


Competition between *Ambrosia artemisiifolia* and *Ambrosia trifida*: Is there a threat of a stronger competitor?

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Abstract

Recent reports of the presence of *Ambrosia trifida* (AT) in areas infested by *A. artemisiifolia* (AA) in Serbia warn of the impending establishment of a more damaging crop weed. Here, we test the potential competitive effects of these two weed species. We conducted a field competition study in 2016 and 2017 as a replacement series experiment arranged in a split plot, with main plots (20.5 m × 2 m) at total plant densities of 10 and 100 plants/m², and sub-plots (3 m × 2 m) at the proportion of AT to AA of 100:0, 80:20, 60:40, 40:60, 20:80 and 0:100. Individual plant biomass (IPB) for AT was lowest when grown in monoculture, while AA reached its highest IPB in its monoculture. With AT < 40%, the AT IPB was larger than (2017) or the same as AA (2016). With AT > 40%, its IPB decreased due to increased intraspecific competition. We obtained the lowest sub-plot biomass (SPB) of AT + AA in mixtures with 40:60 and 60:40 ratios, and also the highest SPB of other weed species. We show that despite a larger leaf area, AT may not fully replace AA and thus not become a new threat to crops, as it not only suffers from intraspecific competition at high densities, but also from interspecific competition with AA. Therefore, crops may benefit from a stable coexistence of both species as compared to highly dominant AT or AA. Further studies in the presence of crops are needed to confirm this hypothesis.

KEYWORDS

interspecific competition, intraspecific competition, plant density ratio, plant invasion, multispecies competition

1 | INTRODUCTION

To be successful in establishing in crop fields, weeds must tolerate soil disturbance, synchronise their germination time and emergence with the crop and with management interventions as well as with the growth of neighbouring plants to reduce competition (Tominaga and Yamasue, 2004). In addition, fields are fertilised and irrigated;

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therefore to become established, a successful weed species should be able to monopolise resources in favour of its own growth and to increase its suppressive effect (Kaur et al., 2018). Another important characteristic of weeds is their ability to grow at high density and still maintain high reproductive output (Yannelli et al., 2017).

Ambrosia artemisiifolia L. (common ragweed), hereafter referred to as AA, is both a highly noxious plant due to its negative impacts on human health caused by its allergenic pollen and an important weed of spring sown crops (Kazinczi et al., 2008). A recent study reported that around 13.5 million people suffer from common ragweed-induced allergies in Europe, causing economic costs of

approximately Euro 7.4 billion annually (Schaffner et al., 2020). Besides crop fields, it is also invading natural and semi-natural habitats and cities, and spreads along linear transport structures such as roads, railway tracks and rivers (Essl et al., 2015). Human mediated dispersal such as through contaminated seed and grain mainly favoured the spread of the large number of seeds produced by this plant among cultivated fields (Kazinczi et al., 2008; Lavoie et al., 2007), but also zoochory, including endo-zoochory (Kazinczi et al., 2008) and rarely ecto-zoochory (Marza, 2010) can be a dispersal mechanism for *Ambrosia* seeds. High phenotypic plasticity and regrowth capacity enable AA to adapt to variable environments. It has invaded areas outside its native range in all continents except Antarctica. In Europe, it has been considered a weed since the early 1920s (Csontos et al., 2010) and is presently invasive in more than 30 countries (Essl et al., 2015). In Serbia, AA was first recorded from the Pannonian Plain (Bačka region [Voyvodina province]: sites Sremski Karlovci and Novi Sad) (Slavnić, 1953), and today, it is widely distributed across the country in crop and non-crop fields (Vrbničanin et al., 2008). Species distribution models predict a northward spread of AA under climatic change both for the introduced European and East Asian populations (Sun et al., 2017) as well as the native North American range (Case and Stinson, 2018).

Ambrosia trifida (giant ragweed), hereafter referred to as AT, also originates from North America, where it is widespread in Canada, the United States and northern Mexico. It has been widely introduced into Europe (Lawalree, 1947) and is reported from many regions of Europe and Asia (Follak et al., 2013). The first records of AT in Serbia were from the Pannonian Plain (Banat region [Voyvodina province]: site Čoka) (Koljandzinski and Šajinović, 1982), and Malidža and Vrbničanin (2006) reported new sites of AT from crop and non-crop fields in the Bačka region, both in the Voyvodina province. Based on a recent Pest Risk Analysis, it was added to the A2 List, indicating a high phytosanitary risk of AT for the European and Mediterranean region with risks to agricultural production, the economy and human health (European and Mediterranean Plant Protection Organization: EPPO, 2019). The species is an annual herbaceous plant that usually grows to a height of 2 m, but can reach a height of 6 m in nutrient-rich and moist soils. With the capacity to adapt to disturbed habitats such as roadsides and crop fields, AT is harmful to wild and crop plants because of its competitive ability. Moreover, the large amount of pollen produced by AT is known as a significant human allergen and in various regions of its distribution, residents report allergic symptoms (Qu et al., 2019).

Both AA and AT have been reported to invade the same crops. AA can cause 30% loss to maize and sunflower yields (Kazinczi et al., 2009), and up to 70% loss in soybean (Weaver, 2001). *Ambrosia trifida* can cause 76%–87% yield loss to maize (Harrison et al., 2001), more than 75% yield reduction in soybean (Webster et al., 1994), and has the potential to decrease sunflower biomass by 50% (Vrbničanin et al., 2012).

The newly reported simultaneous presence of AA and AT in crop fields suggests the potential for new ecological interactions between the two *Ambrosia* species. AT and AA coexist in Serbia along roads,

between settlements and at the margins of sunflower, maize, soybeans and sugar beet fields (Vrbničanin et al., 2015). In their native range, the two species also occur in the same states in the United States (e.g. in Ohio, Indiana, Wisconsin and Nebraska) (Leif et al., 2000; Regnier et al., 2016), and they have been observed to grow in the same sites in Nebraska including crop fields and non-crop land (S. Z. Knezevic, personal communication). Hybridisation of AA and AT has been studied, provoked by fears of the origin of a weed species more detrimental to human health, agriculture or natural environments (Vincent and Cappadocia, 1987). Coexistence of AA and AT in crop fields also warns of impending competition between the two *Ambrosia* species. Both *Ambrosia* species have a similar ecological niche, but AT prefers slightly more moist and nutrient-rich soils than AA (Bassett and Crompton, 1982). The invasion of AT into the distribution range of AA may further reduce crop yield due to AT's larger growth form and larger leaves. The ability of AT to overtop less competitive crops, even when placed at a competitive disadvantage by delayed emergence, reinforces concerns about introducing a more troublesome weed than AA (Page and Nurse, 2015).

Information about the interspecific interactions of AT and AA is scarce (Savić et al., 2019). Predicting species distributions across fields or natural areas requires a good understanding of a plant's ecology within a multispecies community (Huisman and Weissing, 2001), as the response of plants may vary from their typical growth when alone. Above- or below-ground competition among plant species can alter the growth habit and biomass accumulation (Mudrák et al., 2016), the root to shoot ratio (Mašková and Herben, 2018), growth rates, the canopy structure and the timing of reproduction (Walsh et al., 2018). AT and AA interactions may influence the other weed species in the community. Miller and Werner (1987) reported that AA interactions with a multispecies mixture were asymmetric, with AA severely suppressing other weed species, while the presence of other weed species did not influence AA growth. Regarding the competitive traits of AT, we assume that its introduction to a new area will also highly affect the composition and abundance of the other weeds. Therefore, we conduct the current study within a site with a severe infestation of AA, and a diverse weed flora of monocotyledons, for example *Echinochloa crus-galli* (L.) P.B. (barnyard grass), *Setaria viridis* (L.) P.B. (green foxtail), *Sorghum halepense* (L.) Pers. (Johnson grass) and dicots, for example *Cirsium arvense* (L.) Scop. (Canada thistle), *Chenopodium album* L. (lamb's quarters), *Plantago lanceolata* L. (ribwort plantain), *Polygonum aviculare* L. (prostrate knotweed) and *Erigeron annuus* (L.) Pers. (annual fleabane).

Here, we present the results of experiments to study the interaction between AT and AA under field conditions at two densities and in a series of different density ratios of the two species. Outcomes were quantified at the level of individual plant performance and at the plot level, including changes in the other weed species. More specifically, we ask the following questions: (a) what is the effect of six different ratios of the two *Ambrosia* species on individual plant biomass (IPB), (b) what is the effect of the six ratios on total sub-plot biomass (SPB), (c) how do these effects differ between two overall densities, and between 2 years, and (d) how do the other weed

species respond to the overall plant densities and the proportion of AT to AA. Results will provide the basis to assess the invasion potential of AT into AA infested areas and its expected effects on crop yield.

2 | MATERIALS AND METHODS

Two field experiments were carried out at a farm near Dobrić, Republic of Serbia (44°41'N, 19°34'E) during 2016 and 2017. Unlike AA, which forms dense populations in this area and greatly impacts crop production, AT has not yet been recorded in this part of Serbia. This site was selected for the field trial to obtain a measure of the competitive strength of AT when it invades a habitat where AA is already well established at high density. Seeds of AT were collected in autumn 2015 from infested crop fields in Central Bačka (45°30'N, 19°31'E; c. 130 km from the study area) and subsequently stored for three months at 4°C before sowing. Climatic conditions and soil properties are similar in the two areas, and average temperature and precipitation at the study site during the experiments are presented in Table 1.

The experimental field was known to have severe infestations of AA. It remained fallow for two years prior to the experiment, and previously cultivated with maize and wheat in rotation for many years. The field was prepared with two shallow discs followed by a cultivator in April 2016 and 2017. Soil samples were taken in April 2016 after soil preparation from each sub-plot and subsequently analysed for physical and chemical properties (Table 2).

The experiment consisted of a split-plot design with four replications (blocks) and arranged as a replacement series (de Wit, 1960). Each block comprised two main plots, and each main plot consisted of six sub-plots of 3 m × 2 m. Main plots size was 20.5 m × 2 m (we separated sub-plots by a 0.5 m distance). The main plot treatments were total plant densities of 10 or 100 plants/m², and the sub-plot treatments were the proportion of AT to AA of (a) 0:100, (b) 20:80, (c) 40:60, (d) 60:40, (e) 80:20 and (f) 100:0. As shown in Figure 1, each of the four blocks contained two main plots (low and high density) that were randomly placed within each block, and within each main plot, the six sub-plots (the proportion of AA to AT) were also randomly assigned (6 density ratios × 2 densities × 4 blocks = 48 sub-plots). The sub-plots were further divided into six quadrats of 1 m² for sequential destructive plant sampling. For AA, we used its natural infestation, as we observed a relatively even distribution of AA with well over 100 plants/m² prior to the experiments. AT was sown on 8 April in both years to mimic an invasion of AT into a site with a well-established AA population. Due to the strong similarity in soil, climate and management (both are from crop fields) properties of the experimental field and the site where the AT seeds originated, we assumed potential home-site advantage of AA over AT to be minimal. The sowing density in main plots was 1,000 seeds/m² for high density and 100 seeds/m² for low density. To facilitate the even distribution of AT seeds, they were mixed with soil before sowing. The soil was levelled by a rake at a depth of 1 cm. Four quadrats per sub-plot were used for measurements of vegetative plant growth in July, August, September and October, while the remaining

TABLE 1 Monthly weather conditions during the field trials

Month	Mean monthly temperatures (°C)		Precipitation (mm)	
	2016	2017	2016	2017
April	13.6	12.1	25.2	61.6
May	16.3	17.7	58.4	59.4
June	20.9	24.3	109.2	165.6
July	22.2	23.2	40.8	108.9
August	20.4	23.6	33.2	40.8
September	17.9	16.6	45.2	69.6

TABLE 2 Soil properties of the experimental field. Soil samples were taken from each sub-plot in April 2016 prior to the experiment

pH		P ₂ O ₅ (mg/100 g)	K ₂ O (mg/100 g)	Humus (%)
KCl	H ₂ O			
3.9–4.3	5.1–5.7	3.18–5.30	12.35–15.14	2.01–2.83

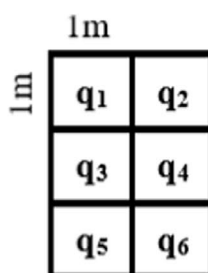
Note: Covariance analysis did not reveal any significant difference among sub-plots ($p > 0.5$).

two quadrats served for another study not presented here. Data from the last two assessments (September and October) were similar, so we used only data from September. July, August and September samplings (in both 2016 and 2017) were coincident with BBCH (Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie) stages of 34–36, 57–59 and 69–71, respectively, for AT, and 36–39, 57–59 and 69–71, respectively, for AA (Hess et al., 1997).

As AT does not occur in the study area, care was and will continue to be taken to avoid permanent establishment of AT in adjacent crop fields and after the end of the experiment by manually removing plants, herbicide applications and mowing as needed.

The emergence of AA and AT was roughly simultaneous. Plants of AA and AT were selected to achieve the required densities and marked by tying the red thread around the stems 14 days after emergence, and every 7 to 10 days during the entire season, all newly established ragweed plants were removed. This was achieved by hand-thinning, and care was taken to reach a uniform distribution of ragweed plants in approximately the same growth stages within each sub-plot. As mortality of the marked plants was below 1%, this allowed us to maintain the required number of AA and AT per unit area after establishment and throughout the duration of the experiments. Other weed species were not removed. They were more or less homogeneously distributed across the experimental field (as described below in *Statistical analyses*), with the most abundant species being *Setaria viridis* (L.) P.B., *Echinochloa crus-galli* (L.) P.B., *Sorghum halepense* (L.) Pers., *Polygonum aviculare* L., *Cirsium arvense* (L.) Scop., *Chenopodium album* L., *Plantago major* L. and *Erigeron annuus* (L.) Pers. For identification, we follow the taxonomy of Flora of R. Serbia (Josifović, 1970–1980).

Individual plant biomass and SPB were determined during July, August and September by destructively harvesting one quadrat

Main-plots:H: High Density (100 plants/m²)L: Low Density (10 plants/m²)**Sub-plots:**A: 100% *AT*B: 80% *AT*: 20% *AA*C: 60% *AT*: 40% *AA*D: 40% *AT*: 60% *AA*E: 20% *AT*: 80% *AA*F: 100% *AA***Each sub-plot**

Samples were taken from quadrats as follows:

q₂, q₃, q₄ – July, August, September, respectively for both 2016 and 2017 (height, width, number of leaves, biomass of *AT* and *AA*, as well as number, percent cover and biomass of other weed species). Data of q₁, q₅, and q₆ are not used for the current manuscript.

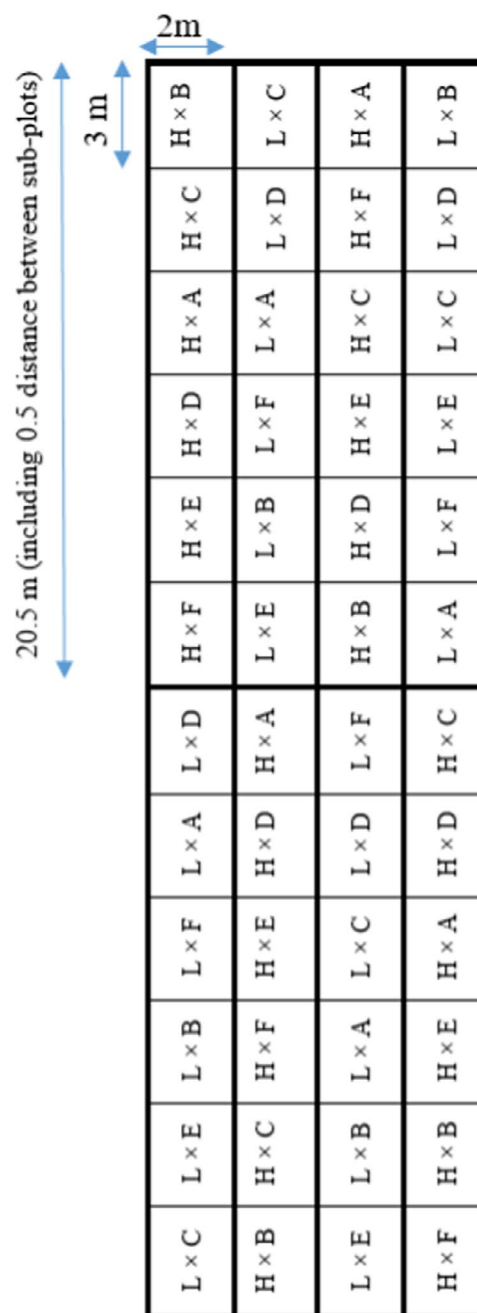


FIGURE 1 Schematic of this study's experimental design (see text for details)

within each sub-plot. For this, a total of 10 plants (*AT* + *AA*) were individually harvested by cutting the above-ground biomass, air-dried for a few days in the laboratory, oven dried for 48 hr at 80°C, and then weighed to determine IPB and thereby calculate SPB.

2.1 | Statistical analyses

Mixed models were used to analyse the main effects of total plant density (main plots), *AT*:*AA* ratio (sub-plots) and their interaction. Total plant density and density ratios were considered as fixed

effects in the model, whereas year was considered as a random effect. Data analysis was performed in R-studio version 1.1.453 (RStudio Team, 2020) using the package 'lme4' (Bates et al., 2018). As there was no significant deviation from normality, no data transformation was required. The interaction terms were significant, so the main effects of total density and the density ratios are not shown. We used protected least significant difference (LSD) for the comparison of means. The standard error of means were also calculated and shown. To assess whether other weed species and soil properties were distributed homogeneously across the study site, we performed analysis of covariance.

3 | RESULTS

Mixed effects model analysis was conducted separately for data from each sampling month and as the effect of year was significant for all three months, the results of both years are shown. Interactions between total density (low or high) and AT:AA ratio were significant for both AT and AA for the IPB and their SPB ($p < 0.01$). Covariate analysis of the biomass of other weed species in July, and of soil properties measured prior to experiments did not reveal any significant difference among sub-plots ($p > 0.5$). Therefore, differences in the density of other weed species in September were interpreted as treatment effects. Furthermore, the non-significant block effect ($p > 0.6$) confirms the homogeneity in soil properties and biomass of other weed species at the field site across our study plots.

3.1 | Ambrosia performance in low density (10 plants/m²)

In 2016, in a pattern that became stronger over sequential sampling months, AT produced the least IPB in monoculture, and the IPB of AT increased with increasing AA in the proportion of species. In contrast, AA produced its highest IPB in monoculture. When grown together, the IPB of the two species did not differ, irrespective of the proportion of the species, but in monocultures, AA produced higher IPB than AT (Figure 2).

Consistently, in 2017 AA produced highest IPB in its monoculture (39 g), while AT produced its lowest IPB (21 g) in monoculture. The highest IPB for AT (52 g) occurred with an AT:AA ratio of 20:80.

When comparing the greatest IPB produced between AT and AA, in 2016, AA had higher IPB than AT (24 g vs. 17 g), while, in 2017, AT had higher IPB than AA.

3.2 | Ambrosia performance in high density (100 plants/m²)

In 2016, IPB was marginally lower for AA than AT for the July and August assessments, while in September, AA had greater IPB than AT (Figure 2). The highest IPB of AA was in its monoculture (16 g) and decreased to a minimum IPB of 13 g in the proportion of 80AT:20AA.

In 2017, AT produced a much higher IPB than AA in 20AT:80AA in the September assessment. However, with increasing AT density, we observed an exponential decrease in the IPB of AT. The highest IPB of AT was 94 g that decreased to about 27 g with increasing proportion of AT to AA.

For both years, as in the low-density plots, monocultures yielded the lowest IPB for AT and the highest IPB for AA. The highest IPB of AA (50 g) occurred in AA monoculture, and its minimum IPB was with 80AT:20AA (20 g).

3.3 | Biomass production at plot level: interaction between AT and AA

Results from the two years were not consistent. In 2016, biomass per square meter was higher in low than high density, while in 2017, high-density plots produced higher biomass (Figure 3). However, in both low and high densities, the highest biomass production occurred in monocultures (Figure 3). With low density, the lowest total biomass (AT + AA) per plot occurred at an AT:AA ratio of 80:20, and with high density, it occurred at ratios of 40:60 and 60:40.

In 2017, AT monoculture produced higher SPB than AA, and this difference was larger in high density (Figure 3). In low density, AT:AA ratios of 20:80 and 40:60 produced the lowest total (AT + AA) biomass per m². To summarise, when the two species co-occur, total biomass production was significantly lower compared to monocultures.

3.4 | Effects of total density and AT:AA ratio on other weed species

In 2016, among the other weed species, *S. viridis*, *C. album*, *P. aviculare* and *E. annuus* were the most abundant (with average plant density > 5 plants/m²), while in 2017, *S. viridis* and *P. aviculare* were the most abundant other weed species. The biomass of other weed species was significantly lower in high density than in low-density sub-plots ($p < 0.001$, Figure 4) and the interaction between total density and AT:AA ratio was significant in both years (2016: $p < 0.02$, 2017: $p < 0.05$). In 2016, for both low and high densities, the highest biomass of other weed species occurred with AT:AA ratio 60:40, that is when the interspecific competition between AT and AA was highest, causing the lowest total biomass per m² of AT + AA (Figure 3). The AT monoculture at high density resulted in lower biomass of the other weed species than in AT monoculture at low density. In 2017, with high density, the lowest biomass of other weed species occurred with AA monoculture (Figure 3), while with low density it occurred with AT:AA ratio 60:40.

4 | DISCUSSION

Both AA and AT are reported to be invasive and strong competitors in crop fields (Barnes et al., 2018). Compared to AA, AT suffered more from intraspecific competition in our experiments, while AA produced its highest IPB in monoculture. Our results showed that AT had a larger IPB than AA if its density was $< 40\%$ in the AT:AA ratio. Increasing AT $> 40\%$ enhanced intraspecific competition, which led to a significant decrease in the IPB of AT. Studies of competition across varying habitats (including agriculture, grassland and forest) based on 527 plant species pairs reported in 39 publications have revealed that intraspecific competition is on average four to five times stronger than interspecific competition (Adler et al., 2018). Here, we found severe intraspecific competition in AT, with its taller and more expansive canopy. In contrast, greater plasticity of some species in allocating

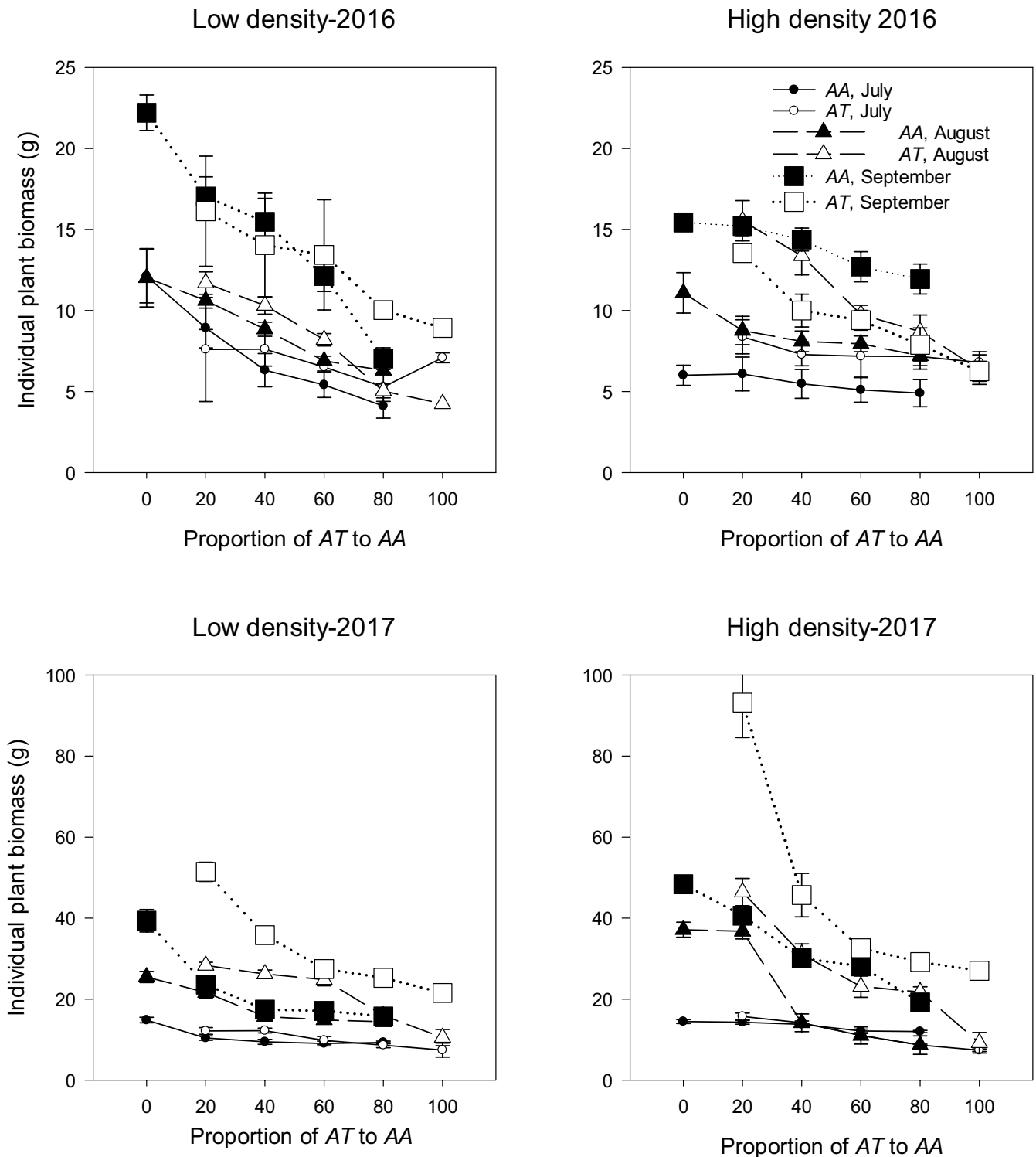


FIGURE 2 Individual plant biomass (IBP) of *Ambrosia trifida* (AT) and *A. artemisiifolia* (AA) with increasing AT density in combination at low (10 plants/m²) and high density (100 plants/m²) in July, August and September for 2016 and 2017. Bars on mean values are standard errors

resources to growth allows them to grow taller and thinner without collapsing and thereby potentially escape shading and mortality even at high densities (Leicht-Young et al., 2011). AA is an example of such a species, capable of producing considerable above-ground biomass at various pure stand densities (Patracchini et al., 2011).

Ambrosia trifida had higher IPB than AA in 2017 but not in 2016 (Figure 2). This may have been caused by the fact that in 2016, seeds of AT were sown in the field, whereas in 2017, seeds remained in the soil from the previous year and these may have germinated earlier. Therefore, if both AT and AA become naturalised in the area, the

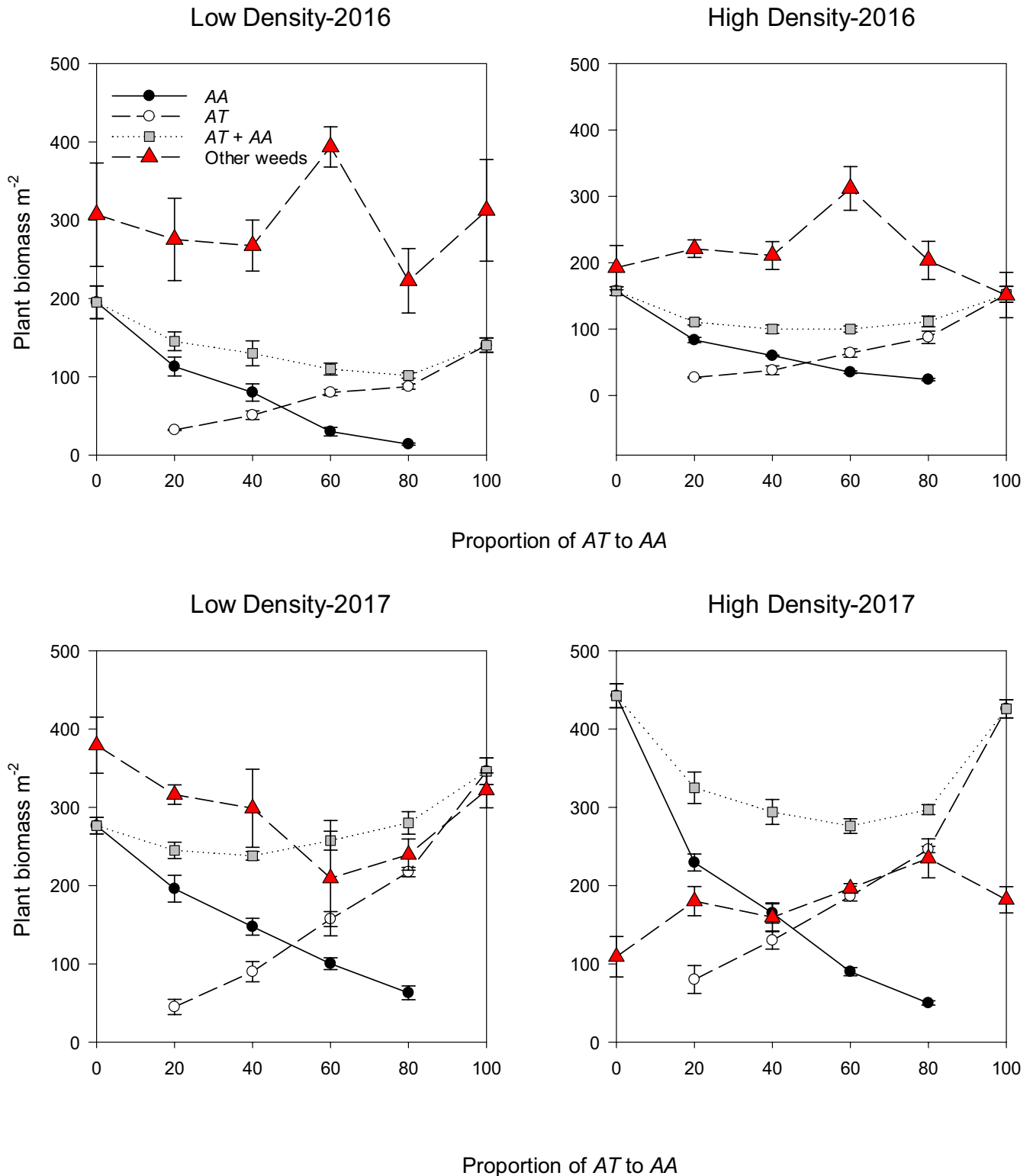


FIGURE 3 Sub-plot biomass (SPB) of *Ambrosia trifida* (AT), *A. artemisiifolia* (AA), AT + AA and of other weed species per square meter with increasing AT density in combination. Low (10 plants/ m^2) and high density (100 plants/ m^2) in 2016 and 2017 are shown. Bars on mean values are standard errors

competitive ability of AT might be further increased. Moreover, the growth of AT might have been favoured by the higher average temperature and precipitation in 2017 (Table 1). Models predicting the impact of climate change on AT and AA suggest that both species

will increase in abundance in Europe under future climate conditions (Rasmussen et al., 2017).

Measuring SPB production showed that monocultures of each species produced higher SPB than mixtures of 40AT:60AA and 60AT:40AA.

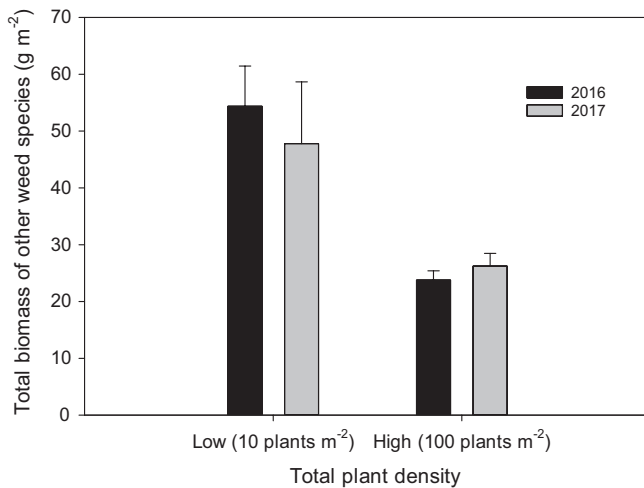


FIGURE 4 Biomass of other weed species as affected by total *Ambrosia* plant density (main plot effect: high or low) in 2016 and 2017. Bars represent standard errors of means. Total biomass of other weed species is significantly higher in low density than in high density of *Ambrosia* for both years (compared using protected LSD, $p < 0.001$)

This may be due to interspecific competition being less severe than intraspecific competition and/or due to allelopathic effects (Lehoczyk et al., 2011). In addition, we found that a higher biomass of other weed species was also obtained in the mixtures of ratio 40:60 and 60:40 (Figure 3). Competition between two dominant species, either directly or indirectly, will influence other species present and may allow greater growth of other weed species (Tilman, 1987). Gibson et al. (2017) suggested that crops may benefit from interspecific competition among weeds in a multispecies setting. They found that when crops were grown with a more diversified weed community, weed biomass decreased by 83% over the gradient of weed species evenness, whereas crop productivity increased by 23%. Thus, diversified weed communities limited the negative effect of competitive and dominant species on crop productivity (Adeux et al., 2019). We thus propose that crops may benefit from the reduced biomass of *Ambrosia* when both *Ambrosia* species grow together. However, further studies in the presence of crops are needed to confirm this.

5 | CONCLUSIONS

Ambrosia trifida is sensitive to intraspecific competition and therefore produces less IPB at high densities, while AA produces its highest IPB in monoculture. At close to even mixtures, total SPB (AT + AA) was lowest, suggesting that interspecific competition decreases the biomass of both species. Such mixtures may favour crop yield, as we found the highest biomass of other weed species at these mixtures. Despite its larger canopy, AT is not predicted to replace AA or become a new threat to crops, as it not only suffers from intraspecific competition at high density in monoculture, but also from interspecific competition with AA. Further studies in the presence of crops with natural infestations of both AA and AT and in variable

environments are required to confirm our hypothesis that invasion of this additional weed species may actually benefit crop yield.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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