



Biomass development and CO₂ gas exchange of *Ambrosia artemisiifolia* L. under different soil moisture conditions

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ABSTRACT

Ambrosia artemisiifolia L. is an annual plant species whose pollen is produced in high quantities and may cause allergies and asthma. Originating from North America, it has become established in several European countries. This leads to increasing costs in the public health sector of these countries. The aim of our study was to characterize aspects of the species' growth and ecophysiology, to assess the probability of a further spread and widespread establishment in Central Europe.

For this purpose *Ambrosia* seedlings were cultivated under different soil moisture conditions. Growth, root and stem tissue porosity, leaf chlorophyll contents and biomass allocation were measured. Additionally, gas-exchange measurements at leaf level were conducted.

Ambrosia grew best and had the highest net photosynthesis rates under moist soil conditions. Under dry or waterlogged soil conditions the plants remained smaller, produced less seeds, and had lower assimilation rates. However, even under waterlogged soil conditions *Ambrosia* was able to survive over months and finally to produce seeds. Under such conditions root porosity increased 2.5 times as compared with plants from dry soil. This reasonably improved the O₂ transport within the waterlogged plant. The measured gas exchange rates were comparable to those reported from the species' native range of occurrence. Light saturation of CO₂ uptake was reached at 300 μmol photons m⁻² s⁻¹.

The results suggest that a further spread in Central Europe is very probable because of the broad hydrological amplitude of the species and its generalist character concerning irradiation. Thus, control measures should be started, respectively intensified, timely.

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Introduction

Common Ragweed (*Ambrosia artemisiifolia* L., Asteraceae) is an annual plant species native to North America which has become a widespread neophyte in several European countries (e.g. Chauvel et al., 2006; Török et al., 2003). In Germany, the species has not been able to establish on a large scale, so far. Since several years, however, there are reports of increased appearance of *Ambrosia* even in neighbouring countries, e.g. Austria and Switzerland (Alberternst et al., 2006). Also in Germany more and more reports appear about expanding local populations (Otto et al., 2008) most of them probably resulting from ragweed achenes that contaminate imported birdseed. *Ambrosia* seems to benefit from higher minimum temperatures and fewer days with frost encountered in recent years in the context of climate change (Schmitz, 2004; Walther et al., 2002), since it flowers late in the year and does not start seed-production until September/October.

Because of its highly allergenic pollen the species is considered as a risk for human health. About 20% of people suffer from allergic reactions (e.g. Taramarcaz et al., 2005). In Hungary *A. artemisiifolia* occupies the fifth position of a list of the most problematic plants (Schrader, 2004). Also in other European countries like Italy (northern areas; Mandrioli et al., 1998), Switzerland (Clot et al., 2002), Austria (Jäger, 2000) and the Czech Republic (Rybníček et al., 2000) increasing amounts of *Ambrosia* pollen were measured during the last few years. Furthermore, the number of days increased with a critical pollen concentration (Puc, 2006).

Moreover, *Ambrosia* flowers in Europe from August until October when most other species producing allergenic pollen ceased flowering. This means a longer exposure to pollen for allergic people (Brandes and Nitzsche, 2007), a fact also leading to higher costs for the public health sector (Bohren et al., 2005). To avoid or reduce these effects, the species is already fought in many countries (Taramarcaz et al., 2005).

Although there are studies about the allergenicity and the present state of its establishment in Germany (Otto et al., 2008), so far we only know little about spreading mechanisms, growth, ecophysiological parameters, and habitat requirements when growing

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under Central European climate conditions. However, these factors should be considered, especially in the context of the changing climatic conditions. In fact, it is still uncertain whether *Ambrosia* will be able to spread and establish permanently in regions of Germany with not as favourable climatic conditions.

Therefore, the aim of this study was to investigate the survival, growth and biomass development of *Ambrosia artemisiifolia* growing under the influence of different soil moistures. Furthermore, the gas exchange was investigated. The results may contribute to predict if there will be a serious danger of the species' spreading and establishing widely in Central Europe and to estimate how urgent control measures will be.

Materials and methods

Plant material

Mature *Ambrosia artemisiifolia* achenes (in the following also called "seeds") were collected in autumn 2006 from a site of spontaneous occurrence near the Heinrich-Heine University campus of Düsseldorf, Germany. Air dried seeds were stored at room temperature before stratification at 7 °C in a fridge for at least 3 weeks before the beginning of the experiments. The investigations were conducted outdoors in the experimental fields of the Botanical Garden, University of Düsseldorf (51°11'N, 6°48'W), in summer 2007.

Growth experiments

To investigate the influence of different soil moisture regimes upon the species' growth it was germinated and seedlings were planted into 301 pots. The pots were filled with sand and fertilized every three weeks with a nutrient solution containing 9% N, 6% K₂O, 4% P₂O₅, 0.04% Fe; the stock solution was thinned to a ratio 1:80 with tap water. Two weeks after planting each of the pots was adjusted to one of three different water levels: Five pots were filled up to 2 cm above soil surface (=waterlogged), other five pots were watered up to 17 cm below soil surface (=moist), the last five pots had holes on the bottom (=dry). The soil moisture of each treatment was measured during the whole experiment using TDR-sensors (Delta-T Device Ltd., Cambridge, UK) connected to a data logger (Squirrel 1250, Driesen & Kern, Bad Bramstedt, Germany). The pots were placed in a randomised block design under a rain shelter under otherwise natural temperature and irradiation conditions (screen effect: approx. 5% light reduction). To avoid position effects pot positions were randomised four times during the experiment. The water content of each cultivation group was kept constant during the experiment. At the end of the experiment all plants were harvested. Biomass of leaves, shoots, roots, male flowers and female flowers/seeds was determined separately after drying at 65 °C to a constant dry-weight (dw).

Gas exchange measurements

As the individuals showed different growth rates between the different soil-moisture treatments, for each plant group diurnal courses of leaf gas exchange were measured using a leaf chamber analyser porometer (LCA4, ADC, Hoddesdon, UK). For the measurements, adult but not yet senescent leaves were used. For each soil-moisture group at least five diurnal courses of CO₂ gas exchange were measured along with leaf temperature and photosynthetically active photon flux density (PPFD) at leaf level. Intervals of measurements were 6 minutes. Since *Ambrosia* leaves are pinnate and thus, do not fill in the gas exchange chamber completely, the measured values related to a window size of 6.25 cm² of the porometer chamber had to be re-calculated. For this, after each diurnal the area of the leaf enclosed in the chamber was determined

by scanning the respective leaf (UMAX, Astra 4700) and calculating its area from the number of pixels. The measured CO₂ exchange rate was related to this leaf area.

Dependencies of CO₂ gas exchange upon environmental parameters (leaf temperatures and PPFD) were determined by plotting all CO₂ exchange data from the diurnal courses against the corresponding values of the respective environmental parameter. Following Jarvis (1976), the upper limit of the cloud of scattered data points indicates the response to the respective variable (PPFD and leaf temperature). Lower values result from limiting affects on CO₂ exchange caused by other variables.

Chlorophyll contents

The chlorophyll content of leaves was measured twice, on 23 August 2007 and 1 October 2007. Following Ziegler and Egle (1965) chlorophyll was extracted by using an acetone–tris(hydroxyaminoethane)-buffer (ratio 80:20; tris–hydroxyaminoethane as 0.05 m aqu. solution). The chlorophyll concentration of the solution was measured with a spectral photometer (Novaspec II, Pharmacia Biotech, Cambridge, UK) at 647 nm, 664 nm and 750 nm, respectively. Chlorophyll contents were calculated using the equations:

$$C_a = 11.78 \times E_{664} - 2.29 \times E_{647} \quad (1)$$

$$C_b = 20.05 \times E_{647} - 4.77 \times E_{664} \quad (2)$$

$$C_{\text{tot}} = \left[\frac{(C_a + C_b) \times L}{1000} \right] / g \text{ dw} \quad (3)$$

where C_a, C_b = concentration of chlorophyll a, b in the given dilution [mg/l]; E_{647, 664, 750} = extinction-value at the respective wavelength; L = volume of the assay [ml]; C_{tot} = total chlorophyll content, related to the sample dry weight [mg/g dw].

Porosity of roots and shoots

Since the species showed a high survival rate even under waterlogged soil conditions, we investigated if there was an increased porosity of axial tissues which might enable the survival. The porosity (POR) due to aerenchyma spaces of shoots and roots was determined using a 25-ml pycnometer. Small pieces of roots, respective shoots were gently blotted dry on tissue paper and weighed exactly. After that, the roots or shoots were placed in the pycnometer which was filled with double deionized water and reweighed. In a second step, the plant material was removed from the pycnometer, crunched completely using mortar and pestle, returned into the pycnometer and weighed again. The porosity was calculated using the following equation:

$$\text{POR} = \frac{\text{PG} - \text{PR}}{P + R - \text{PR}}$$

where PG = mass of pycnometer with crunched roots or shoots and water, PR = mass of pycnometer with intact pieces of roots or shoots and water, P = mass of water-filled pycnometer, and R = mass of roots or shoots (Burdick, 1989).

Statistical analysis of the data

Statistical analysis was conducted with JMP (SAS Institute Inc., Cary, NC). Data from the harvest, aerenchyma volume (=tissue porosity) and chlorophyll contents were analysed with analysis of variance (ANOVA). Data were tested for normality and homogeneity of variances and transformed, if necessary. Significant differences were identified by using the contrast procedure of JMP, testing hypotheses about the least squares means.

Table 1

Survival rates, biomass allocation, and shoot/root ratio of *Ambrosia artemisiifolia* cultivated under different soil moisture conditions (moist, dry, waterlogged). Numbers show mean $\pm$ SD, $n = 15$. Different superscript letters in a line indicate significant differences with $P < 0.05$ for shoot biomass and $P \leq 0.01$ for all other categories.

	Soil moisture treatment		
	Moist	Dry	Waterlogged
Survival rates [%]	100	93.3	93.3
Total biomass [g dw]	9.55 $\pm$ 2.10 ^a	6.34 $\pm$ 0.93 ^b	3.47 $\pm$ 1.23 ^c
Biomass shoot [g dw]	2.21 $\pm$ 0.89 ^a	1.75 $\pm$ 0.67 ^a	0.98 $\pm$ 0.43 ^b
Biomass leaves [g dw]	1.69 $\pm$ 0.46 ^a	1.32 $\pm$ 0.20 ^a	0.51 $\pm$ 0.10 ^b
Biomass male flowers [g dw]	0.47 $\pm$ 0.10 ^a	0.43 $\pm$ 0.12 ^a	0.20 $\pm$ 0.09 ^b
Biomass female flowers [g dw]	1.49 $\pm$ 0.37 ^b	1.05 $\pm$ 0.22 ^a	0.47 $\pm$ 0.10 ^c
Biomass roots [g dw]	3.60 $\pm$ 0.86 ^b	1.72 $\pm$ 0.45 ^a	1.25 $\pm$ 0.73 ^a
Shoot/root ratio	1.70 ^b	2.79 ^a	2.16 ^{ab}

Results

Survival and biomass allocation

The three soil moisture levels were: “waterlogged”, that corresponds to soaked soil with water contents $\geq 39\%$ (v/v), “moist”, corresponding to 22% water content, and 5% under “dry” soil conditions. Different soil moisture levels had no effect on the survival of *Ambrosia*. The seedlings survived under the three imposed water levels and showed a survival rate of nearly 100% in all treatments (Table 1). However, soil moisture level had a significant influence on the biomass produced by the species. Most biomass was accumulated under moist soil conditions (9.55 $\pm$ 2.10 g dw), significant less biomass ($P < 0.01$) was accumulated under dry and waterlogged soil conditions (6.34 $\pm$ 0.93 g dw, 3.47 $\pm$ 1.23 g dw, respectively). Under waterlogged conditions the biomass was reduced by 63.7%. The differences in dry weight were consistently different in all plant parts under the three soil moisture treatments (Table 1).

Until the end of June, all plants grew slowly with growth rates of 1 mm per day. Main growth started at the end of June and increased continuously until the middle of August. Maximal growth rates were observed between the 01 August 2007 and the 16 August 2007; after this time the growth slowed down. The soil treatments had no influence on the period of maximal and minimal growth. However, the amount of growth was influenced by soil moisture: plants under moist but aerated soil conditions had higher growth rates, the waterlogged plants had lowest growth levels, and the dry ones were in between. During the time of main growth the plants could grow up to 20 cm shoot length per week. Under waterlogged conditions, however, the maximal shoot growth rate was 10 cm per week.

Tissue porosity

In the shoots we did not find differences in tissue porosity between the treatments. Furthermore, the variance within each soil treatment was high (Fig. 1). In the roots, however, there were significant differences between the moisture treatments ($P < 0.001$). Under dry conditions, the roots had a porosity of 9.6 $\pm$ 4.5%. With increasing soil water content this value increased. Under moist and waterlogged conditions the root porosity was significantly higher (moist: 20.2 $\pm$ 3.5%, waterlogged: 26.3 $\pm$ 4.2%, Fig. 1).

Chlorophyll content

Under waterlogged conditions the chlorophyll content of the leaves was significantly lower than in the other treatments (Table 2). The ratio of chlorophyll a/b, however, depended upon the ontogenetic status of the plants. 30 days after exposure to different soil moistures the content of total chlorophyll was different

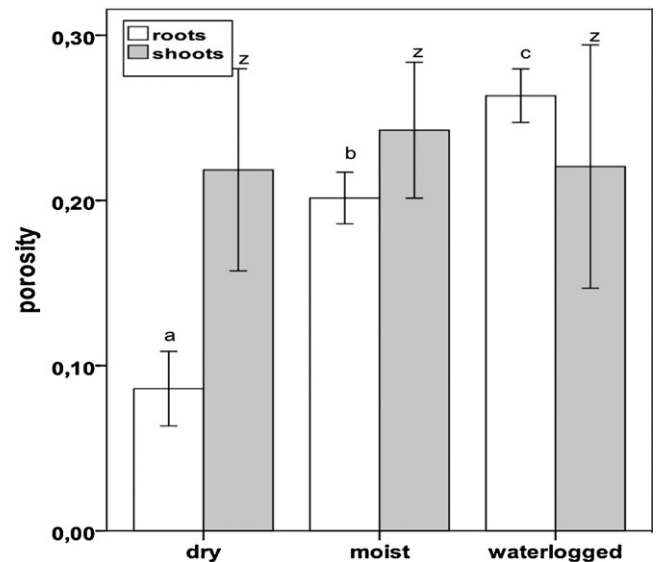


Fig. 1. Tissue porosity of roots and shoots (mean $\pm$ standard error) of Common Ragweed cultivated under different soil moisture regimes ($n = 15$). Different letters above root-related columns indicate significant differences ($P < 0.001$).

Table 2

Leaf chlorophyll content after one and two months plant growth of *Ambrosia artemisiifolia* under different soil moisture conditions. Numbers show mean $\pm$ SD, $n = 15$. Different superscript letters in a line indicate significant differences, $P < 0.01$ for (1), (4), $P < 0.05$ for (2).

	Soil moisture treatment		
	Moist	Dry	Waterlogged
(1) Chlorophyll content after 30 days [mg g^{-1}]	8.8 $\pm$ 0.6 ^a	8.0 $\pm$ 0.7 ^a	7.0 $\pm$ 0.5 ^b
(2) Chlorophyll content after 69 days [mg g^{-1}]	7.3 $\pm$ 0.5 ^a	7.0 $\pm$ 1.3 ^a	5.8 $\pm$ 0.7 ^b
(3) Chlorophyll a/b ratio after 30 days	3.43 $\pm$ 0.28	3.44 $\pm$ 0.54	3.45 $\pm$ 0.69
(4) Chlorophyll a/b ratio after 69 days	2.89 $\pm$ 0.11 ^a	3.98 $\pm$ 0.60 ^b	3.80 $\pm$ 0.19 ^b

between the treatments, but the ratio chlorophyll a/b was constant. However, 69 days after the start of the experiment, also this ratio differed significantly between the soil treatments.

Gas exchange

Under moist conditions *Ambrosia* had a maximal net photosynthesis rate of 31.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$, under dry or waterlogged conditions the highest values were 16.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 14.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively (Fig. 2). CO_2 uptake was highest in August when the plants were adult but did not show any senescence yet. In October, even under a high PPFD the net photosynthesis rates were lower, probably due to insufficient availability of chlorophyll which became partly degraded in fall (Table 2). The light compensation point was low at about 7–40 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Low light intensities are obviously sufficient for the species to harvest energy and assimilate carbon. Light saturation was reached already at 300 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ under all imposed soil moisture conditions; higher light intensities did not much increase CO_2 uptake rates (Fig. 2).

When related to leaf chlorophyll contents, CO_2 uptake showed highest values under moist conditions (442 $\mu\text{mol mg}^{-1}$ chloroph. h^{-1}). Plants under dry or waterlogged conditions were much less effective (326 $\mu\text{mol mg}^{-1}$ chloroph. h^{-1} , 235 $\mu\text{mol mg}^{-1}$ chloroph. h^{-1} , respectively). Thus, the reduced

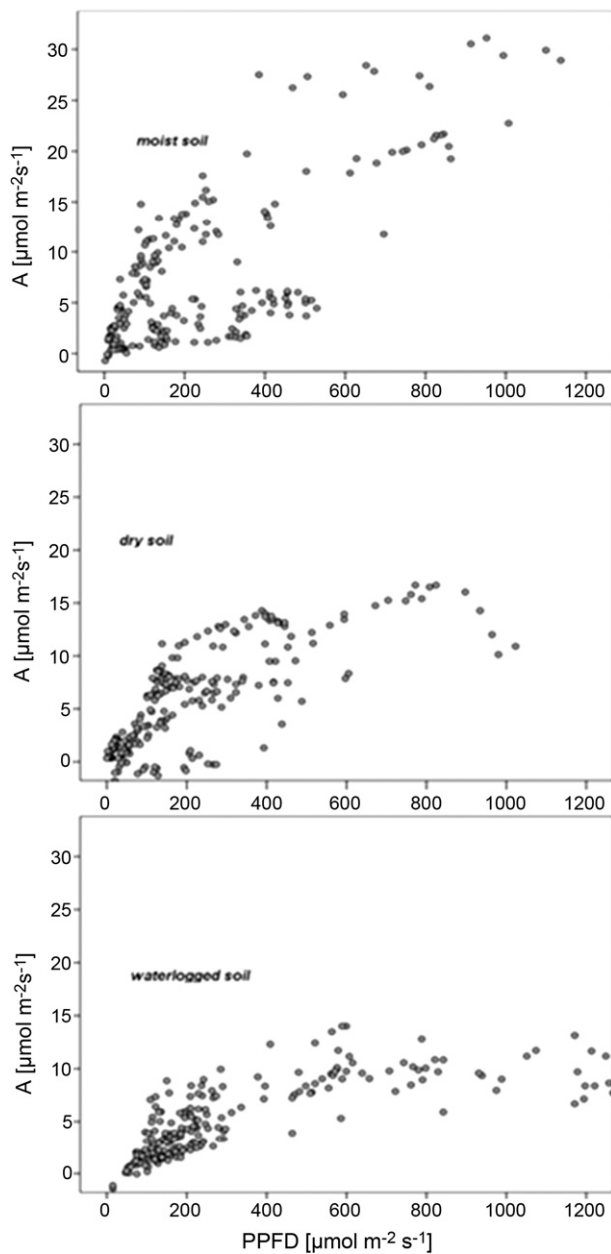


Fig. 2. Net CO₂ gas exchange (A) of Common Ragweed cultivated under different soil moisture regimes in dependency to light intensity (PPFD); top: moist, middle: dry, bottom: waterlogged; data are used from measurements of diurnal courses of gas exchange under outdoor conditions.

photosynthesis rates under less favourable growth conditions cannot be explained only by the reduced chlorophyll content.

In the dry treatment we consider the reduced leaf conductance as the most important factor explaining the lower achieved net photosynthesis levels. In comparison to optimal conditions with a mean conductance of $0.32 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ (Fig. 3), the mean leaf conductance under dry conditions was reduced by 80%. Also under waterlogging the mean stomatal conductance was lower ($0.24 \text{ μmol H}_2\text{O m}^{-2} \text{ s}^{-1}$). The observed transpiration values up to $18.4 \text{ mmol m}^{-2} \text{ s}^{-1}$ under moist soil conditions were consistent with results previously reported by Bazzaz (1974). Under dry conditions, we observed lower transpiration rates (max. $6.6 \text{ mmol m}^{-2} \text{ s}^{-1}$) due to the lower water availability in this treatment which lead to a closure of the stomata.

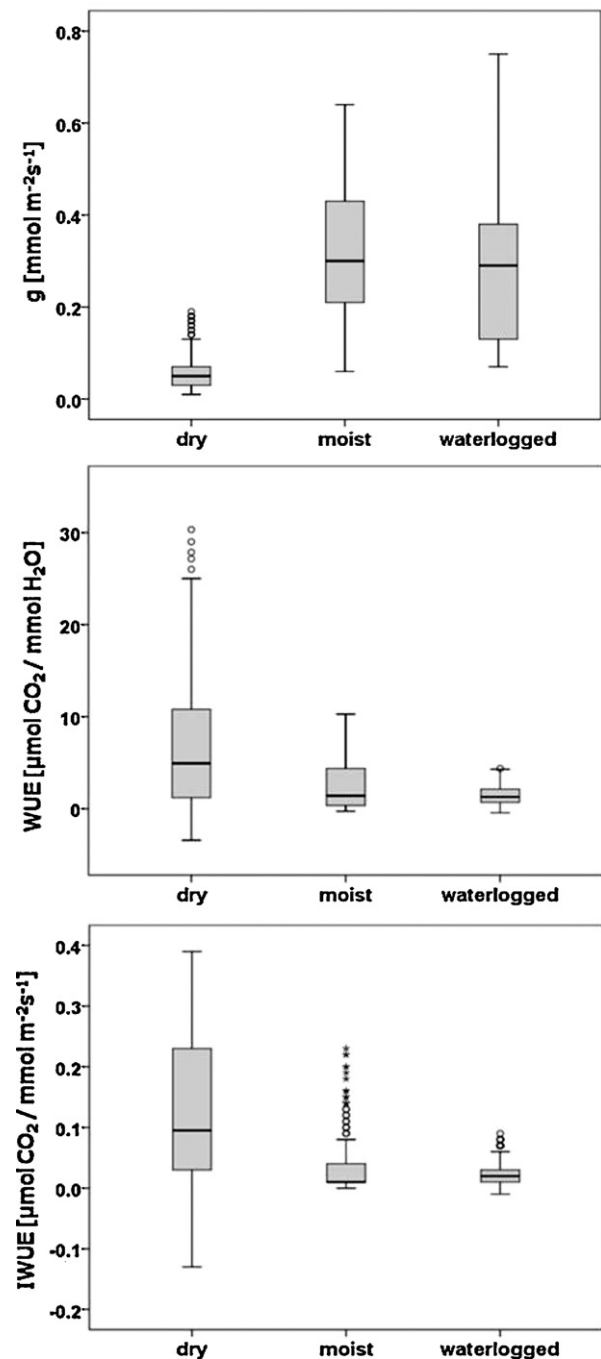


Fig. 3. Stomatal conductance (g) and water use efficiency (WUE=net photosynthesis per transpiration rate) and intrinsic water use efficiency (IWUE=net photosynthesis per stomatal conductance) of Common Ragweed under different soil moisture regimes.

Water use efficiency [WUE=net photosynthesis (A) per transpiration rate (E)] and intrinsic water use efficiency [IWUE=net photosynthesis (A) per stomatal conductance (g)] was highest under conditions of dry soil (Fig. 4). Between the moist and waterlogged soil conditions no differences in both WUE and IWUE were found.

Optimal temperatures for CO₂-fixation were between 20 °C and 30 °C (Fig. 4) which is a typical range found in herbaceous sun-light plants from temperate regions (Larcher, 2001). Above and below these temperatures the net CO₂ exchange was lower, e.g. at a temperature of 35 °C the rate was reduced by 50% (Fig. 4).

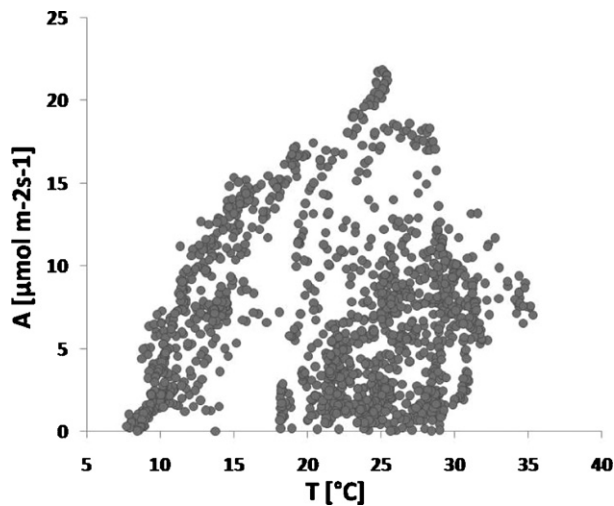


Fig. 4. Net CO₂ gas exchange (A) of Common Ragweed depending on temperature (T). Data are used from measurements of diurnal courses of gas exchange under outdoor conditions.

Discussion

Ambrosia artemisiifolia showed a high endurance against adverse effects from different soil moisture treatments. It was able to survive under all imposed water-levels, even under waterlogging, and – which is most important for an annual plant species like *Ambrosia* – to produce seeds. All individuals produced achenes and were able to fulfill their life cycle this way. Under moist soil conditions the growth was highest and, in consequence most seeds per plant were produced. When grown under dry or waterlogged conditions the plants attained lower heights and produced less seeds.

Under waterlogged soil, O₂ availability to roots is reduced which may lead to problems in growth, nutrient and water uptake and hormonal balance (Jackson and Colmer, 2005). Furthermore, less energy can be provided and microbiological processes in the soil produce toxic substances which may damage the plants. Generally, also non-wetland plants may develop higher amounts of aerenchyma in their roots when suffering from low oxygen concentrations in the soil (Lösch, 2003). *Ambrosia artemisiifolia* showed a significant higher root aerenchyma content (porosity) under waterlogged conditions. Hence, following Smirnoff and Crawford (1983) the species may be classified as (moderately) flood-tolerant species which is able to survive waterlogging even over several months. Mesophytic plants growing under dry conditions usually show aerenchyma contents of less than 7% (Justin and Armstrong, 1987), which was also measured for *Ambrosia* growing on aerated soil.

Both waterlogged and dry conditions are less optimal for the species. This also became evident from the lower level of photosynthesis and the lower leaf chlorophyll contents. Moist but aerated soil conditions, however, lead to optimal chlorophyll contents and highest photosynthesis rates. Lower chlorophyll contents under waterlogging were described for wetland plants by Elakovitch and Wooten (1989). The low chlorophyll content of *Ambrosia* leaves under less favourable conditions partly explains the lower assimilation rates. But also an insufficient opening of the stomata influences CO₂ uptake. Plants are assumed to adapt physiologically to drier conditions by decreasing stomatal conductance and thereby increasing their water use efficiency (Zangerl and Bazzaz, 1984). Marshall and Zhang (1994) found a higher IWUE in evergreen and deciduous species along a decreasing rainfall gradient; such results were also found in *Ambrosia* growing on soil with different moisture. Generally, waterlogged plants may attain low leaf conductances (Liao and Lin, 2001; Pezeshki, 2001). For *Ambrosia*,

however, the leaf conductance did not differ reasonably between moist and waterlogged soil conditions.

The measured net CO₂ uptake levels under optimal (moist) soil conditions are consistent with results previously reported for ragweed in its native range in Central North America (Bazzaz, 1974). The present climatic conditions in Central Europe are certainly less continental than those in the areas of origin of *Ambrosia artemisiifolia*, but obviously suitable for a good development of the species as well. In the experiments, light saturation of CO₂ uptake was already reached at 300 μmol photons m⁻² s⁻¹. This may explain why irradiation has shown to have only an influence on *Ambrosia* growth and development when combined with low temperature stress (Deen et al., 1998).

The maximal measured gas exchange values achieved under different soil moisture were related to leaf chlorophyll contents of the respective plant. Under moist conditions the CO₂ gain per chlorophyll is with 442 μmol mg⁻¹ chloroph. h⁻¹ nearly twice as high than under waterlogged/dry conditions. This can be explained by a lower quantum efficiency of the Photosystem II, as regularly found when plants are waterlogged (e.g. Close and Davidson, 2003; Smethurst and Shabala, 2003). Under dry soil conditions, the lower photosynthesis can be attributed to a reduced stomatal conductance.

However, even with somewhat reduced vigor *Ambrosia* could stand both extremes, dry and waterlogged conditions. This broad hydrological amplitude in its ecological niche will enable ragweed to grow on most soil types and under different water regimes. In addition, also the gas exchange data indicate a generalist character of this species with concern to irradiation conditions of the habitat: It can occupy places from shadow and semi-shadow up to bright sun. Therefore, *Ambrosia* does not seem to be strongly limited by important abiotic habitat conditions.

The main growing time of the individuals was equal, irrespective whether the plants were under moist, dry or waterlogged conditions. The degree of growth, however, differed. This clearly resulted from the differences in assimilation rates we found between the hydrologically different substrates. Time of flower and fruit set, however, was not as much influenced by the soil conditions. Just the amount of generative organs per plant was higher under the optimal situation of a moist, but aerated growth substrate. Flowering and fruit set also under unfavourable conditions, in some species starting even precociously, is typical for annual plants with high phenotypic plasticity (Sultan, 2000).

However, similar as other annuals *Ambrosia* will face difficulties to establish in dense vegetation. This became obvious also with the spontaneous source population the seeds of which were used in the present study: Situated at a meadow-pond ecotone, offsprings germinated in the dense grass vegetation remained stunted, and no spread occurred into the dense vegetation. But there are enough open sites in densely men-populated Central Europe where founder populations of the invader may establish. Therefore, it can be anticipated that *Ambrosia* will spread widely, if no measures will be taken constraining this process.

Under the actual climate, the probability to reproduce successfully also under Central European conditions is high. Wayne et al. (2002) predict that an increasing CO₂-concentration of the atmosphere will even lead to a higher amount of *Ambrosia* pollen produced per plant. In addition, Singer et al. (2005) describe an increasing Amb a 1-content, the most crucial allergen in *Ambrosia*, with rising CO₂-concentration. Consequently, with an increasing CO₂-concentration to 600 ppm which is predicted for the middle of the 21st century (e.g. Houghton et al., 1996). *Ambrosia* pollen pollution of the air should seriously increase, resulting from increased occurrences of the invader, from higher pollen amounts per plant, and from their more severe allergenic properties. In the USA Barnes et al. (2001) reported a statistically significant effect of temper-

ature on the pollen content in the air. We conclude that under near future climate change conditions (rising temperatures, rising CO₂-concentration) humans will get more often in contact with the allergenic pollen than they do now. With *Ambrosia* spread in Central Europe the number of allergy-suffering persons surely will increase and additional costs in the public health sector will occur.

Generally, containment of undesired neophytes is only efficient if measures are taken in the beginning of their spread (Rejmánek et al., 2005) – the situation presently given for *Ambrosia* in Germany. Control measures against it should be intensified respective started at the actual stage of an incipient spread. For this, it will be most efficient to halt the introduction via bird seed. In addition, existing populations should be removed by tearing out. With incomplete removal or early mowing the species is able to re-sprout (Bohren et al., 2005), late mowing increases the risk of increased distribution of already developed seeds. Efficient containment measures are timely to prevent an *Ambrosia* invasion over big parts of Germany.

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References

- Alberternst, B., Nawrath, S., Klingenstein, F., 2006. Biologie, Verbreitung und Einschleppungswege von *Ambrosia artemisiifolia* in Deutschland und Bewertung aus Naturschutzsicht. Nachr.bl. Dtsch. Pflanzenschutzdienst 58, 279–285.
- Barnes, C., Pacheco, F., Landuyt, J., Hu, F., Portnoy, J., 2001. The effect of the temperature, relative humidity and rainfall on airborne ragweed pollen concentrations. *Aerobiologia* 17, 61–68.
- Bazzaz, F.A., 1974. Ecophysiology of *Ambrosia artemisiifolia*: a successional dominant. *Ecology* 55, 112–119.
- Bohren, C., Delabays, N., Mermillod, G., Keimer, C., Kündig, C., 2005. *Ambrosia artemisiifolia* in der Schweiz – eine herbologische Annäherung. *Agrarforschung* 12, 71–78.
- Brandes, D., Nitzsche, J., 2007. Verbreitung, Ökologie und Soziologie von *Ambrosia artemisiifolia* L. in Mitteleuropa. *Tuexenia* 27, 167–194.
- Burdick, D.M., 1989. Root aerenchyma development in *Spartina patens* in response to flooding. *Am. J. Bot.* 76, 777–780.
- Chauvel, B., Dessaint, F., Cardinal-Legrand, C., Bretagnolle, F., 2006. The historical spread of *Ambrosia artemisiifolia* L. in France from herbarium records. *J. Biogeogr.* 33, 665–673.
- Close, D.C., Davidson, N.J., 2003. Long-term waterlogging: nutrient, gas exchange, photochemical and pigment characteristics of *Eucalyptus nitens* saplings. *Russ. J. Plant Physiol.* 50, 843–847.
- Clot, B., Schneiter, D., Tercier, P., Gehring, R., Annie, G., Thibaudon, M., 2002. *Ambrosia* pollen in Switzerland – produced locally or transported? *Allerg. Immunol. (Paris)* 34, 126–128.
- Deen, W., Hunt, T., Swanton, C.J., 1998. Influence of temperature, photoperiod, and irradiance on the phenological development of common ragweed (*Ambrosia artemisiifolia*). *Weed Sci.* 46, 555–560.
- Elakovich, S.D., Wooten, J.W., 1989. Allelopathic potential of sixteen aquatic and wetland plants. *J. Aquat. Plant Manage.* 27, 78–84.
- Houghton, J.T., Meiro Filho, L.G., Callander, B.A., Harris, N., Kattenburg, A., Maskell, K. (Eds.), 1996. *Climate Change 1995: The Science of Climate Change*. Cambridge University Press, Cambridge.
- Jackson, M.B., Colmer, T.D., 2005. Response and adaptation by plants to flooding stress. *Ann. Bot.* 96, 501–505.
- Jäger, S., 2000. Ragweed (*Ambrosia*) sensitisation rates correlate with the amount of inhaled airborne pollen. A 14-year study in Vienna, Austria. *Aerobiologia* 16, 149–153.
- Jarvis, P.G., 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 273, 593–610.
- Justin, S.H.F., Armstrong, W., 1987. The anatomical characteristics of roots and plant response to soil flooding. *New Phytol.* 106, 465–495.
- Larcher, W., 2001. *Ökophysiologie der Pflanzen. Leben, Leistung und Streßbewältigung der Pflanzen in ihrer Umwelt*. 6. Aufl., UTB, Stuttgart.
- Liao, C., Lin, C., 2001. Physiological adaption of crop plants to flooding stress. *Proc. Natl. Sci. Coun. Repub. China* 25, 148–157.
- Lösch, R., 2003. Wasserhaushalt der Pflanzen. 2. Aufl., Quelle & Meyer, Wiebelsheim.
- Mandrioli, P., Di Cecco, M., Andina, G., 1998. Ragweed pollen: the aeroallergen is spreading in Italy. *Aerobiologia* 14, 13–20.
- Marshall, J.D., Zhang, J., 1994. Carbon isotope discrimination and water-use efficiency in native plants of the north-central Rockies. *Ecology* 75, 1887–1895.
- Otto, C., Alberternst, B., Klingenstein, F., Nawrath, S., 2008. Verbreitung der Beifußblättrigen Ambrosie in Deutschland. Problematik und Handlungsoptionen aus Naturschutzsicht. BfN-Skripten 235, Bonn-Bad Godesberg.
- Pezeshki, S.R., 2001. Wetland plant responses to soil flooding. *Environ. Exp. Bot.* 46, 299–312.
- Puc, M., 2006. Ragweed and mugwort pollen in Szczecin, Poland. *Aerobiologia* 22, 67–78.
- Rejmánek, M., Richardson, D.M., Pysek, P., 2005. Plant invasions and invasibility of plant communities. In: van der Maarel, E. (Ed.), *Vegetation Ecology*. Blackwell, Oxford, pp. 332–355.
- Rybníček, O., Novotná, B., Rybníčkova, E., Rybníček, K., 2000. Ragweed in the Czech Republic. *Aerobiologia* 16, 287–290.
- Schmitz, U., 2004. The potential effects of climate change on the growing season and degree of naturalization of alien *Amaranthus* species on banks of the river Rhine. In: Kühn, I., Klotz, S. (Eds.), *Biological Invasions: Challenges for Science*. Neobiota 3, 135–145.
- Schrader, G., 2004. Risikoanalyse von gebietsfremden Pflanzen – Das neue Konzept der EPPD. *Gesunde Pflanzen* 56, 75–79.
- Singer, B.D., Ziska, L.H., Frenz, D.A., Gebhard, D.E., Straka, J.G., 2005. Increasing *Ambrosia* pollen content in common ragweed (*Ambrosia artemisiifolia*) pollen as a function of rising atmospheric CO₂ concentration. *Funct. Plant Biol.* 32, 667–670.
- Smethurst, C.F., Shabala, S., 2003. Screening methods for waterlogging tolerance in lucerne: comparative analysis of waterlogging effects on chlorophyll fluorescence, photosynthesis, biomass and chlorophyll content. *Funct. Plant Biol.* 30, 335–343.
- Smirnov, N., Crawford, R.M.M., 1983. Variation in the structure and response to flooding of root aerenchyma in some wetland plants. *Ann. Bot.* 51, 237–249.
- Sultan, S.E., 2000. Phenotypic plasticity for plant development, function and life history. *Trends Plant Sci.* 5, 537–542.
- Tamarcaz, P., Lambelet, C., Clot, B., Keimer, C., Hauser, C., 2005. Ragweed (*Ambrosia*) progression and its health risks: will Switzerland resist this invasion? *Swiss Med. Wkly.* 135, 538–548.
- Török, K., Botta-Dukát, Z., Dancza, I., Németh, I., Kiss, J., Mihály, B., Magyar, D., 2003. Invasion gateways and corridors in the Carpathian Basin: biological invasions in Hungary. *Biol. Invasions* 5, 349–356.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395.
- Wayne, P., Foster, S., Connolly, J., Bazzaz, F., Epstein, P., 2002. Production of allergenic pollen by ragweed (*Ambrosia artemisiifolia* L.) is increased in CO₂-enriched atmospheres. *Ann. Allergy Asthma Immunol.* 88, 279–282.
- Zangerl, A.R., Bazzaz, F.A., 1984. Effects of short-term selection along environmental gradients on variation in populations of *Amaranthus retroflexus* and *Abutilon theophrasti*. *Ecology* 65, 207–217.
- Ziegler, R., Egle, K., 1965. Zur quantitativen Analyse der Chloroplastenpigmente. I. Kritische Überprüfung der spektralphotometrischen Chlorophyll-Bestimmung. *Beitr. Biol. Pfl.* 41, 11–37.