Growth and development of *Artemisia annua* L. on different soil types

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Synopsis

Artemisia annua, a neophyte from the temperate zone in Asia, became established within 30 years on the banks of the middle course of the river Elbe. One reason for the fast expansion and the success of this plant is its settlement ability on different soil types, which was tested with field and greenhouse experiments. *A. annua* displays a remarkable phenotypic plasticity, comparable to successful weeds such as e. g. *Chenopodium album*. Available nutrients are readily utilized for an increase of biomass and diaspore production. The relatively low demands on its environment paired with the ability to exploit resources successfully help *A. annua* to colonize different sites of the river banks.

Artemisia annua, sweet wormwood, population dynamics, neophyte, phenotypic plasticity

Artemisia annua, Einjähriger Beifuß, Populationsdynamik, Neophyt, phänotypische Plastizität

1 Introduction

River banks are characterized by temporary inundation and substrate shifting, as long as they are still in a relatively natural condition, as for example in the middle course of the river Elbe. Such disturbances regularly create vegetation free patches and allow settlement of numerous annual neophytes. Next to the good supply with water and nutrients in riparian habitats, the possibility for diaspores to use the water as dispersal agent is a key factor for the immigration of new species. So it was possible for e. g. *Bidens frondosa* and *Xanthium albinum* to become established in the Elbe flood plains. Another neophyte, which appears at the middle course of the river Elbe since 1964, is *Artemisia annua* (BRANDES & JANSSEN 1991). During the last thirty years it experienced a strong expansion and at some locations it builds large stands today. *A. annua* settles on varying sites, such as sand, gravel or silty soil. According to the different settlement habitats it shows distinct differences in its course of growth, growth height as well as diaspore production. Extensive investigations on the population biology of *A. annua* were conducted (see MÜLLER 1996) to give insight into the reasons for the fast expansion and the success of this neophyte. In this article the emphasis is put on the settlement ability on different soil types, which was tested with field and greenhouse experiments.

2 Information on *Artemisia annua*

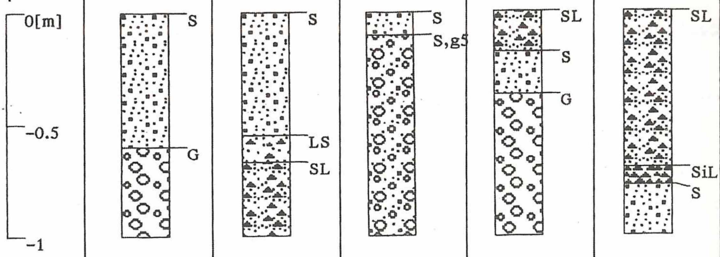
According to MEUSEL & JÄGER (1992), *A. annua* is a continental species from the temperate zone in Asia with origin in sandy banks of rivers, lakes and wadis in the semi deserts and steppes. The occurrences in central Europe, central Russia, North America and Japan are classified as synanthropic. In Germany *A. annua* has frequently been recorded in the Elbe valley downstream of the Saale mouth (BRANDES & SANDER 1995). Already in the sixties RAUSCHERT (1966) reported many findings of *A. annua* in villages at the Saale. It is probable, that the neophyte reached the Elbe from its occurrence in the vicinity of Halle using the Saale as dispersal agent. Own experiments show that the diaspores are able to swim and to germinate after a storage in water for about two months.

In Europe *A. annua* is most often reported from disturbed ruderal sites. BRANDES (1987) describes rich stands on the outskirts of Verona, in Vienna it grows on parking lots and road sides (FORSTNER & HÜBL 1971), and also in the flora of Turkey locations such as fields and rubble tips are given (DAVIS 1975). In Wackersleben, Western Sachsen-Anhalt, *A. annua* is reported from the whole village. Plant sociological tables of these stands are given in S. BRANDES & D. BRANDES (1996).

A. annua is a summer annual species and in the blossom time, beginning in mid August, it builds numerous little flower buds (2–5 mm in diameter) in a racemose or paniculate inflorescence. The mostly red coloured stem, the three to four times pinnately divided light green leaves and the intensive aromatic scent are characteristic features. The very small achenes (0.5–1.5 mm length) are ripe at the end of September and do not possess a pappus. Observations in the field show that most of the mature achenes are found near the adult plant which is also known from

Table 1
Information on vegetation and soil profiles of investigated 1 m² quadrates on sand (S1–S7) and loam (L1–L6); S: sand; G: gravel; SL: sandy loam; LS: loamy sand; SiL: silty loam; S, g5: very gravelly sand (50–75 vol. % gravel).

site	S1-S4	S5	S6	S7	L1-L6
soil profile					
germination	end of April	end of April	beginning June	beginning May	end of May
vegetation cover [%]	30-65	30-65	25	95	100
dominant species	*Eragrostis albensis*	*Eragrostis albensis*	sparsly covered with single species	*A. annua*	*Elymus repens* *Urtica dioica* *A. annua*



Artemisia herba-alba a species with achenes of comparable size (FRIEDMAN & ORSHAN 1975). Therefore, wind does not seem to play a major role in dispersal.

In China *A. annua* has long been known for its medical value. Already 2000 years ago, it was used in the treatment of fever (KLAYMAN 1993). With the isolation of Artemisinin, a substance with antimalarian effect, *A. annua* gained great importance in the pharmaceutical research (e. g. FEIRREIRA & JANICK 1995).

3 Material and methods

3.1 Study site

The study site covers a small section of the Elbe river bank north of Magdeburg (river kilometre 39.5 to 39.8). This Elbe section is situated at the edge of the »Mitteldeutsches Trockengebiet« with an annual precipitation of 500 mm. In the flood plain small scale variation of different soil types can be found. The soil texture of the lower bank is characterised by sandy gravelly material, which is partly covered with a thin mud layer. On the upper bank the soil becomes more silty (sandy loam).

3.2 Field observations

Transect-survey

In August 1994, three transects from the water surface to the beginning of the lower terrace were established (10–44 m length). Every 1–3 m along these transects 1 m soil profiles were taken (with Pürckhauer) in order to describe the soil type. The dominant plant species were noted and shoot lengths of *Artemisia annua* recorded. The following representative transect covered a distance of 39 m and had a south-southeast exposed slope with a slight inclination of 4 %. The upper bank fell dry at the end of April, whereas areas on the lower bank were covered with water until mid June. Therefore, the start of germination for plants differed for up to 6 weeks.

Course of growth of individually marked plants

To eliminate possible effects of differing starts of germination of *A. annua*, two additional sites with different soil types were selected on which the plants germinated simultaneously at mid June. Here *A. annua* plants were marked individually, and their growth was determined by regular measurements of the shoot length. One observation site was located on the upper bank. Here the top 58 cm of the soil profile were dominated by a high proportion of silt. The second site was situated on the lower bank on which the sandy soil was covered by a 8 cm thick loam layer. In both areas the water-level had sufficiently sunken at the end of May until the beginning of June.

Production of flower buds on different soil types

For detailed observation, 1 m² quadrates were established, seven on sand (S1–S7) and six on sandy loam (L1–L6). Here again, the substrate was described with 1 m soil profiles and the shoot length and the production of flower buds of *A. annua* were determined. Table 1 represents the soil profiles and gives information on conditions of location.

3.3 Experiments in the greenhouse

In addition to field observations, several experiments concerning the ecology of *A. annua* were conducted from May until September 1994 in the greenhouse. The diaspores for these tests were collected in October 1993 in the field and stored under dry conditions until their employment.

Growth on different soil types

One experiment was designed to analyze differences in growth on varying soil types. *A. annua* plants were raised on silt (loess) and quartz sand (middle sand) respectively (density: 4 plants/pot, equivalent to 242 plants/m^2) with two repeats for each variant. The growth was determined by regular measurements (every 7–14 days) of the shoot length.

Influence of different fertilizer quantities

A second experiment should investigate the influence of fertilizer. Here, *A. annua* plants (density: 3 plants/pot, equivalent to 79 plants/m^2) were watered with different amounts of liquid fertilizer. The given quantities of fertilizer were calculated to 30, 60 and 120 kg N/ha. At the end of the vegetation period the dry weight and the number of flower buds per plant were determined. The tests were performed with three repeats for each variant.

4 Results

4.1 Field observations

Transect-survey

Along the transect significant differences in growth of *A. annua* can be noted (fig. 1). Figure 2 shows the average growth height of *A. annua* in correlation with the soil profile. In order to determine average values for the shoot lengths, all *A. annua* individuals in areas of similar plant communities were grouped together (for dominant species see legend of

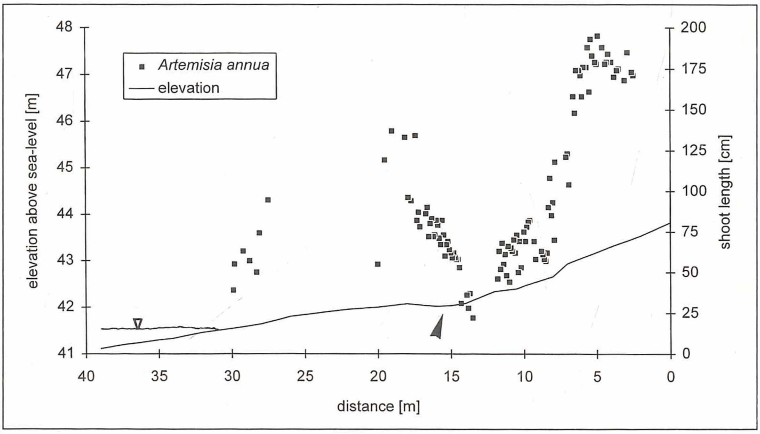


Fig. 1
Shoot length of individual *A. annua* plants along the transect (arrow indicates hollow) from the water edge to the beginning of the lower terrace of the river Elbe.

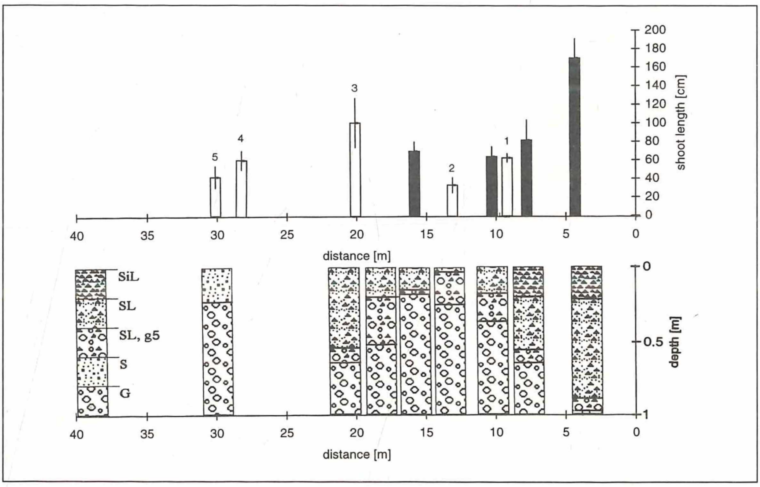


Fig. 2
Average shoot lengths of *A. annua* along the transect with corresponding 1 m soil profiles. Black bars indicate *A. annua* dominated stands, white bars show *A. annua* heights in communities dominated by other species (1: *Bromus inermis*, 2: *Portulaca oleracea*, 3: *Polygonum lapathifolium*, 4: *Phalaris arundinacea*, 5: *Eragrostis albensis*); SiL: silty loam; SL: sandy loam; SL, g5: very gravelly sandy loam (50–75 vol. % gravel); S: sand; G: gravel.

fig. 2). On the upper bank silty loam and sandy loam, respectively, are the prevailing components of the top 90 cm in the soil profiles. Here, the densest stands of *A .annua* with heights of up to 195 cm are found. Further to the water the loam layer decreases to a thickness of 8 cm in the area of *Portulaca oleracea* stand. Below the loam layer sandy gravel is found. Correspondingly, the average shoot length of *A. annua* diminishes to 22 cm. In the following hollow (see arrow in fig. 1) the proportion of loam as well as the growth height of *A. annua* increases again to shoot lengths of up to 150 cm. In the area of 21 m and 27 m of the transect, *Polygonum lapathifolium* and *Bidens frondosa* dominated the flora and no *A. annua* plants occurred. At the water edge the loam layer is absent, and sand forms the top 20 cm of the soil profile above gravel. In this area the average shoot length accounts to 32 to 74 cm.

Course of growth of individually marked plants

The detailed course of growth of *A. annua* on two locations is shown in figure 3. On the first site on the upper bank the plants reach a mean height of 136 cm and show a typical sigmoid course of growth, which can be described by the logistic growth function by VERHULST and PEARL (see RICHTER 1985). On the second sandy site individuals do not only achieve lesser shoot lengths in total, but also have a slower growth. Since they interrupt their growth from beginning until end of July when precipitation is rare, their course of growth is not sigmoid.

Production of flower buds on different soil types

Like the shoot lengths the numbers of flower buds per plant show considerable variation (tab. 2) between the different soil types (tab. 1). On the sandy soil plants reach average height of 24.9 cm to 66.5 cm and the mean number of buds varies between 27 to 3930 buds per plant. Even the smallest individuals produce diaspores. On S5 the tallest of three *A. annua* plants had a shoot length of 101.5 cm and 10677 flower buds. The single plant on sandy gravelly substrate (S6) and a three weeks delayed start of germination attained a height of 66 cm and produced 2207 flower buds.

Plants on the loamy soil (L1–L6) germinated at the end of May and gained significantly larger shoot lengths (U-test, P< 0.01) and carried significantly more flower buds (U-Test, P< 0.01; see tab. 2).

4.2 Greenhouse experiments

Growth on different soil types

As in the field, *A. annua* plants in the greenhouse stay small on the sandy soil and reach only heights of 22 (± 8.9) cm in the first and 23 (± 3.4) cm in the second pot (fig. 4). On the silty loam, however, growth is better and individuals gain average shoot lengths of up to 80.8 (±18.5) cm and 77.7 (± 17.1) cm. Both variants show a sigmoid course of growth, that can be described as logistic growth. Not only the shoot length varies according to the soil type but also the production of flower buds. Whereas the plants on the quartz sand produce on average 66 to 68 flower buds per plant, they have 870 to 1300 buds per plant on the silty loam. When the number of achenes per flower bud are taken into account, which was done in 9 representative buds for each variant, it shows that plants growing on sand possess considerably less achenes per bud than plants growing on the silty loam.

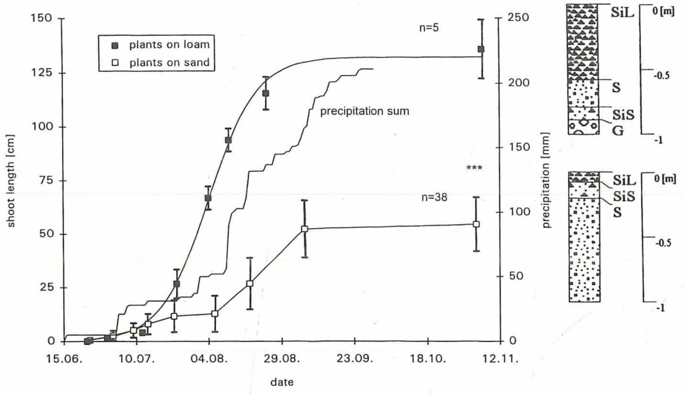


Fig. 3
Course of growth of *A. annua* in the field on sand and loam; SiL: silty loam; SiS: silty Sand; S: sand; G: gravel; * the means are significant different (U-test, P<0.01); results of parameter estimation and asymptotic standard error: K=132.1 (3.2) cm; r = 0.121 (0.010) 1/d; y_0 = 0.809 (0.329) cm; R^2 = 0.997; logistic growth function:**

$$y(t) = \frac{K \cdot y_0}{y_0 - (y_0 - K) \cdot e^{-r \cdot t}}$$

Artemisia annua on sand			*Artemisia annua* on loam		
site	shoot length [cm]	number of flower buds	site	shoot length [cm]	number of flower buds
	mean (s.d.)	mean (s.d)		mean (s.d.)	mean (s.d.)
S 1 (56 plants)	24.9 (9.9)	219 (224) °	L 1 (1 plant)	88.8	8712
S 2 (24 plants)	11.9 (5.6)	27 (24)	L 2 (1 plant)	78.7	4343
S 3 (65 plants)	21.0 (9.2)	97 (108)	L 3 (1 plant)	120.0	11160
S 4 (38 plants)	26.1 (9.7)	121 (151)	L 4 (9 plants)	87.4 (19.3)	4984 (4517) °
S 5 (3 plants)	65.4 (33.5)	3930 (5853)	L 5 (31 plants)	126.3 (23.4)	7553 (9093) °
S 6 (1 plant)	66.5	2207	L 6 (35 plants)	135.5 (25.4)	7335 (10117) °
S 7 (136 plants)	55.9 (10.8)	392 (398) °			
S 1 to S 7	38.8 (23.0)	999 (1503)	L 1 to L 6	106.1 (23.9)**	7348 (2492)**

Table 2
Shoot length and number of flower buds per plant of *A. annua* in 1 m^2 quadrates on sand (S1–S7) and loam (L1 – L6); s. d.: standard deviation; °: determination of bud numbers by measurement of lateral branch lengths (previously established correlation between allometric growth of branches and bud numbers allowed the calculation of buds); **significant differences between means on sand and loam (U-test, $P < 0.01$).

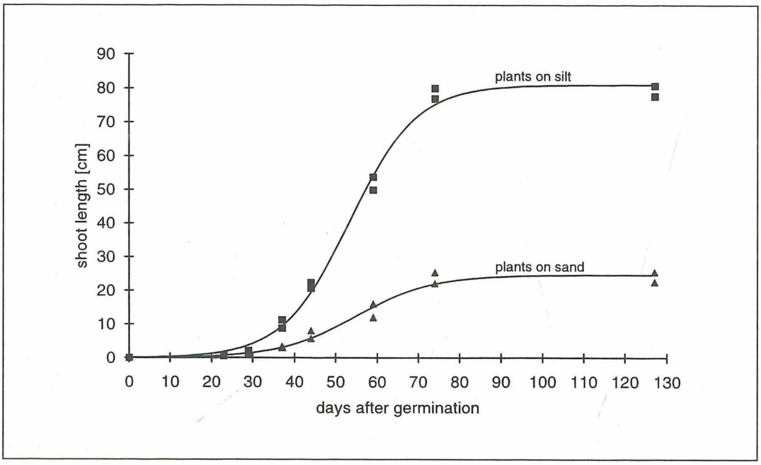


Fig. 4
Course of growth of *A. annua* in the greenhouse on quartz sand and silt (loess); the means of the two pots (density: 4 plants/pot) of each variant are shown; results of parameter estimation (logistic growth) and asymptotic standard error: quartz sand: $K = 24.7$ (1.0) cm; $r = 0.109$ (0.013) 1/d; $y_0 = 0.063$ (0.042) cm; $R^2 = 0.992$; silt: $K = 81.1$ (2.1) cm; $r = 0.124$ (0.010) 1/d; $y_0 = 0.110$ (0.058) cm; $R^2 = 0.997$; logistic growth function see fig. 3.

In the first case they had 12 (± 2) achenes on average, in the second case the mean number of achenes was 20 (± 3) per bud.

Influence of different fertilizer quantities

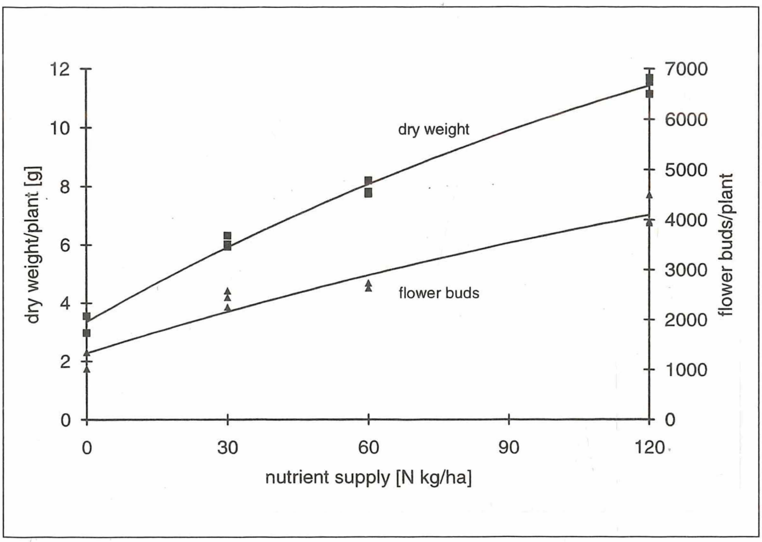
The dry weight and the number of the flower buds increase significantly with the amount of fertilizer (fig. 5). The correlation, however, is not linear, since dry weight as well as bud number reach an upper limit regardless of further increase in the given N-fertilizer quantities. The measurements are in accordance with the MITSCHERLICH function (see RICHTER 1985), that says that continuous enhancement of fertilization will increase yield only up to a certain limit.

The number of produced buds rises by a factor of 3.5 from 1192 (± 291) in the unfertilized controls to 4146 (± 315) in the pots with highest N input. The dry weight per plant increases by the same factor from 3.27 (± 0.41) to 11.47 (± 0.28). A spot check of 7 to 17 flower buds revealed an increase in the numbers of achenes per bud from 15 (± 6) in the unfertilized variant to 27 (± 10) in plants in the 120 kg N/ha variant. The experiments show, that a raised nutrient input correlates with an increased production of diaspores.

5 Discussion

The evaluation of the transect shows a clear correlation between the shoot length of *Artemisia annua* and the different soil types (fig. 1 and fig. 2). With increasing thickness of the loam layer plants can reach considerable heights, which is supported by the favourable water and nutrient conditions. On the sandy gravel, however, they stay small. Here, the usually paniculate inflorescence is often reduced to a

Fig. 5
Correlation between dry weight or number of flower buds of *A. annua* individuals and nutrient supply; the means of the three pots (density: 3 plants/ pot) of each variant are shown; results of parameter estimation (MITSCHERLICH-function) and asymptotic standard error: dry weight: K = 19.73 (3.43) g; a = 0.006 (0.002) ha/kg; b = 33 (5) kg/ha; R^2 = 0.992; flower buds: K = 8223 (6150); a = 0.004 (0.005) ha/kg; b = 41 (20) kg/ha ; R^2 = 0.935; MITSCHERLICH-function: $y(x) = K \cdot (1 - e^{-a(x+b)})$



double or single raceme (FÖRSTER 1985). In comparison to *A. annua* plants within the *Portulaca oleracea* stand on sand (distance 13–14 m in fig. 2), the individuals in direct proximity to the water – but also on nutrient poor sand – are on average 6–28 cm taller. A possible explanation is the better water supply throughout the vegetation period.

For the greater heights of plants on the upper bank, the earlier start of germination is a crucial factor as well. *A. annua* is a short-day plant, i. e. flower induction depends on day length. The critical photo period for flower induction in climate chamber experiments was 14.5 h to 15 h (MÜLLER 1996), which corresponds to day lengths in August. Results of FEIRRARA (1995) on cloned *A. annua* plants in controlled environments showed also critical day lengths of 12 h to 16 h. With the start of flower induction the plants finish their vegetative growth, so that earlier germinated plants have higher final shoot lengths and more flower buds than later germinated individuals (MÜLLER 1996). The ability to germinate at low temperatures of 10 °C to 15 °C to a high percentage of around 87 % allows *A. annua* a germination early in the year (MÜLLER 1996). GALAMBOSI (1976), who conducted field scale cultivation of *A. annua* in Hungary, recommends end of march to mid April as best sowing time. These plants reach heights of 200 cm to 250 cm in August.

The course of growth of marked *A. annua* plants on different soil types (fig. 3), that had all germinated at the same time, shows, that individuals on loamy soil can attain significantly greater shoot lengths than on sand. These findings were confirmed by greenhouse experiments (fig. 4). Next to the deteriorated nutrient supply the increased desiccation of the permeable, sandy soil in times of little precipitation is responsible for the slower growth (fig. 3). An interruption because of drought is also found in *Xanthium album* (BELDE 1995, unpubl.), another neophyte at the river Elbe.

The soil type influences not only the shoot growth but also the production of flower buds (tab. 2). Plants on loamy soil (L1–L6) carry always significantly more buds than plants on the sandy sites (S1–S7). But even individuals on predominantly sandy substrate are able to produce a considerable number of buds, as long as there is a loam layer in the soil as in site S5 (s. tab. 1 and tab. 2). When *A. annua* plants were digged up, larger plants (> 120 cm) showed tap roots of up to 65 cm in length, that can reach deeper situated silt bands in the soil. Because of the better supply with water and nutrients, sites at the water edge (e. g. S6) also allow plants to produce high number of buds and considerable shoot length, regardless of the late start of germination and the sandy substrate. This could already be noted in the transect survey (fig. 1 and fig. 2).

The field results were confirmed in the greenhouse. The soil texture influences not only the shoot growth (fig. 4) but also the production of flower buds. Since the number of achenes per bud is also increased on loam in comparison with sand, the influence of the soil type on diaspore production is considerable. A decrease of diaspore production under deteriorated conditions had already been shown in other experiments. An increased population density, for example, leads to a reduction of achene numbers (MÜLLER 1996), as well as a reduction in nutrient supply. On the other hand, the fertilizer experiment shows (fig. 5), that it is possible for *A. annua* to successfully exploit favourable nutrient conditions for its growth. Increased amounts of Nitrogen-inputs lead to a rise in dry weight and number of flower buds. The additional enhancement of achene production per bud, allows a significant increase in diaspore production.

The ability to make use of available nutrients for an increase of biomass and diaspore production, is one of the reasons for the settlement success of *A. annua* at the river Elbe. This species displays a remarkable phenotypic plasticity, comparable to successful weeds such as e. g. *Chenopodium album* (PALMBLAD 1968, MAILLETTE 1985, MAHN & UDWAL 1991). The production of flower buds ranged between 5 and 50000 buds per plant and shoot length varied between 4 cm and 250 cm. Therefore, *A. annua* cannot only grow on sparsly grown sand banks, but is also fit to compete on the higher bank regions with tall species such as *Atriplex sagittata*. Since even smallest individuals reproduce, the species can colonize nutrient poor soils. So, the relatively low demands on its environment paired with the ability to exploit resources successfully help *A. annua* to colonize different sites of the river banks. In combination with the production of extremely high amounts of diaspores and the possibility of long distance dispersal in riparian habitats, *A. annua* became established along the Elbe river banks within 30 years. The remarkable phenotypic plasticity enables this species to colonize also ruderal sites.

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