treatment	1	749.92630	16.6324	0.0001
Density	3	789.18731	5.8344	0.0013
Mowing * density	3	372.33164	2.7526	0.0488

DF – degrees of freedom; F Ratio – value of the F statistic; p-Value – probability of the F statistic.

respectively (Tab. 2, details not shown). Anthesis (averaged over all inflorescences) was delayed by an average of 17.08 ± 0.7 days by the mowing treatment (Fig. 1), but was not delayed or hastened by plant density (Tab. 2). Although averages are lower for mowed plants, whole plant above-ground biomass was not significantly reduced by the mowing treatment but was reduced by increasing density as higher density plants (12 plants per pot) were 4.59 times smaller than plants growing alone (Tab. 2, Fig. 4). Mowing and increased plant density were both associated with reduced total seed mass and seed counts ($p < 0.01$) (Tab. 2). Mowed and high density plants produced respectively 2.89 and 4.03 times less seed than intact and single plants (Tab. 2, Fig. 5). The seeds produced by mowed plants were also less viable by a factor of 0.62 ($p = 0.0003$; $40.61 \pm 4.82\%$ vs. $65.58 \pm 4.18\%$ viability), while plant density did not alter viability percentages ($p = 0.8258$, details not shown). Allocation to seed biomass was reduced by the mowing treatment ($p < 0.001$), but was not modified by plant density ($p = 0.5337$, Tab. 2). Biomass allocation to male inflorescences at the whole plant level could not be evaluated because too many plants had discarded inflorescences. However, pollen count per inflorescence mass was reduced by a factor of 1.82 by the mowing treatment (-55.8% , $p < 0.001$), but not by density ($p = 0.5618$) (data not shown).

DISCUSSION

Pollen production per inflorescence. The pollen production of *Ambrosia artemisiifolia* inflorescences could be fairly well estimated by inflorescence length alone. Rogers *et al.* [40] also observed that inflorescence length was a very good predictor of pollen production. Days to anthesis was also a good predictor of pollen production. During our experiment, the inflorescences that started flowering earlier produced the most pollen. Therefore, as days between germination and anthesis onset increased, pollen

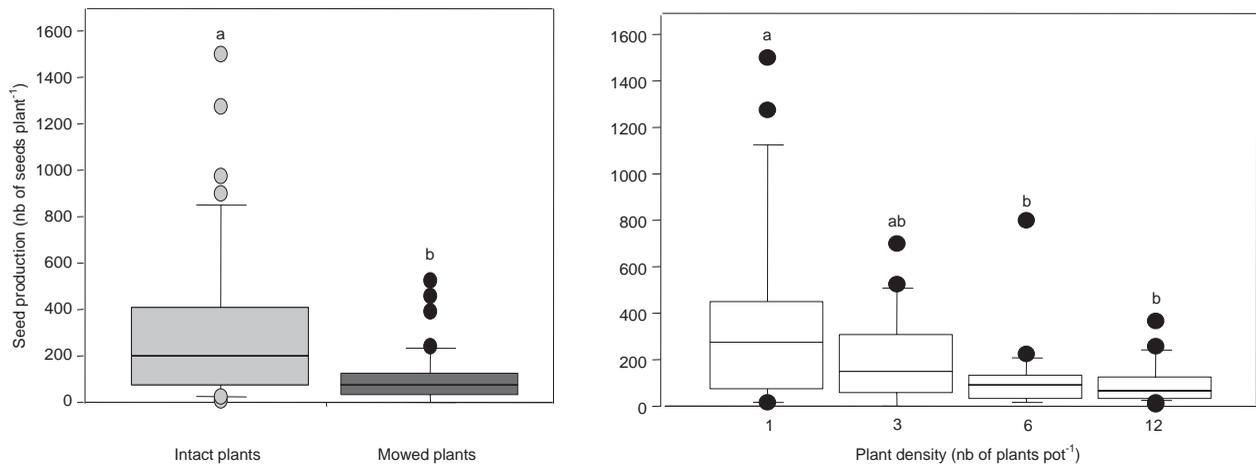


Figure 5. Box plots of seed production per plant for intact and mowed plants (left) and all plants growing at different densities (right) in the greenhouse. Mowed plants were cut at 10 cm height when they reached 25 cm height (twice). Boxes topped by the same letter are not significantly different ($\alpha=0.05$).

production decreased. Within a plant, resource allocation to late flowering inflorescences is generally lower than to early flowering ones. However, these observations on allocation are generally based on the seed production of hermaphroditic flowers [33]. Our results indicate that the reproductive success of male inflorescences of *A. artemisiifolia* varies in a similar fashion. Mowing modified the relationship between inflorescence length and pollen production as mowed plants produced less pollen per unit of inflorescence length. Allocation to male fitness was probably reduced as mowed plants invested in secondary branching below cutting height. Plant density altered pollen production per inflorescence, indicating that inflorescences suffering from higher competition for light and/or nutrients (we did not separate effects), produced less pollen. However, density did not alter pollen production per unit of inflorescence length. Although plant density alters allocation to male fitness in *A. artemisiifolia* [37], these changes are probably mostly generated by a reduction in the number of flowers (inflorescence length and mass) than by a reduction in pollen production or size per flower. Therefore, the inflorescences formed from regrowth after our mowing treatment did not produce less pollen per unit length at higher plant density than those located on single plants. This indicated that at the whole plant level, plant density did not alter the effect of our mowing treatment.

Mowing and whole plant pollen production. The ability of ragweed to produce new stems after being cut has been observed [4, 14, 15, 49]. A single cut, 5 cm from the ground when the plants start to flower, can reduce the total biomass of inflorescences (both male and female) by 49–55% while total biomass will be reduced by 9–34% [49]. Our results from 2 cuts at 10 cm in the greenhouse when plants reach 25 cm show a 70.2% reduction in male inflorescence length and a slight but not significant reduction in total biomass production. The lack of reduction in total biomass can be explained by our high cutting height

and the greenhouse conditions, where lateral growth outside the pot was not limited. Larger pots and higher plant numbers could have limited these edge effects, but would have required at least 4 times the greenhouse space. The reduction in biomass of mowed plants in cities and other areas will likely depend on the competition from surrounding vegetation. Nevertheless, our mowing treatment reduced total pollen production by 88.7% because the mowing treatment predominantly cut male flowers, and male flowers produced by regrowth produced less pollen per unit length and biomass. Our intact plants generally produced over 10^8 pollen grains. High pollen production was expected from this wind pollinated species [20, 40]. Mowing closer to the ground or more often would likely have reduced pollen production even more. However, not all roadsides and weedy areas can be cut below 10 cm (due to the presence of rocks, uneven ground, etc.) and multiplying interventions is expensive.

Mowing and whole plant seed production. Seed production was not reduced as much as pollen production by our mowing treatment. This was expected as female flowers are located lower on the plant. Seed production was reduced by a factor of 2.89 by the mowing treatment. Seed viability was also reduced by a factor of 0.62 by the mowing treatment, leading to a 4.66 reduction in viable seed production. Such a reduction will not reduce the population density of most weeds, including *Ambrosia artemisiifolia*, as most annual weeds produce hundreds of seeds that can germinate the next spring if conditions are suitable [38]. Mowed single plants produced an average of 148.1 seeds plant⁻¹, and mowed high density plants (12 plants per pot) produced 59.4 seeds plant⁻¹. At such a rate, given the high longevity of ragweed seeds in the soil [30, 47], our mowing treatment could potentially increase the seedbank every year. Changing plant density did not significantly alter allocation to seed biomass. Although *Ambrosia artemisiifolia* is self-incompatible [19], single plants did not

produce less seed per biomass unit. Because flowers are uni-ovulate, there was probably enough airborne pollen from the un-bagged inflorescences of the other plants in the greenhouse not to limit seed set. Since allocation to seed was not reduced by increasing density while pollen counts were, gender allocation was slightly increased towards femaleness as density increased, indicating a shading effect of our density gradient [37]. Nevertheless, density did not significantly alter the effect of the mowing treatment on seed production.

CONCLUSION

Ambrosia artemisiifolia can be very abundant along roadsides. Roadside densities can be higher than those of fields or field edges [42]. Field populations are generally managed either with herbicides or mechanically (e.g. in organic crops), while undisturbed field edge populations tend to be overgrown with perennial species that out-compete ragweed. However, along roadsides, the section closest to the pavement is disturbed by vehicles and roadside management (trampling, snow ploughing, cleaning, application of de-icing salt). This is where most of the ragweed plants are located [17]. As herbicide use along roadsides has been somewhat abandoned in a few Canadian provinces, ragweed is basically controlled by mowing [17]. Our research indicates that mowing twice (10 cm from the ground) when the plants reach 25 cm in height will reduce pollen and seed production. Pollen production in the greenhouse was reduced by a factor of ca. 9 by this double mowing treatment while the production of viable seed was reduced by a factor of ca. 5. Nevertheless, millions of pollen grains and dozens of seeds were still produced per mowed plant. If these numbers are converted per area, over 2×10^9 pollen grains m^{-2} and 140 seeds m^{-2} or 86 viable seeds m^{-2} (of greenhouse pot) were produced by mowed plants. Given that less than 50 pollen grains m^{-3} are probably necessary to trigger an allergic reaction [3, 43], evaluations of actual airborne pollen concentrations following mowing treatments would be required. Long-distance transport of exogenous pollen will also increase local pollen concentrations [28, 29, 41] and a fraction of deposited pollen grains can be potentially re-deposited on human feet [27] and in houses [18]. As for the seed production of mowed plants, if 15% of the *A. artemisiifolia* seed bank was to emerge the following season and 30–40% of seeds that did not germinate remain viable in the soil for one year [11], and then take decades to be entirely depleted [30, 47], our results suggest this type of mowing strategy would steadily increase or maintain a very persistent seed bank. More effective management strategies would probably be necessary to observe an *A. artemisiifolia* population decline along roadsides. Otherwise, roadsides will remain important refuges for *A. artemisiifolia*.

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