

The influence of nitrogen, water and competition on the vegetative and reproductive growth of common ragweed (*Ambrosia artemisiifolia* L.)

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Abstract As common ragweed (*Ambrosia artemisiifolia* L.) spreads across Europe and other regions, it is becoming both a health and an economic threat. To better understand which environmental conditions facilitate the spread of the invasive species, in 2010, a greenhouse experiment was conducted determining the effects of various nitrogen levels (10, 50 and 100 kg N/ha), soil moisture level (low and high) and competition levels (no competition, medium competition and high competition) on the growth parameters of ragweed. Single-grown ragweed responded favourably to the medium nitrogen and water increase, whereas the ragweed growth parameters in competition stands increased only when high levels of nitrogen and water were added. High competition reduced the total dry matter of ragweed by up to 83%, but the ragweed continued to increase its relative growth rate during the full-flowering stage and allocate its dry matter to reproductive parts, producing up to 70 seeds per plant. Ragweed is a poor competitor when there is high resource availability; however, under disturbance

and in the shortage of nutrients and water conditions, the intensity of competition decreases and the ragweed performance is minimally affected. The addition of medium levels of nitrogen to promote the growth of competitive species, prevention of disturbance and establishment of plant communities with stress-tolerant species is measures that should help to prevent the further spread of ragweed.

Keywords Nitrogen · Water availability · Competition · Common ragweed · *Lolium multiflorum* L. · Invasive

Introduction

Invasive plants generally possess physiological, morphological or life history traits that allow them to colonize disturbed areas quickly and rapidly grow in response to a high resource availability (Grotkopp et al. 2002; Rejmanek et al. 2005). Increased growth and competitive ability occur because of variations in the environmental conditions (nutrients, temperature and water) and from inherent differences in plant characteristics, such as the relative growth rate (RGR) (Grotkopp et al. 2002), seed size (Stanton 1985), emergence time (Van Baalen et al. 1984) and phenological development (Godoy et al. 2009). In combination, these traits enable the plants to use resources more efficiently than native species (Vitousek 1990).

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This advantage is conferred by factors such as a greater rooting depth (Lopez-Zamora et al. 2004), late flowering (Godoy et al. 2009), the lack of natural enemies (Cappuccino and Carpenter 2005) and the production of novel allelochemicals (Hierro and Callaway 2003; Fan et al. 2010).

Common ragweed (*Ambrosia artemisiifolia* L., Asteraceae), hereafter referred to as ‘ragweed’, is a wind-pollinated annual plant that is native to the prairie regions of North America. Introduced to Central Europe in the late 19th century, ragweed has greatly increased its range and abundance in recent years (Chauvel et al. 2006). Because of its high germination rate and rapid growth during the juvenile phase, common ragweed is considered a highly competitive species, with the potential to spread widely in disturbed habitats (Brandes and Nitzsche 2006). Research on this problem has increased because the ongoing expansion of ragweed in Europe and other regions threatens agricultural production; moreover, ragweed is of particular concern because many people develop an allergic reaction to its pollen, causing health problems (Tamarcaz et al. 2005). Despite extensive studies focused on the geographical distribution, management of ragweed and its adverse impacts on health and agricultural production (Simard and Benoit 2010; Buttenschön et al. 2009; Brandes and Nitzsche 2006; Tamarcaz et al. 2005), relatively little is known about the growth and development of ragweed in the presence of competitors and at different levels of resource availability. Among nutrients, N is generally a limiting resource in plant communities (LeBauer and Treseder 2008). Plant growth is enhanced by higher soil N levels, but the level of responsiveness differs considerably between species (Blackshaw et al. 2003). Furthermore, increased competitive advantage of invasive species compared with native species has been contributed to higher N availability (Quinn et al. 2007). Competing species can differ in the neighbouring size (Weiner et al. 2001), N acquisition (Miller et al. 2007), seasonal patterns of growth rate (Mamolos 2006) or other life-history traits, thus altering N and water availability over time. This temporal variation in resource supply can influence the intensity of competitive interactions (James and Richards 2007; Novoplansky and Goldberg 2001) and could potentially affect the outcome of plant competition (Berkowitz 1988; Troeh and Thompson 1993).

The objective of this study was to describe the growth and development of common ragweed when it is influenced by various N, competition and water levels. Specifically, this study aimed to examine the effects of these factors and their interaction with different growth parameters, such as the leaf, stem and total biomass, the leaf area, the RGR and the seed production. A better understanding of ragweed ecology might provide improved control methods and more effective management of areas infested with this species.

Materials and methods

A greenhouse experiment was conducted at the Agricultural Institute of Slovenia, Ljubljana, between May and October of 2010. The experiment consisted of a randomized-block factorial design in which the experimental units (pots) were arranged in five temporal blocks, with each block harvested at a different time throughout the growing season. Each temporal block contained four replicates of each combination of N availability (three levels), competition (three levels) and water availability (two levels). In total, 360 pots were used in the experiment. Over the growing season, the total N addition levels were 0.08 g/pot (10 kg/ha-low N level), 0.4 g/pot (50 kg/ha-medium N level) and 0.8 g/pot (100 kg/ha-high N level). The competition levels were no competition (one ragweed plant in the pot), medium competition (one ragweed and one grass plant) and high competition (one ragweed and five grass plants); Italian ryegrass (*Lolium multiflorum* L.) was chosen as a competitor. In central and southern Europe, Italian ryegrass is a common grass species in moderately disturbed habitats, such as managed grasslands, field and road margins, in which the naturalized ragweed populations often have their highest densities (Fumanal et al. 2008). Additionally, because of its rapid growth, Italian ryegrass is frequently a main constituent of the seed mixtures used in the revegetation of soil disturbed during construction projects (e.g. along roadsides). Furthermore, it is used when converting croplands to grasslands, both of which are sites prone to ragweed invasion.

The soil water content in the pots was held at 50 and 90% of the pots’ water-holding capacity (WHC) for the low and high water level, respectively and the

WHC was continuously monitored over the duration of the experiment. The soil water measurements were obtained using six soil tensiometers (UMS T4, Munich, Germany) connected to an automatic regulation system and a Delta T system with a data logger (Delta T devices, Cambridge, UK). The sensors were inserted into the pots at depths of 4, 6 and 10 cm. The sensor settings were determined by a pilot growth experiment in 2009 in which the pots were weighed daily and the consumed water was measured to maintain a constant soil water content. On 26 May 2010, the ragweed and grass seeds were planted 2-cm deep in each pot; the pots were 15-cm tall and 19-cm wide and contained a mixture of peat (70%), perlite (10%), vermiculite (10%) and sand (10%). Two weeks after planting (WAP), the ragweed and grass plants were thinned to achieve the desired densities. The pots were watered as needed until the ragweed plants reached the V6 stage (6-leaves). Subsequently, different amounts of water were applied for the low and high water treatments. At three WAP, 10% of the total N treatment was uniformly applied as aqueous NH_4NO_3 ; the remaining amount of N was divided into four applications and supplied in the 2-week period before the first sampling. To ensure that the plant growth was not limited by elements other than N, other macro- and micronutrients were added separately on a schedule similar to that of the N application. At each application, a single pot received 200 mL of modified non-nitrogen Hoagland solution containing 0.2 mM KH_2PO_4 , 1 mM KCl, 1 mM $\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$, 0.4 mM $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 1 mM H_3BO_3 , 1 mM $\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$, 1 mM $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$, 1 mM $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$, 1 mM $\text{H}_2\text{MoO}_4 \cdot \text{H}_2\text{O}$ and 1 mM Fe-EDTA. Five harvests were conducted throughout the experiment at the following stages of ragweed growth: V6 (6 leaves at 4 WAP), V10 (10 leaves at 6 WAP), V14 (14 leaves at 8 WAP), V22 (full flowering at 12 WAP) and physiological maturity (20 WAP). The ragweed plants were harvested at ground level and divided into the leaf, stem and reproductive components. The leaves were scanned immediately after harvest and the images were analysed using the AnalySIS image analysis software (Soft Imaging System, GmbH, Munster, Germany). The leaf, stem and inflorescence dry weights were determined after drying at 45°C until a constant mass was achieved. The inflorescences were threshed, the seeds were cleaned and the number of seeds per plant was counted and weighed. The harvest

Table 1 Growth stages of *Ambrosia artemisiifolia* L. with corresponding harvest dates and growing degree days-GDD (after planting)

Growth stage	Harvest date	GDD (after planting)
V6 (6-leaf)	June 27, 2010	360.0
V10 (10-leaf)	July 7, 2010	486.2
V14 (14-leaf)	July 21, 2010	688.9
V22 (full flowering)	August 18, 2010	1004.8
Physiological maturity	October 12, 2010	1301.2

dates, corresponding growth stages and growing-degree days (GDD) after planting are presented in Table 1.

Throughout the growing season, temperature data loggers made hourly recordings of the greenhouse temperatures. Using the following equation, the temperatures were then converted to cumulative GDD for the corresponding harvest dates (Gilmore and Rogers 1958):

$$\text{GDD} = \sum ([T_{\max} + T_{\min}]/2 - T_{\text{base}}), \quad (1)$$

where T_{\max} and T_{\min} are the daily maximum and minimum, respectively, air temperatures (°C), with a lower limit of 10°C and T_{base} is the base temperature (10°C). The T_{base} of 10°C was chosen on the basis of the minimum germination temperature for ragweed (Brandes and Nitzsche 2006).

The leaf relative water content (LRWC) of ragweed was determined at the V14 stage according to Turner (1981). Between 10 and 14 h, the youngest fully expanded leaves were selected and the leaf tissue without veins was excised, placed in pre-weighed vials and stored in a cooler. The vials with fresh ragweed leaves were weighed before hydration for 6 h at 10°C in distilled water to ensure full turgidity. To remove excess water, the fully turgid leaves were placed on filter paper, before being weighed. The samples were then oven-dried at 80°C until a constant mass was achieved and then weighed to determine the dry weight.

LRWC of the fresh leaves was calculated using the following equations (Kirkham 2005):

$$\text{LRWC} (\%) = ([F_w - D_w]/[T_w - D_w]) \times 100, \quad (2)$$

where F_w is the leaf fresh weight, T_w is the leaf turgid weight and D_w is the leaf dry weight.

The RGR was estimated according to Causton and Venus (1981) using the following equation:

$$\text{RGR} = (\ln W_2 - \ln W_1)/(t_2 - t_1), \quad (3)$$

where W_1 is the treatment mean of the total shoot dry matter at time t_1 and W_2 is the individual total shoot dry matter sample of the subsequent harvest at time t_2 .

Statistical analysis

A factorial ANOVA was performed using the PROC GLIMMIX procedure in SAS (SAS Institute, 2010) to test for significant effects ($P < 0.05$) of the N level, the water level, the competition level and the growth stage (GDD) and their replications and interactions based on the leaf, stem, total dry matter and leaf area data. The assumption of normality was checked graphically. The assumption of homogeneity of variance between the treatments was tested using Levene's test. The data are presented separately for each N level, competition level and water level, with GDD as the x -axis (Figs. 1, 2, 3).

The leaf, stem, total shoot dry matter and leaf area per plant were also analysed using the following four-parameter log-logistic model in which the C term was fixed to 0 (Seefeldt et al. 1995):

$$Y = C + (D - C)/(1 + \exp[B(\log X - \log E)]), \quad (4)$$

where Y is the response (e.g., leaf dry matter), C is the lower limit, D is the upper limit, X are the GDD calculated after crop planting, E is the GDD that provides a 50% response between the upper and lower limit (also known as the inflection point, I_{50} or ED_{50}) and B is the slope of the line at the inflection point. Curve fitting was performed with nonlinear regression using the least-squares method. The graphs were plotted using the R program (R Development Core Team 2006) and its dose–response curve (drc) package (Knezevic et al. 2007). A lack-of-fit test ($P < 0.05$) was not significant for any of the dose–response curves tested (Figs. 1, 2, 3), indicating that the log-logistic model was appropriate for the data (Knezevic et al. 2007). Differences among the equation parameters for each combination of competition, water availability and N level were also determined by comparing the standard errors (\pm SE) and the t and F tests at $P < 0.05$.

Significant differences in the remaining parameters (seed weight per plant, seed number per plant and

RGR) among the treatments were determined using ANOVA ($P < 0.05$) and the means were compared using the SE of the difference (SED) at $P < 0.05$ (Webster 2007). For RGR, the treatment effects were determined for each harvest interval. The means \pm SEs of the investigated parameters are presented in the tables and in the text.

Results

The effects of N, competition and water level on the relative water content of ragweed leaves

The water level significantly influenced the LRWC of the ragweed ($F_{1,63} = 31.35$; $P < 0.05$), with LRWCs of $64.7\% \pm 1.35\%$ (mean \pm SE) and $51.6\% \pm 1.65\%$ for the high and low water level, respectively (data not shown). Ragweed LRWCs across N and competition levels were not affected by water availability.

The effects of N level, competition level and water level on the leaf, stem and total dry matter production of ragweed

The leaf, stem and total dry matter and the leaf area per plant at the initial (V6) harvest stage of the ragweed were similar ($P < 0.05$), which indicates that both competing species were similar in size at the onset of the experiment. The leaf dry matter was significantly influenced by the N level ($F_{2,270} = 4.05$; $P < 0.05$), competition level ($F_{2,270} = 331.56$; $P < 0.05$), water level ($F_{1,270} = 10.55$; $P < 0.05$) and GDD (growth stage) ($F_{4,270} = 140.46$; $P < 0.05$). Similarly, the stem dry matter was affected by the N level ($F_{2,270} = 19.94$; $P < 0.05$), competition level ($F_{2,270} = 204.02$; $P < 0.05$), water level ($F_{1,270} = 9.80$; $P < 0.05$) and GDD ($F_{4,270} = 222.69$; $P < 0.05$). The total shoot dry matter production was also influenced by the N level ($F_{2,270} = 29.22$; $P < 0.05$), competition level ($F_{2,270} = 266.10$; $P < 0.05$), water level ($F_{1,270} = 11.07$; $P < 0.05$) and GDD ($F_{4,270} = 201.70$; $P < 0.05$). For the leaf, stem and total shoot dry matter production, interactions were observed among the N level, competition level, water level and GDD; the data are presented separately at the different competition levels for each N level and each water level (Figs. 1, 2; Appendix Tables 2, 3).

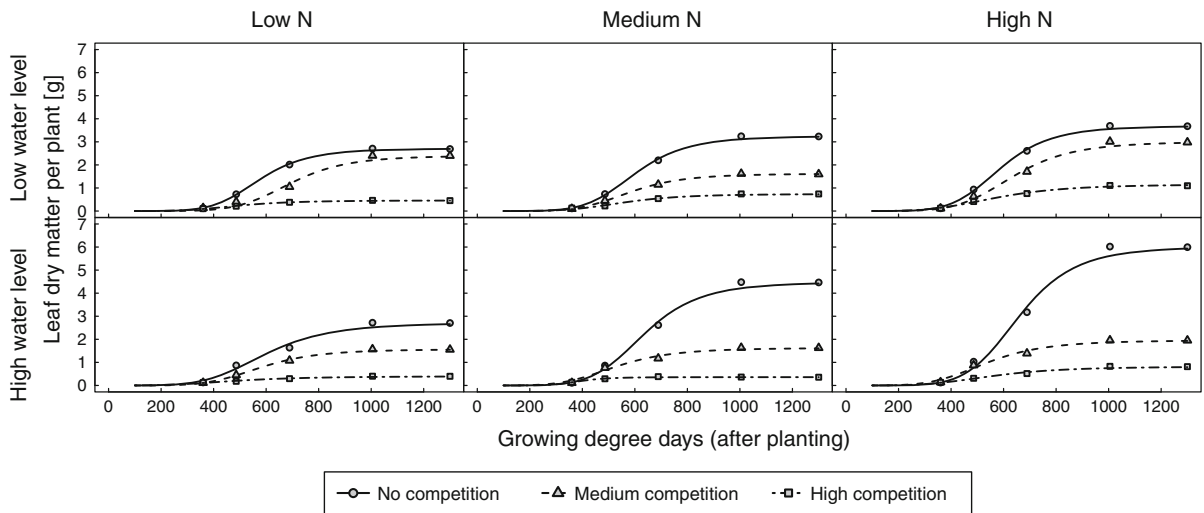


Fig. 1 Effects of nitrogen (N), soil water and competition level on leaf dry matter production of *Ambrosia artemisiifolia* L. over time (represented by growing degree days after planting) in the greenhouse experiment. Nitrogen levels chosen were low (10 kg/ha), medium (50 kg/ha) and high (100 kg/ha) with water levels set to low (50% WHC) and high (90% WHC) water levels. Competition levels tested were no competition (one

ragweed in the pot), medium (one ragweed and one grass in the pot) and high competition (one ragweed and five grasses in the pot) and the harvest growth stages were V6 (6-leaf), V10 (10-leaf), V14 (14-leaf), V22 (22-leaf; full flowering) and physiological maturity. The regression lines were plotted using Eq. 4 and the parameter values are reported in the Appendix Table 2

The three-way interaction between the N level, the competition and the GDD was significant for the leaf dry matter ($F_{16,270} = 2.51$; $P < 0.05$), stem dry matter ($F_{16,270} = 2.90$; $P < 0.05$) and total shoot dry matter production ($F_{16,270} = 2.85$; $P < 0.05$). Up to the full-flowering stage (V22), the single-grown ragweed increased with the medium and high additions of N; however, only the highest N level increased the dry matter during the physiological maturity stage (V30). The ragweed in the competition stands evenly increased its performance up to the V10 stage and was severely suppressed thereafter. However, in the period before flowering (V14 to V22), the competition effect of the Italian ryegrass diminished and the ragweed significantly increased its leaf, stem and total dry matter. The three-way interaction between the water level, competition level and GDD was also observed for the leaf ($F_{8,270} = 3.49$; $P < 0.05$), stem ($F_{8,270} = 2.86$; $P < 0.05$) and total dry matter production ($F_{8,270} = 3.29$; $P < 0.05$). The single-grown ragweed responded to an increased water supply throughout the entire growth period, whereas the ragweed in the competition stands increased its leaf, stem and total dry matter only during the initial growth stage (V6 to V10) and with the exception of the leaf

dry matter in the period before flowering (V14 to V22). Conversely, at this growth stage an increased water supply even reduced the ragweed's leaf dry matter when compared with a low water level, regardless of the N level. At the highest N level, the leaf dry matter decreased from 3.0 to 1.96 g and from 1.16 to 0.82 g under medium and high competition, respectively.

Regardless of the N and water levels, competition generally decreased the leaf dry matter. For example, at the high N and higher water levels, medium competition reduced the leaf dry matter from 6 to 1.96 g (−67%), and high competition reduced it to 0.82 g (−86%). A similar but weaker effect was observed at the low water and N levels (Fig. 1; Appendix Table 2). The stem dry matter was also significantly reduced by competition, regardless of the N and water levels (data not shown). A similar competition effect was observed for the total shoot dry matter: the single-grown ragweed total shoot dry matter values under the lower water treatment were 5.89, 8.22 and 10.1 g at low, medium and the high N levels, respectively, whereas these values decreased to 2.89 (−51%), 3.48 (−58%) and 6.12 g (−39%), respectively, under medium competition. Under high

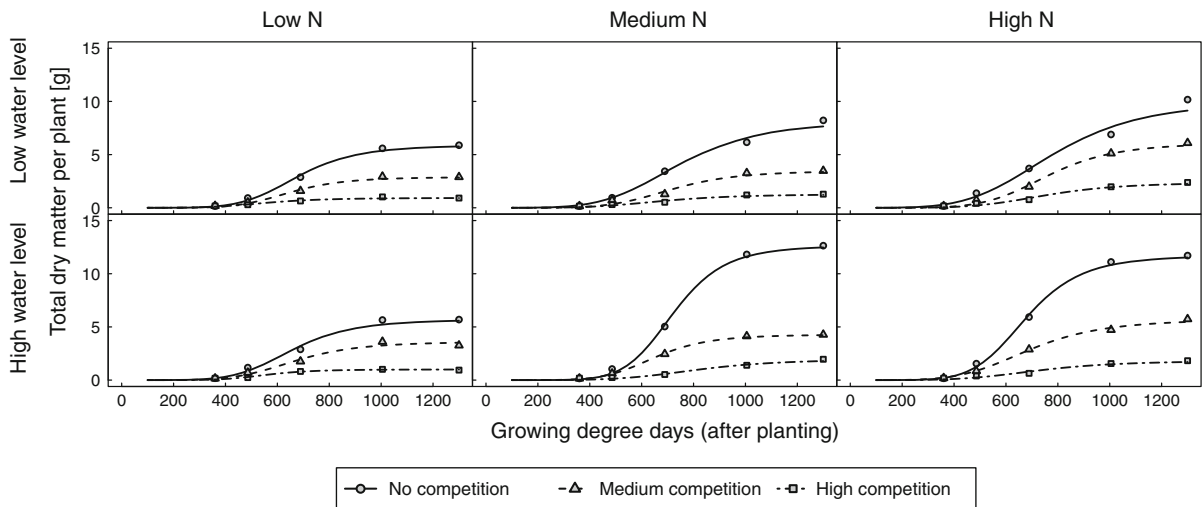


Fig. 2 Effects of nitrogen (N), soil water and competition level on total dry matter production of *Ambrosia artemisiifolia* L. over time (represented by growing degree days after planting) in the greenhouse experiment. Nitrogen levels chosen were low (10 kg/ha), medium (50 kg/ha) and high (100 kg/ha) with water levels set to low (50% WHC) and high (90% WHC) water levels. Competition levels tested were no competition (one

competition, these values decreased further to 0.72 (−88%), 1.28 (−85%) and 2.38 g (−76%), respectively (Fig. 2; Appendix Table 3).

The effects of N, competition and water level on the leaf area production of ragweed

The N level ($F_{2,216} = 48.90$; $P < 0.05$), water level ($F_{1,216} = 20.71$; $P < 0.05$), competition level ($F_{2,216} = 377.44$; $P < 0.05$) and GDD (growth stage) ($F_{3,216} = 143.67$; $P < 0.05$) significantly influenced the leaf area per plant of ragweed. The data are presented separately at the different competition levels for each N level and water level (Fig. 3; Appendix Table 4).

The three-way interaction between the N level, competition level and GDD was significant for the leaf area production ($F_{12,216} = 3.53$; $P < 0.05$), which indicates that the interaction between the N level and the competition level changed over time. Throughout the entire growing period, the leaf area per plant of the single-grown ragweed increased with the addition of the medium and high N levels. Under competition conditions, this response was observed only for the combination with the high N level during the initial growth stages (V6 to V10) and in the period before flowering

ragweed in the pot), medium (one ragweed and one grass in the pot) and high competition (one ragweed and five grasses in the pot) and the harvest growth stages were V6 (6-leaf), V10 (10-leaf), V14 (14-leaf), V22 (22-leaf; full flowering) and physiological maturity. The regression lines were plotted using Eq. 4 and the parameter values are reported in the Appendix Table 3

(V22). The strongest competition effect was observed during the V14 stage in which the ragweed leaf area remained similar with the addition of N. The competition level \times water level interaction also changed over time ($F_{6,216} = 6.33$; $P < 0.05$). The single-grown ragweed responded to an increased water supply throughout the entire growing period, whereas the ragweed in the medium competition stands responded up to the V14 stage and the ragweed in the high competition stands responded favourably only during the initial growth stage (V10). At the lower water level, the leaf areas per plant of the ragweed grown at low, medium and high N levels without competition were 386, 652 and 871 cm², respectively; under medium competition, these values decreased significantly to 196 (−49%), 245 (−62%) and 332 cm² (−62%), respectively, and decreased further to 46 (−88%), 78 (−88%) and 145 (−83%) cm², respectively, under high competition. Similar trends occurred with the higher water level (Fig. 3; Appendix Table 4).

The effects of N, competition and the water level on the seed weight and seed number of ragweed

The seed number and seed weight per ragweed plant were significantly influenced by the N level

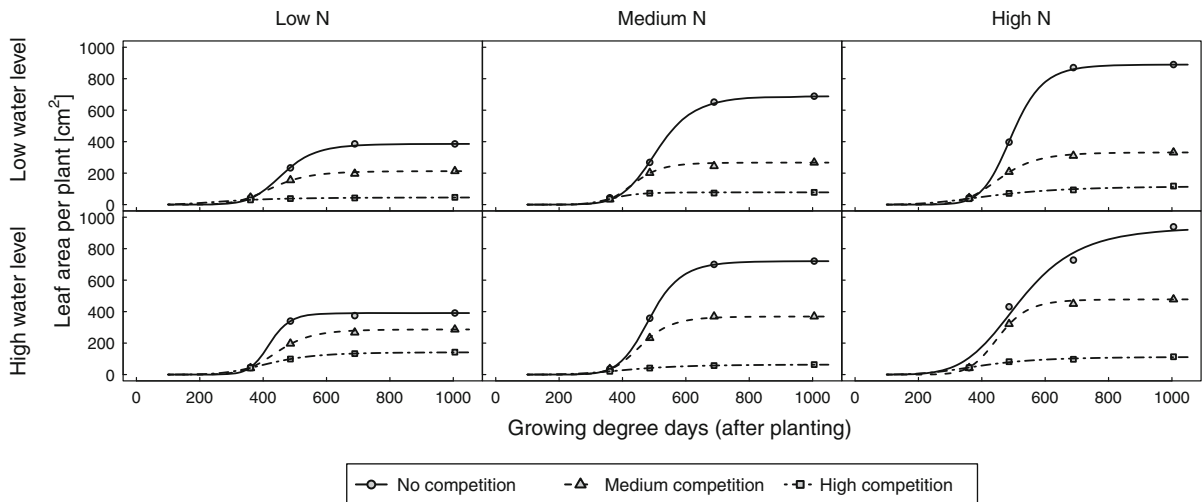


Fig. 3 Effects of nitrogen (N), soil water and competition level on leaf area production of *Ambrosia artemisiifolia* L. over time (represented by growing degree days after planting) in the greenhouse experiment. Nitrogen levels chosen were low (10 kg/ha), medium (50 kg/ha) and high (100 kg/ha) with water levels set to low (50% WHC) and high (90% WHC) water levels. Competition levels tested were no competition (one

ragweed in the pot), medium (one ragweed and one grass in the pot) and high competition (one ragweed and five grasses in the pot) and the harvest growth stages were V6 (6-leaf), V10 (10-leaf), V14 (14-leaf) and V22 (22-leaf; full flowering). The regression lines were plotted using Eq. 4 and the parameter values are reported in the Appendix Table 4

($F_{2,62} = 13.96$; $P < 0.05$) and competition level ($F_{2,62} = 57.55$; $P < 0.05$). There was a significant two-way interaction between the N level and the competition level ($F_{4,62} = 4.51$; $P < 0.05$). For the seed number and seed weight per plant, yet there was no effect of the water supply. Thus, the data were combined across all of the N levels and competition levels and are presented separately for each N level at the different competition levels (Fig. 4).

The ragweed grown without competition had a significantly higher seed weight per plant (2.71 ± 0.46 g) at the high N level when compared with the medium ($1.99.0 \pm 0.21$ g) or low (1.02 ± 0.08 g) N level. A similar effect was observed at the high competition level. At the medium competition level, however, the seed weight per plant was not affected by increasing the N levels. The ragweed grown without competition at the low N level produced 1.02 ± 0.08 g of seeds per plant and the seed weight per plant significantly decreased under the medium (0.45 ± 0.08 g) and high competition (0.11 ± 0.04 g) levels. A similar trend was observed for the high N level (Fig. 4).

The seed number per plant followed trends similar to those of the seed weight, i.e. it increased with the addition of N and decreased with an increasing competition level. The highest seed number

(628.6 ± 103 seeds per plant) was obtained in the single-grown ragweed at the high N level, and the lowest seed number (26.4 ± 10 seeds per plant) was obtained in the plants grown at the low N level in high competition stands (data not shown).

The effects of N, competition and water level on the RGR of ragweed

The RGR was significantly influenced by the N level ($F_{2,216} = 3.04$; $P < 0.05$), competition level ($F_{2,216} = 60.48$; $P < 0.05$) and growth stage (GDD) ($F_{4,216} = 481.55$; $P < 0.05$). Additionally, an ANOVA was performed for each harvest stage, and the means were compared with the SED difference at $P < 0.05$. The results are presented at each N level, water level and competition level separately for the corresponding harvest dates (Fig. 5).

When the RGR data of the single-grown ragweed plants were averaged for each harvest interval (Table 1), the highest RGR (188 ± 4 mg/g/day) was recorded at the V10 growth stage, followed by stages V6 (106 ± 6 mg/g/day), V14 (77 ± 2 mg/g/day) and V22 (33 ± 7 mg/g/day).

The N level had a significant effect on the RGR only at the V10 stage ($F_{2,216} = 3.73$; $P < 0.05$) in

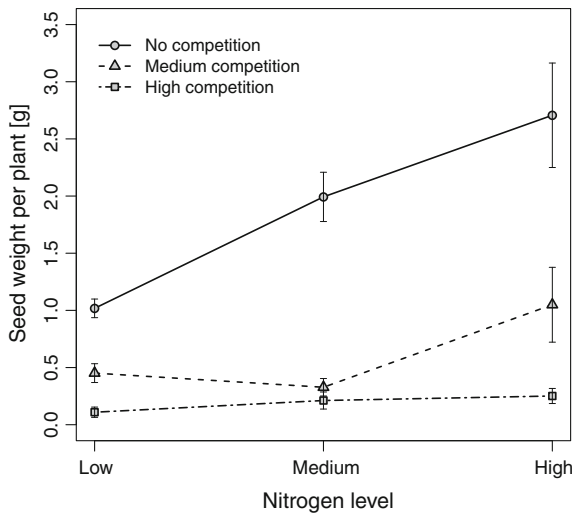


Fig. 4 Seed weight of *Ambrosia artemisiifolia* L. as influenced by nitrogen (N) and competition level. Nitrogen levels chosen were low (10 kg/ha), medium (50 kg/ha) and high (100 kg/ha) and competition levels tested were no competition (one ragweed in the pot), medium (one ragweed and one grass in the pot) and high competition (one ragweed and five grasses in the pot). Vertical bars represent SE of the means

which the ragweed plants growing at a high N level had a significantly higher RGR when compared with the ragweed plants growing at the low and medium N levels (Fig. 5). In general, the RGR decreased with the

increasing competition levels, except during the V22 stage in which a significant three-way interaction between the competition level, the water level and the GDD ($F_{8,216} = 3.51$; $P < 0.05$) was observed. The RGR of ragweed without competition responded to the higher water level (an increase from 29.2 ± 1.4 to 37.7 ± 2.1 mg/g/day); however, the increased water availability under conditions of competition significantly decreased the RGR. The RGR at the medium competition level decreased from 49.0 ± 3.2 to 28.0 ± 4.9 mg/g/day and from 33.2 ± 6.0 to 24.0 ± 4.6 mg/g/day at the high competition level for the low and high water levels, respectively (Fig. 5).

Discussion

The results of the single-grown ragweed growth parameters were as expected: growth increased with increased levels of nitrogen and water. A response to the water increase was observed throughout the entire growing period, whereas only the highest N level was sufficient to enhance the growth after the full-flowering stage. Lehoczky (2008) also reported that common ragweed requires a sufficient N supply (e.g. 100 or 200 mg N/kg soil) for optimal growth, although our findings suggest that ragweed performs well even under

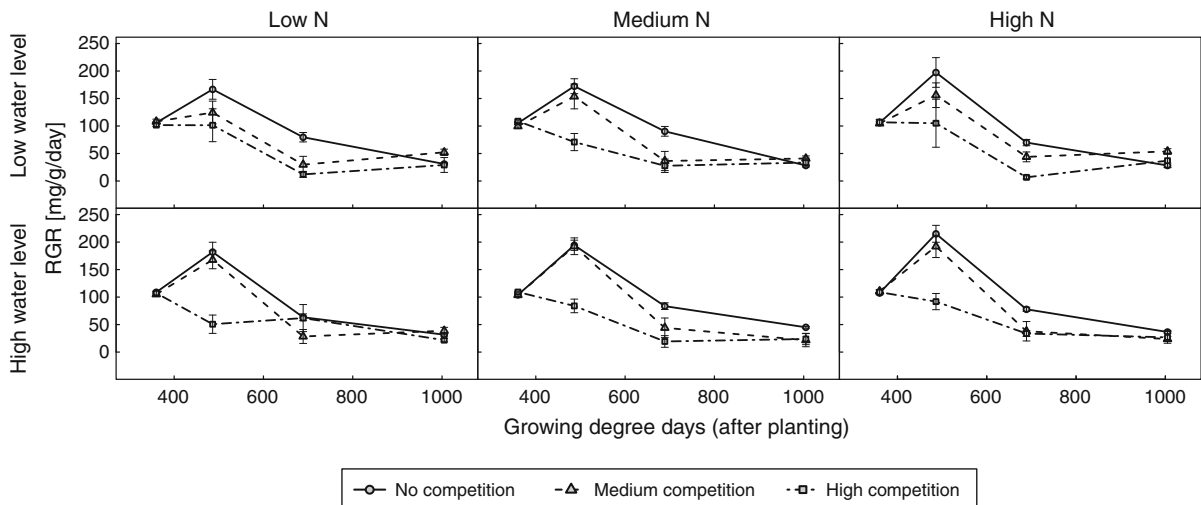


Fig. 5 Relative growth rate (RGR) of *Ambrosia artemisiifolia* L. over time (represented by growing degree days after planting) as influenced by nitrogen (N), competition and soil water level. Nitrogen levels chosen were low (10 kg/ha), medium (50 kg/ha) and high (100 kg/ha) with water levels set to low (50% WHC) and high (90% WHC) water levels. Competition levels tested

were no competition (one ragweed in the pot), medium (one ragweed and one grass in the pot) and high competition (one ragweed and five grasses in the pot) and the harvest growth stages were V6 (6-leaf), V10 (10-leaf), V14 (14-leaf) and V22 (22-leaf; full flowering). Vertical bars represent SE of the means

lower N conditions. However, the ragweed performance in the competition stands was not increased with the medium N addition but only at the highest N level, which is partially consistent with previous findings in which N addition did not facilitate invasion success (Thomsen et al. 2006). Our results suggest that the Italian ryegrass had a competitive advantage and dominated over the ragweed owing to its increased resources (data not shown). The outcome of competition depends primarily on resource availability and the competitive ability of neighboring species (Lonsdale 1999). Our results are not surprising because Italian ryegrass is a fast-growing competitive species adapted to a high resource availability (D'Aoust and Taylor 1968; García de Arévalo et al. 1994), whereas ragweed exhibits a ruderal strategy (Fumanal et al. 2008). Similar to the increased N levels, the ragweed did not respond to higher water levels under competition; however, the ragweed did produce thinner leaves with a greater leaf area ratio, which could be a potential mechanism to achieve greater resource capture and a higher RGR (Poorter and Remkes 1990). The N level increased the RGR of the ragweed only during the initial growth stages. Consistent with our conclusions, such observations that the RGR remains similar under various N treatments have been previously reported (Zhao et al. 2010; Shipley and Keddy 1988). In contrast, James (2008) and Hua et al. (2010) reported increased RGR with the addition of N. Because the RGR is positively correlated to the plant-N content (Peng et al. 2011), these differences might be the result of the very broad range of applied N when compared with the N rates applied in our experiment.

In our study, the RGR was strongly reduced by competition. Surprisingly, at the full-flowering stage (V22), the ragweed in the competition stands exhibited higher RGRs when compared with the single-grown ragweed plants, resulting in dry matter increases and allocation to reproductive parts. Our experiment also demonstrated that the competition effect was enhanced at high N and water levels, thus a greater decrease in the ragweed leaf, stem and total dry matter and leaf area per plant was observed. We also observed a temporal changes in the competition intensity, which can be explained by previous reports (Connolly et al. 1990; Goldberg and Landa 1991), where variations, intensity, frequency and periodicity of competitive interactions between species have been contributed to the stage of the species life cycle, patterns of physiological activity

and temporal resource availability (Novoplansky and Goldberg 2001; James and Richards 2007). Our findings are contradictory to Goldberg et al. (1999) meta-analysis suggesting that competition intensity declines with increasing productivity, while they are consistent with several reports, where competition intensifies relatively with the increased water and N availability (Briones et al. 1998; Lowe et al. 2003). Our results also support Grime's (2001) hypothesis that competition is not constant along the site productivity gradient and there are two factors limiting the competition intensity within a plant community: disturbance and stress. Numerous studies exist (Burke and Grime 1996; Leishman and Thomson 2005) that show the importance of disturbance in the spread and success of invasive plant species. In his meta-analysis, Daehler (2003) demonstrated that invasive species are often competitively inferior to native species in comparative growth studies, which indicates that traits other than competitiveness (such as the phenological development, absence of enemies, dispersal capacity and seed bank longevity) often influence the success of the invasive species (Richardson and Pyšek 2006; Rejmanek and Richardson 1996). Our results indicate that very high seed production could be one of the potentially important traits for the invasion success of this species. The ragweed performance was strongly suppressed by competition, especially during the initial growth stages; however, in the period before flowering, the ragweed continued to increase its dry matter and allocate resources to reproductive parts, resulting in the production of approximately 25–70 seeds per plant. Such a number is sufficient to maintain the population size. Furthermore, such seed production might even enable the further spread of the species, considering that an extremely high rate of seed germination and seedling survivorship were reported and the seed bank even in its native range remains scarcely affected by seed predation (MacDonald and Kotanen 2010).

Several studies reported that species with wide environmental tolerances are likely to succeed in new habitats (Goodwin et al. 1999) because of the advantage of having a high plasticity in heterogeneous environments (Rice and Bazzaz 1989). Fumanal et al. (2008) demonstrated the high ecological tolerance of ragweed: it can be found in various plant communities, soil types and site productivities (arable lands, roadsides and construction sites) but it requires disturbance (e.g., trampling, mowing, soil cultivation) to lower the

competition from neighboring species. Unfortunately, Fumanal et al. (2008) did not attempt to determine the competition intensity within a ragweed-infested community (e.g., by estimating the importance of the total plant cover in the vegetation samples).

Our results indicate that ragweed is a highly adaptable plant but a poor competitor in resource-rich environments. However, under resource-limiting conditions, such as drought and nutrient stress, the performance of ragweed is not strongly affected by moderate competition. Environmental stressors, such as disturbance or shortages of water and nutrients, appear to be the main factors that facilitate a successful invasion and further spread into new areas. Along roadsides, ragweed is often confined to the most stressed environment, one marked by poor soil conditions (shallow soil, high levels of gravel, and poor nutrient availability) and limited competition (personal obs.) Measures should be taken to increase the magnitude of competition, which would, in turn, reduce the frequency and intensity of disturbance and the severity of stress. On newly constructed road verges, the soil depth might be increased to decrease the probability of drought and nutrient shortages, thus promoting competitor species, such as grasses of the

Festuca, *Brachypodium* or *Lolium* genera, which would successfully suppress the growth and fitness of ragweed.

The addition of moderate levels of N to minimize possible stressful conditions due to nitrogen shortages and in areas where N management is not possible the establishment of plant communities dominated by stress-tolerators could be appropriate measures to prevent the enhanced performance of ragweed. The data presented here might lead to improved N and vegetation management, which would prevent disturbance and other environmental stressors and constrain the spread of common ragweed and its pollen-induced health problems.

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Appendix

See Tables 2, 3 and 4.

Table 2 Regression parameters (\pm SE) for leaf dry matter production of *Ambrosia artemisiifolia* L. as influenced by nitrogen, competition and soil water levels (Fig. 1)

Response	Soil water level	Competition level	Nitrogen level	Regression parameters (\pm SE)		
				Slope (<i>B</i>)	Inflexion point (<i>I</i> ₅₀)	Upper limit(<i>D</i>)
Leaf dry matter	Low	No	Low	-6.2 (0.4)	574.2 (8.2)	2.71 (0.14)
		No	Medium	-6.1 (0.6)	601.6 (16.9)	3.25 (0.13)
		No	High	-6.1 (0.6)	587.8 (11.6)	3.69 (0.20)
		Medium	Low	-5.2 (0.9)	607.8 (23.5)	2.40 (0.42)
		Medium	Medium	-5.7 (0.6)	578.4 (12.8)	1.62 (0.14)
		Medium	High	-5.7 (1.0)	637.5 (24.9)	3.01 (0.16)
		High	Low	-4.5 (0.6)	491.6 (14.5)	0.46 (0.13)
		High	Medium	-4.8 (0.9)	557.9 (25.7)	0.74 (0.01)
	High	High	High	-5.7 (1.0)	637.5 (24.9)	1.16 (0.18)
		No	Low	-4.8 (1.0)	598.6 (32.6)	2.72 (0.11)
		No	Medium	-6.0 (0.9)	637.1 (20.2)	4.48 (0.32)
		No	High	-6.2 (1.3)	660.6 (23.7)	6.02 (0.28)
		Medium	Low	-4.9 (0.9)	603.6 (27.6)	1.57 (0.17)
		Medium	Medium	-4.8 (1.1)	528.4 (30.4)	1.63 (0.24)
		Medium	High	-4.8 (1.0)	536.3 (28.8)	1.96 (0.24)
		High	Low	-3.3 (0.7)	484.0 (32.8)	0.40 (0.20)
	High	Medium	-6.9 (1.4)	386.6 (12.7)	0.36 (0.08)	
	High	High	-4.0 (0.9)	559.9 (34.9)	0.82 (0.12)	

Regression parameters are estimated using Eq. 4

B the slope of the line at the inflection point, *I*₅₀ the growing degree days giving a 50% response between the upper and lower limit (also known as inflection point), *D* the upper limit

Table 3 Regression parameters (\pm SE) for total shoot dry matter production of *Ambrosia artemisiifolia* L. as influenced by nitrogen, competition and soil water levels (Fig. 2)

Response	Soil water level	Competition level	Nitrogen level	Regression parameters (\pm SE)		
				Slope (<i>B</i>)	Inflexion point (<i>I</i> ₅₀)	Upper limit (<i>D</i>)
Total dry matter	Low	No	Low	-5.9 (0.7)	679.8 (0.7)	5.89 (0.29)
		No	Medium	-4.71 (0.6)	749.1 (25.8)	8.22 (0.24)
		No	High	-4.5 (0.8)	784.0 (4.6)	10.10 (0.48)
		Medium	Low	-6.1 (1.1)	649.0 (23.3)	2.89 (0.39)
		Medium	Medium	-5.7 (1.7)	717.5 (39.3)	3.48 (0.38)
		Medium	High	-5.9 (0.8)	764.4 (20.2)	6.12 (1.12)
		High	Low	-4.9 (1.3)	556.9 (39.2)	0.72 (0.35)
		High	Medium	-4.6 (1.3)	682.8 (49.6)	1.28 (0.17)
	High	No	Low	-5.1 (1.2)	756.9 (37.9)	2.38 (0.51)
		No	Medium	-5.6 (1.1)	659.0 (26.4)	5.70 (0.49)
		No	High	-6.4 (0.5)	678.5 (9.7)	11.71 (1.50)
		Medium	Low	-5.4 (1.4)	689.0 (33.9)	3.61 (0.37)
		Medium	Medium	-6.3 (0.4)	651.9 (7.8)	4.28 (0.76)
		Medium	High	-4.8 (0.4)	692.6 (15.6)	5.73 (0.70)
		High	Low	-6.3 (1.9)	559.2 (27.7)	1.11 (0.27)
		High	Medium	-5.1 (1.2)	817.4 (42.8)	1.96 (0.50)
		High	High	-4.6 (1.2)	727.6 (46.3)	1.82 (0.35)

Regression parameters are estimated using Eq. 4

B the slope of the line at the inflexion point, *I*₅₀ the growing degree days giving a 50% response between the upper and lower limit (also known as inflexion point), *D* the upper limit

Table 4 Regression parameters (\pm SE) for leaf area production of *Ambrosia artemisiifolia* L. as influenced by nitrogen, competition and soil water level (Fig. 3)

Response	Soil water level	Competition level	Nitrogen level	Regression parameters (\pm SE)		
				Slope (<i>B</i>)	Inflexion point (<i>I</i> ₅₀)	Upper limit (<i>D</i>)
Leaf area	Low	No	Low	-8.8 (0.6)	461.1 (4.0)	386 (44)
		No	Medium	-8.8 (0.5)	509.7 (3.2)	652 (46)
		No	High	-10.2 (0.7)	495.7 (2.1)	871 (47)
		Medium	Low	-7.3 (0.7)	428.3 (6.3)	196 (26)
		Medium	Medium	-9.8 (1.5)	435.3 (8.4)	245 (37)
		Medium	High	-7.8 (0.5)	465.6 (3.6)	332 (49)
		High	Low	-5.9 (1.5)	335.7 (13.9)	46 (14)
		High	Medium	-8.5 (1.4)	366.0 (5.2)	78 (14)
	High	No	High	-7.8 (0.5)	456.6 (3.6)	145 (31)
		No	Low	-13.0 (1.2)	420.3 (5.8)	475 (37)
		No	Medium	-9.9 (0.2)	486.5 (0.5)	721 (37)
		No	High	-5.5 (1.1)	521.2 (23.5)	939 (36)
		Medium	Low	-8.1 (0.9)	444.1 (6.5)	257 (32)
		Medium	Medium	-9.5 (0.6)	458.7 (0.6)	369 (56)
		Medium	High	-9.7 (1.3)	452.7 (6.3)	450 (37)
		High	Low	-5.6 (0.1)	419.2 (2.0)	133 (35)
		High	Medium	-4.5 (0.1)	424.2 (2.9)	116 (18)
		High	High	-4.1 (0.7)	397.7 (13.2)	116 (23)

Regression parameters are estimated using Eq. 4

B the slope of the line at the inflexion point, *I*₅₀ the growing degree days giving a 50% response between the upper and lower limit (also known as inflexion point), *D* the upper limit

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