University of Rostock, Faculty of Agricultural and Environmental Sciences, Crop Health, Rostock, Germany

# Important maize weeds profit in growth and reproduction from climate change conditions represented by higher temperatures and reduced humidity

Kristian Peters*, Bärbel Gerowitt

## Summary

Climate change is predicted to result in rising temperatures and reduced precipitation during spring and summer in Central Europe. As a consequence, crops and weeds will be affected. Our study focuses on the three weed species in maize *Amaranthus retroflexus*, *Echinochloa crus-galli* and *Setaria viridis*. These weeds occur numerously in European maize fields and populations are likely to further increase. Yet, there is a lack of knowledge about particular biological strategies of the weeds. Our study focuses on how the weed species respond biologically to the climate change conditions. Experiments were conducted in two climate chambers with a 2 °C difference in temperature and the warmer one with 13 % less humidity. Emergence, development, biomass and seed production were determined of the weeds grown individually in pots and grown within maize. All tested weed species were taller during the first weeks under the climate change scenario. At later growth phases there was a trade-off between traits measured during vegetative growth and at the time when seeds were produced. To summarize the results, the weed species profited in the order *E. crus-galli*, *S. viridis* and *A. retroflexus* from the climate change conditions. Knowledge of the weeds biological responses to the predicted conditions helps to reduce their long-term population development by targeting crop protection measures at specific growth phases of the weeds. To ensure control of the tested weed species under climate change conditions various weed management strategies are necessary.

## Introduction

Climate change will result in rising temperatures (TUBIELLO et al., 2007) and modified precipitation (ROBINSON and GROSS, 2010). Summer droughts will be more likely and will affect weeds in spring-sown crops. According to PATTERSON et al. (1999) temperature and precipitation are the most important factors for the geographical distribution, the growth and the competitive abilities of weeds. Our study focuses these two climate variables. We have chosen three important Central European $C_4$ weeds in maize: *Amaranthus retroflexus*, *Echinochloa crus-galli* and *Setaria viridis*, since currently a shift of the local weed flora is occurring in favour of weeds of the $C_4$ photosynthesis type. Most of these weeds are late germinators and emerge from early summer to early autumn. Thus, they are considered thermophilous in Central Europe and these weeds are expected to migrate further north with changes in climate conditions (WALTHER et al., 2002). These weeds are already most numerous and most competitive in maize fields of Southern Europe (NOVÁK et al., 2009). They may also extend their damage potential in spring-sown crops, such as maize, under the predicted future conditions in Central Europe. Therefore, our study focuses on three thermophilous $C_4$ weeds, whose future status and biological strategies are not well understood for Central European populations.

*Amaranthus retroflexus* L. (redroot pigweed) is a successful weed in maize (OVEISI et al., 2013). Fast growth and indeterminate flowering enable a single plant to produce up to 500,000 seeds (STECKEL et al., 2004). The reaction of European populations to warming and different humidity is not well studied so far (HYVÖNEN, 2011). Nevertheless, because the species produces more biomass and more seeds in a warmer climate in North America and Canada (SCHIMPF, 1977), we expect the species to develop better with warmer conditions in Europe as well (KIGEL et al., 1977; OVEISI et al., 2013).

*Setaria viridis* (L.) P. Beauv. (green foxtail) is currently the most wide-spread species of the *Setaria* genus in Europe (DEKKER, 2003). It generally emerges after the last herbicide treatment in maize fields. Thus, plants are often not affected by herbicides (MEHRTENS et al., 2005; BECKIE and TARDIF, 2012). A high genetic variability enables the species to grow under a great range of temperatures (DEKKER, 2003). Plants of North-American populations produce less biomass but increase generative reproduction under warmer conditions (SWANTON et al., 1999).

*Echinochloa crus-galli* (L.) Beauv. (barnyard grass) exhibits high phenotypic plasticity (BARRETT and WILSON, 1981; MAUN and BARRETT, 1986). Central European populations are most competitive under high temperatures, high nutrient availability and mid level humidity (OTTE et al., 2006). The species benefits from higher temperatures but not from dry conditions (BARRETT and WILSON, 1981; CHAUHAN and JOHNSON, 2011).

Most studies focus on the development of weeds under various agricultural practices or on their resistance to herbicides (BARRETT and WILSON, 1981; POTVIN, 1986; CHAUHAN and JOHNSON, 2011). With a special focus on European populations, we ascertain a lack of biological knowledge concerning the vegetative development, the development speed and the generative reproduction for the studied weeds under climate change conditions. The aim of our study is to explore how the three species perform under the predicted future conditions and which distinct biological strategies they realise. Furthermore, this study attempts to assess which biological weed properties are important with climatic changes. Based on these biological data, a better framework for weed management and crop protection can be devised. To achieve this, the effects of the raised temperature and less humidity on the weeds were studied combined in the experiment.

## Materials and methods

The three weed species *Amaranthus retroflexus*, *Setaria viridis* and *Echinochloa crus-galli* used in the experiments were collected near Göttingen, Germany in 2007. Seeds originated from different field populations in that area and were stored for two years until the experiments started in 2009. Preliminary germination tests showed high germination rates (approx. 50-75 % germination percentage). Thus, the seeds were not subjected to any special treatment.

The experiment was conducted in two climate chambers, 2.15 m in width, 3.45 m in length and 2.10 m in height. Temperature, humidity and light were independently adjustable. The first climate chamber had temperatures that represent the conditions of the current

* Corresponding author

climate of Northern Germany. The humidity (air moisture content) was raised slightly with water nozzles when compared to the second chamber that represented predicted future climate conditions (Tab. 1). Mean humidity was set to 68 % in the climate chamber with current conditions and was 13 % lower in the other chamber due to the disabled water nozzles. As light source ten Phillips Son-T Agro 400 were used, which were embedded in the ceiling of each climate chamber. Light levels at the centre of the chambers were 24,900 lux measured 90 cm from the ground and 120 cm below the lights. This is equal to a PPFD of approx. 400 $\mu$mol/s/m$^2$ at the aforementioned distance.

The chosen conditions were based on the A1B scenario of the IPCC (2013), which predicted an increase in temperatures of 2 °C until 2070 for Central Europe and less humidity during summer months. Thus, daily minimum and maximum temperatures were always set 2 °C higher in the second chamber (Tab. 1). The day-length was the same in both chambers, but adjusted over time to simulate an advancing season. To ensure the intended climate levels (Tab. 1), temperate and humidity in the chambers were continuously adapted and monitored with data loggers 5 cm above ground and with additional air temperature sensors 1.60 m above ground.

Each climate chamber had two large plant tubs, 1.30 m x 1.10 m in size and a depth of 0.90 m. The bottom of each tub was equipped with a 2 cm thick layer of small stones to allow excessive water to run off through small holes at the bottom-side of the tubs. Gauze was stretched above the stone layer to prevent soil from the 60 cm thick soil layer above to agglutinate at the bottom. Maize seeds were sown directly into the tubs' soil (at a depth of 3 cm) at the beginning of each replication to simulate a row typical for maize fields (80 cm row distance, 10 cm plant distance in row). These tubs were already installed for preliminary studies and thus were equipped with an established soil-bed under the two climate conditions. Due to the resulting weight, they were immovable between the chambers. Therefore, the tubs rested in the same climate chamber under the same conditions in time of the experiment. The tubs were fertilized with 90 g Compo Hakaphos® Blue (equal to 135 kg N and 90 kg P per ha) before the start of each replication and again before weed seedlings were planted.

For studying the emergence of the weed species and to provide seedlings for further experiments, 130 seeds of each species were sown at a soil depth of 1 cm in five germination trays in each climate chamber at the same time. The number of seedlings was counted every day (Fig. 1).
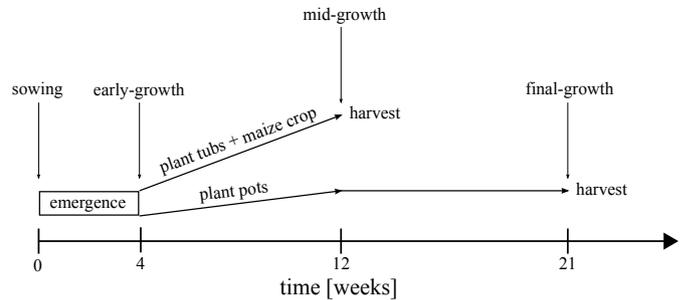


**Fig. 1:** Overview of the treatments performed in each replication in both climate chambers.

In order to characterize, compare and correlate processes during emergence, various parameters were calculated (GRUNDY, 2003). For predicting the cumulative emergence of seedlings, Growing Degree Days (*GDD*) were calculated (DORADO et al., 2009):

$$GDD = \left( \frac{T_{max} + T_{min}}{2} \right) - T_b$$

where $T_{max}$ and $T_{min}$ are the daily maximum and minimum temperatures measured by the dataloggers in the climate chamber. $T_b$ is the base temperature for each weed. The $T_b$ values were taken from various authors: $T_b$=4.0 °C for *A. retroflexus* from GARDARIN et al. (2009), $T_b$=6.2 °C for *E. crus-galli* from GUILLEMIN et al. (2013) and $T_b$=6.1 °C for *S. viridis* from GARDARIN et al. (2010).

In order to estimate and compare the progress of seedling emergence, Mean Emergence Time (*MET*) and Emergence Rate Index (*ERI*) were calculated as follows (DORADO et al., 2009):

**Tab. 1:** Conditions in the two climate chambers. Values given after ± are the mean variations between replications.

| period | factor | chamber with current climate | chamber with predicted future climate |
|---|---|---|---|
| 0-2 weeks | night/day temperature | 7 °C/13 °C ±0.3 % | 9 °C/15 °C ± 0.6 % |
| | night/day length | 12/12 | 12/12 |
| | night/day humidity | 70 %/66 % ± 1 % | 58 %/52 % ± 3 % |
| 2-6 weeks | night/day temperature | 9 °C/18 °C ± 0.3 % | 11 °C/20 °C ± 0.6 % |
| | night/day length | 14/10 | 14/10 |
| | night/day humidity | 70 %/66 % ± 1 % | 58 %/52 % ± 3 % |
| 6-12 weeks | night/day temperature | 11 °C/20 °C ± 0.3 % | 13 °C/22 °C ± 0.6 % |
| | night/day length | 14,5/9,5 | 14,5/9,5 |
| | night/day humidity | 70 %/66 % ± 1 % | 58 %/52 % ± 3 % |
| 12-15 weeks | night/day temperature | 11 °C/20 °C ± 0.3 % | 13 °C/22 °C ± 0.6 % |
| | night/day length | 14/10 | 14/10 |
| | night/day humidity | 70 %/66 % ± 1 % | 58 %/52 % ± 3 % |
| 15-21 weeks | night/day temperature | 9 °C/18 °C ± 0.3 % | 11 °C/20 °C ± 0.6 % |
| | night/day length | 13/11 | 13/11 |
| | night/day humidity | 70 %/66 % ±1 % | 58 %/52 % ± 3 % |

$$MET = \frac{\sum\limits_{i=1}^{n} N_i t_i}{\sum\limits_{i=1}^{n} N_i}$$

$$ERI = \frac{\sum\limits_{i=1}^{n} N_i}{MET}$$

where $N_i$ represents the newly emerged seedlings since the previous count, $t_i$ represents the *GDD* after sowing and $n$ is the number of sampling occasions.

For characterizing emergence speed, the emergence rate at mid emergence ($v_{50}$) was additionally calculated (GARDARIN et al., 2011, modified):

$$v_{50} = \frac{m \cdot b \cdot ln(2)}{2 \cdot (D_{50} - D_0)}$$

where $m$ is the number of emerged seeds until mid emergence, $b$ is a shape parameter correlated with the emergence rate at mid emergence, $D_0$ represents the day after sowing on which first emergence was recorded, and $D_{50}$ is a factor which represents the day on which 50 % the total emerged seedlings were recorded.

The prediction curve of the cumulative emergence $G_i$ was fitted (GARDARIN et al., 2011, modified):

$$G_i = m \left[ 1 - e^{-ln(2)\left(\frac{D_i - D_0}{D_{50} - D_0}\right)^b} \right]$$

where $D_i$ represents the day of measurement.

Seedling height of every emerged seedling was determined after 4 weeks (BBCH stage 15) (Fig. 1, early-growth phase). Ten randomly chosen seedlings of each species were then planted in pots in each climate chamber to study further development. Pots were 30 cm in diameter and 20 cm deep. Another 10 seedlings of each weed were put in the two plant tubs between the maize rows in each climate chamber. Sampling and positioning of the weeds was random.

Both maize and weeds in the large plant tubs were harvested at the end of the mid-growth phase (Fig. 1, beginning of flower onset of maize, BBCH stage 53, after approx. 12 weeks). Plant height and above ground dry mass were determined for each weed and maize plant. Height and development stage (BBCH, HESS et al., 1997) were additionally determined for the weeds in the smaller plant pots.

The remaining weeds in the pots were harvested at the reproduction phase (Fig. 1, after 21 weeks) and their height and vegetative above ground dry mass (without seeds) were determined. Panicles, tillers and seeds of all weed plants were also counted.

The experiment involved three replications, which were conducted consecutively. Each replication in time was set-up independently. The calculated emergence coefficients were tested for significant differences using the t-test (Fig. 3). As described above, two tubs were available within each climate chamber. Hence, the involved factor levels (chambers, tubs) were not arranged orthogonally, excluding classical ANOVA approaches. Instead, for comparing the biological parameters at the end of the early and mid-growth phases, as well as the reproduction phase (Tab. 2, 3), Linear Models with Random Effects (LMER) were used. In these models, climate (temperature and humidity combined) was chosen as fixed factor, whereas replications in time were introduced as random factor. When tubs were involved (Tab. 4), they were also introduced as random factor. Each weed species was tested separately for significant differences between the climate chambers. To investigate the properties of the random coefficients of the LMER, probability values for the parameters of models fitted with LMER were calculated with a Monte Carlo Markov Chain (MCMC) approach, choosing 10,000 sample simulations of the model (BAAYEN et al., 2008). Distribution and homogeneity of variance were visually checked with the help of histograms and diagnostic plots. Data were log or square root transformed before statistical analysis if conditions of normality were not met or to improve homogeneity of variances. The residual vs. fitted plots and the normal qq-plots were examined for each tested parameter according to FARAWAY (2006). Statistical analysis was carried out with the software R (IHAKA and GENTLEMAN, 1997). The additional packages languageR, Hmisc, agricolae and lme4 were used.

## Results

### Seedling emergence

In both climate chambers maize seedlings emerged regularly at the 11th day after sowing, whereas first weed emergence was recorded between the 9th and 13th day after sowing (Fig. 2). First seedlings of *Amaranthus retroflexus* appeared about one day earlier in the climate chamber with future conditions. Only for *Setaria viridis* a significantly different $D_0$ was measured. Seedlings emerged two days earlier under the climate change scenario. Whereas the Mean Emergence Time (*MET*) was significantly different for *A. retroflexus* and *S. viridis* between both climate chambers (Fig. 3), seedlings of

**Tab. 2:** Comparison of the influence of predicted future conditions on plant height [cm] at the end of **early-growth phase**, **mid-growth phase** and **reproduction phase** of plants grown in pots for the three replications, mean and standard error (se) are given for predicted future and current climate, significant $p_{LMER}$-values are bold.

| plant height [cm] / phase | | early-growth phase | | mid-growth phase | | reproduction phase | |
|---|---|---|---|---|---|---|---|
| weed species | measurement | predicted | current | predicted | current | predicted | current |
| *A. retroflexus* | mean | 3.12 | 1.83 | 31.33 | 23.39 | 26.12 | 24.38 |
| | se | 0.07 | 0.04 | 2.21 | 3.08 | 1.85 | 2.42 |
| | $p_{LMER}$ | **0.001** | | **0.040** | | 0.577 | |
| *E. crus-galli* | mean | 13.84 | 8,44 | 92.50 | 73.22 | 107.77 | 102.15 |
| | se | 0.23 | 0.15 | 2.46 | 1.39 | 2.59 | 3.53 |
| | $p_{LMER}$ | **0.001** | | **0.001** | | 0.130 | |
| *S. viridis* | mean | 3.17 | 1.92 | 45.61 | 37.33 | 89.50 | 83.04 |
| | se | 0.08 | 0.05 | 2.31 | 1.73 | 4.98 | 3.23 |
| | $p_{LMER}$ | **0.001** | | **0.002** | | 0.186 | |

**Tab. 3:** Parameters with significant results of plants grown in pots at the end of **reproduction phase** for the three replications; mean and standard error (se) are given for predicted future and current climate, significant differences LMER ($p_{LMER}$) are bold.

| weed species | | *A. retroflexus* | | *E. crus-galli* | | *S. viridis* | |
|---|---|---|---|---|---|---|---|
| factor | measurement | predicted | current | predicted | current | predicted | current |
| panicles | mean | 17.50 | 18.35 | 34.96 | 19.12 | 17.50 | 16.42 |
| per plant | se | 3.18 | 4.92 | 4.20 | 1.44 | 1.30 | 1.61 |
| | $p_{LMER}$ | 0.705 | | **0.001** | | 0.418 | |
| tillers | mean | 2.85 | 2.23 | 15.81 | 18.23 | 15.31 | 15.8 |
| per plant | se | 0.43 | 0.40 | 0.81 | 0.76 | 0.91 | 1.39 |
| | $p_{LMER}$ | **0.035** | | **0.030** | | 0.870 | |
| panicles | mean | 6.05 | 6.60 | 2.35 | 1.07 | 1.18 | 1.14 |
| per tillers | se | 0.52 | 1.12 | 0.29 | 0.08 | 0.08 | 0.10 |
| | $p_{LMER}$ | 0.663 | | **0.001** | | 0.458 | |
| number of seeds | mean | 2135.38 | 2654.46 | 4996.73 | 3553.58 | 2926.35 | 2401.12 |
| per plant | se | 290.76 | 546.14 | 545.57 | 410.86 | 322.13 | 233.77 |
| | $p_{LMER}$ | 0.956 | | **0.002** | | 0.123 | |
| seeds | mean | 73.28 | 46.03 | 150.97 | 187.84 | 171.94 | 171.71 |
| per panicles | se | 7.11 | 4.22 | 7.15 | 17.94 | 18.66 | 19.25 |
| | $p_{LMER}$ | **0.004** | | **0.024** | | 0.976 | |

**Tab. 4:** Parameters of plants grown in tubs at the end of **mid-growth phase** for the three replications; mean and standard error (se) are given for predicted future and current climate, significant differences LMER ($p_{LMER}$) are bold.

| weed species | | *A. retroflexus* | | *E. crus-galli* | | *S. viridis* | | Maize | |
|---|---|---|---|---|---|---|---|---|---|
| factor | measurement | predicted | current | predicted | current | predicted | current | predicted | current |
| height [cm] | mean | 13.37 | 14.15 | 75.33 | 48.97 | 24.30 | 19.40 | 162.55 | 141.05 |
| | se | 1.14 | 1.28 | 3.09 | 2.03 | 2.11 | 1.65 | 2.78 | 1.91 |
| | $p_{LMER}$ | 0.650 | | **0.001** | | **0.034** | | **0.001** | |
| dry mass [g] | mean | 1.06 | 1.34 | 8.17 | 3.94 | 0.76 | 0.57 | 78.91 | 62.15 |
| | se | 0.23 | 0.16 | 1.51 | 0.62 | 0.11 | 0.06 | 9.96 | 7.71 |
| | $p_{LMER}$ | 0.245 | | **0.002** | | **0.026** | | **0.006** | |
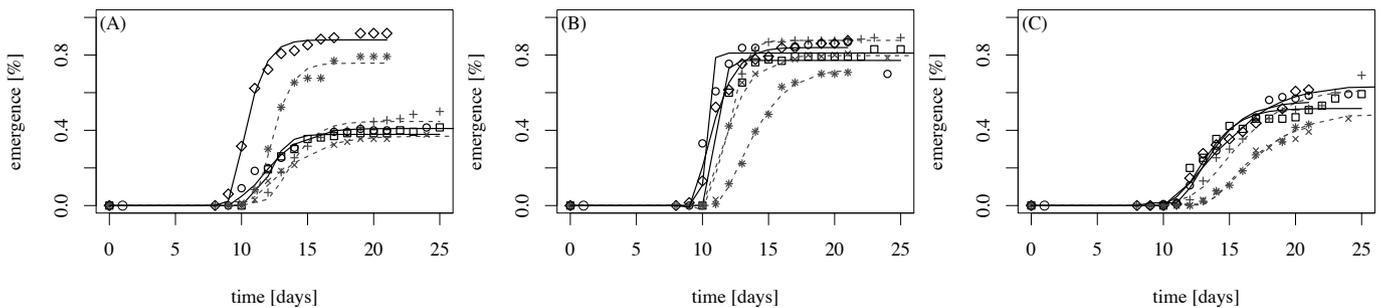


**Fig. 2:** Cumulated **emergence** of weed seeds over time for (A) *Amaranthus retroflexus*, (B) *Echinochloa crus-galli*, (C) *Setaria viridis* for the three replications; square, diamond and circles mark readings in the climate chamber with predicted future conditions; +, x and * mark readings in the climate chamber with normal conditions; normal lines represent fitted curves under predicted future climate, dashed lines represent fitted curves under current climate.

*Echinochloa crus-galli* appeared nearly at the same time in both climate chambers.
The time span from sowing to mid emergence ($D_{50}$) differed significantly for *S. viridis* (Fig. 3). A $D_{50}$ of 13.8 days was recorded in the chamber with the predicted future conditions compared to 16.4 days in the other chamber. The $D_{50}$ of *E. crus-galli* was reached 1.8 days earlier and the $D_{50}$ of *A. retroflexus* was reached 1.5 days earlier under the climate change scenario (Fig. 3). The mid emergence rate ($v_{50}$) differed not significantly for all species between both climate chambers. However, *Echinochloa crus-galli* had the highest $v_{50}$ ratio
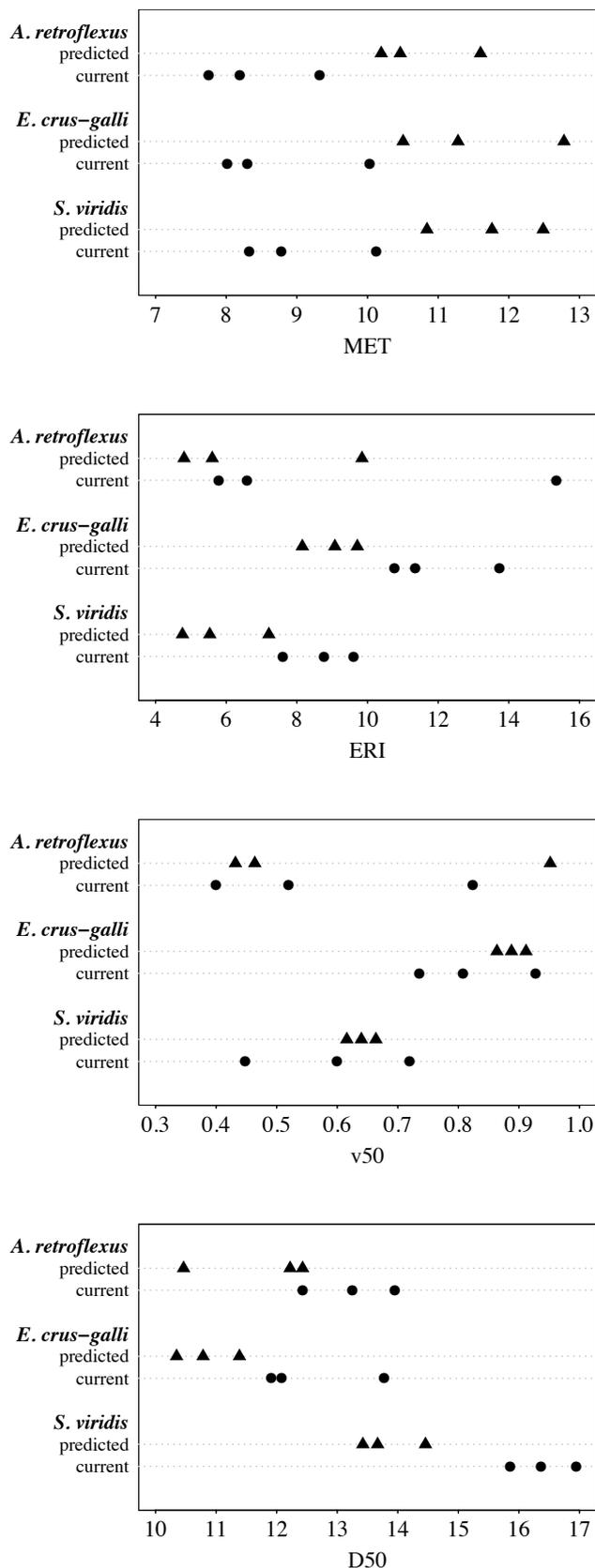
**Fig. 3:** Parameters characterising **emergence**: *MET* = Mean Emergence Time, *ERI* = Emergence Rate Index, $v_{50}$ = emergence rate at time of mid emergence, $D_{50}$ = the calculated day on which 50% the total emerged seeds have emerged; $n$ = 3, triangles show values under predicted future conditions, circles show values recorded under current conditions.

(0.8), whereas *S. viridis* had the lowest $v_{50}$ ratio (0.1) of the tested species (Fig. 3).

The number of emerged *A. retroflexus* seedlings increased with each replication. Whereas in replication one, the ratio was 41 % for current climate conditions and 50 % for the chamber with predicted future conditions after 4 weeks, the ratio was 79 % vs. 91 % in replication three (Fig. 2). The emergence rate of *E. crus-galli* seedlings was high and differences between replications were small four weeks after sowing. A rate of 75 % was reached after four weeks (Fig. 2). For *Setaria viridis* the rate was 58 % after four weeks in both chambers (Fig. 2). Only *E. crus-galli* had a significantly different Emergence Rate Index (*ERI*). The seedlings emerged quicker and more uniformly in the chamber with the predicted future conditions. *A. retroflexus* showed no significant differences (Fig. 3).

**Development without crop competition of plants grown individually in pots**

*Early-growth phase:* Plants of all three species were significantly taller in the climate chamber with the predicted future conditions (Tab. 2). Whereas seedlings of *E. crus-galli* developed quite regularly, the variance of seedling height and development stage of *S. viridis* and *A. retroflexus* were more conspicuous between the different replications. The mean plant height of *E. crus-galli* seedlings was 14 cm in the chamber with the climate change scenario and 8 cm in the chamber with current conditions. Seedlings of *A. retroflexus* and *S. viridis* were significantly smaller under current conditions: 2 cm vs. 3 cm (Tab. 2).

*Mid-growth phase: Amaranthus retroflexus* showed a rather undefined growth habit. Most plants did not grow upright, were less elongated and branched more than plants grown under similar conditions in the field. Plants were also slightly smaller in the climate chamber with current conditions (Tab. 2). No significant differences in development stages between the two climate chambers were found, since first flower buds were developed after only 4 to 5 weeks in both chambers (BBCH stage 71). *Setaria viridis* grew taller under the climate change scenario (Tab. 2). The average time of panicle development was the same in both climate chambers, although variance was higher in the chamber with the predicted future conditions (data not shown). *Echinochloa crus-galli* developed panicles significantly earlier (1 to 2 weeks) under the climate change scenario. Plants grown under the climate change scenario were at stage 67, whereas plants grown under current conditions were still at BBCH 55 on the mean average. Plant height was also increased under the climate change scenario (Tab. 2).

*Reproduction phase:* We observed better growth of all species at the end of early- and mid-growth phase under the climate change scenario. Nevertheless, this relationship diminished at the end of the reproduction phase (Tab. 2). *Amaranthus retroflexus* plants still did not grow upright in both climate chambers (see above). We did not find any significant differences in plant height, panicles and seed production for *A. retroflexus*. The number of seeds per plant varied strongly between plants and replications. However, plants had more tillers per plant and more dry mass under the climate change scenario (Tab. 3). *Echinochloa crus-galli* developed quicker under predicted future conditions. First panicles were visible in the 11th week and flowering occurred over a longer period compared to the chamber with current conditions, which resulted in 550 more seeds/plant under the climate change scenario. The weed developed significantly more panicles with more seeds under the climate change conditions (Tab. 3). *Echinochloa crus-galli* also produced slightly less tillers under this scenario, which resulted also in slightly less vegetative dry matter (Tab. 3). The species was also the tallest of the three
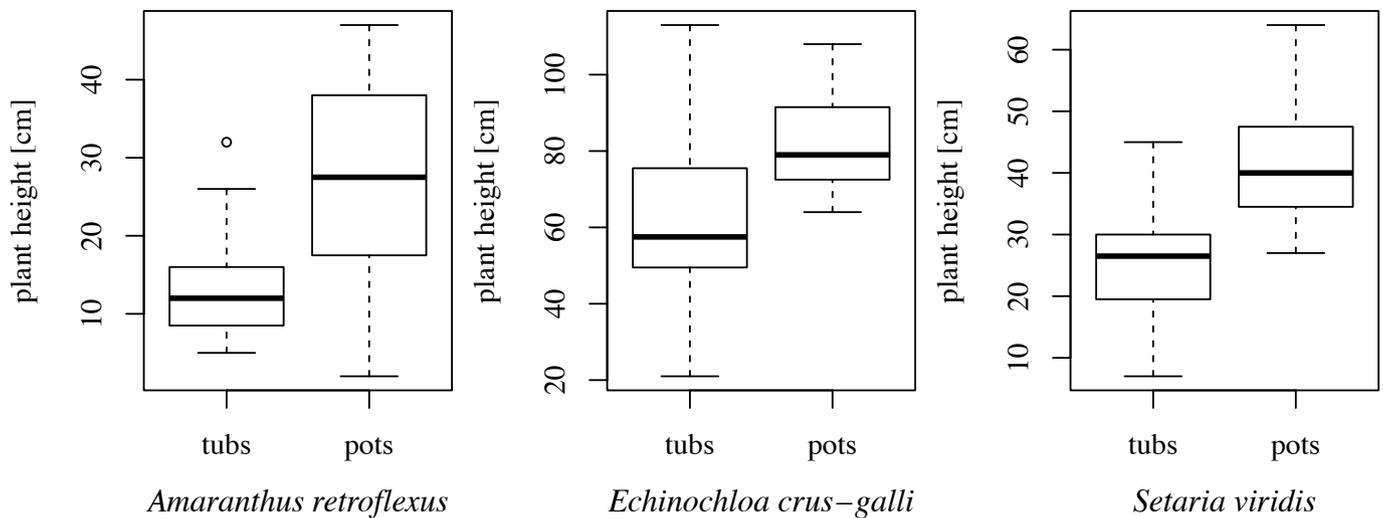
**Fig. 4:** Comparison of the plant height of weeds grown in pots and tubs at the end of **mid-growth phase** for both climate chambers for the three replications.

weed species (Tab. 3). *Setaria viridis* produced first panicles after 17 weeks. They occurred at the same time in both climate chambers. Plant height, the number of panicles and tillers were rather homogeneous after 21 weeks in both climate chambers. The weed tended to develop slightly more seeds under climate change conditions (Tab. 3). Vegetative dry matter was not affected (Tab. 3).

### Development with crop competition in the large plant tubs

Plant height and dry mass of *A. retroflexus* grown in the maize rows in the large plant tubs did not differ significantly between the climate chambers. Both plant height and dry mass were slightly less in the chamber with the predicted future conditions (Tab. 4). Plants of *E. crus-galli* were significantly taller in the chamber with the predicted future conditions. This was also reflected by an increase in dry matter content (Tab. 4). Average height and dry mass of *S. viridis* plants differed strongly between the three replications. Plants grew taller and produced also more dry mass under the climate change scenario (Tab. 4). The maize plants were significantly taller when grown under the predicted future conditions. However, above ground dry mass was similar between both climate conditions (Tab. 4).

All weeds were significantly smaller and had significantly less dry mass when grown in competition with maize in the large plant tubs compared to plants grown individually in smaller pots (Fig. 4). This was true for both climate chambers. Weed plants in the tubs and the pots had the same development stage.

## Discussion

For discussing and evaluating the results, it is crucial to acknowledge that the two factors temperature and humidity were combined in our study. Consequently, we link the discussion mainly to these factors and conclude for climate change.

### Seedling emergence

The growth, speed and timing of weed seedling emergence are important factors for the development and seed production of weeds in maize (SARABI et al., 2011). Our results showed different emergence for all three species, which resulted in species-specific strategies to cope with the predicted future conditions. In summary, the predicted future conditions are beneficial for the tested weed species, as most of their emergence factors were enhanced under these conditions.

This mainly leads to enhanced vegetative growth at later development phases (see below).

The emergence results confirm that *A. retroflexus* seedlings typically emerge under warmer conditions later in the season (STECKEL et al., 2004). Nevertheless, *Amaranthus retroflexus* is also able to germinate in early spring with lower rates (BASKIN and BASKIN, 1985). As the emergence of seedlings is strongly affected by their parent plants, our findings also represent conditions the populations experienced near Göttingen, in Central Germany (KIGEL et al., 1977). The number of emerged *A. retroflexus* seedlings almost doubled in both climate chambers in the third replication. Such high emergence rates are untypical for *A. retroflexus* under low temperatures (GUILLEMIN et al., 2013). Conditions for emergence were equal in all replications. Thus, we expect the dormancy status of the weeds had changed over time of storage. Seeds were stored for a total of 4 years and 2 months before the last replication started. Some other weed species show lower dormancy the longer their seeds were buried (BASKIN and BASKIN, 1985). Our findings that *A. retroflexus* changed its dormancy status over time of storage should be verified by another experiment, as dormancy changes were not reported by other authors (THOMPSON et al., 1997; OMAMI et al., 1999).

Seedlings of *E. crus-galli* are able to grow faster than maize once they find sufficient conditions during the first four weeks. We found that *E. crus-galli* seedlings were less dependent on temperature and humidity, when compared to maize seedlings. CHAUHAN and JOHNSON (2011) reported similar results. The resulting high $v_{50}$ ratio is a good indicator for the effects of higher thermal time (GARDARIN et al., 2009).

The relatively low emergence rate of *Setaria viridis* seedlings confirm that the species typically germinates under warmer conditions later in the season (DEKKER, 2003) and not simultaneously with the sowing of maize as it was defined by the experiment. This also explains why more seedlings emerged considerably earlier under climate change conditions. Current temperature conditions in Northern parts of Central Europe are still below the considered optimum for the species (WALCK et al., 2011). Therefore, *Setaria viridis* will likely benefit more than the other tested weed species from higher temperatures at emergence.

### Development without crop competition

This series of measurements was performed to study various parameters of the weeds at the most important stages of their life and to

provide answers concerning how weeds perform individually under climate change conditions. We found distinct differences between measurements taken at the time of emergence, at the end of the early and mid-growth phase and reproduction phase. The tested weeds balanced their growth and biomass allocation according to abiotic conditions and competition from neighbouring plants. Their response to the predicted future conditions started to become species-specific with the end of the mid-growth phase.

*Early and mid-growth phase:* All tested weed species benefitted from the predicted future conditions at the end of the mid-growth phase. To conclude, greater plant heights under the climate change scenario suggest an increase in vegetative growth and thus, also enhanced interference capabilities of the weeds during the first weeks of their development. This may give them an advantage over single maize plants.

For *A. retroflexus*, we observed no differences in panicle onset speed between the climate chambers, although findings by KNEZEVIC et al. (2001) and STECKEL et al. (2004) suggest a different relationship. *E. crus-galli* had an earlier onset of flowers and a longer flowering time, which increases the opportunities for outcrossing (CLEMENTS and DITOMMASO, 2011). This is in accordance with other studies (POTVIN, 1986). These phenomena can also occur when seedlings emerge later in the season. Thus, climate change conditions may accelerate the life cycle as described by POTVIN (1986) for *E. crus-galli* and by ORYOKOT et al. (1997), KNEZEVIC et al. (2001) and HYVÖNEN (2011) for *A. retroflexus*. This process results in more fertile seeds at the end of the reproductive stage, but probably not in more biomass.

By contrast, *Setaria viridis* develops panicles after midsummer when photoperiods are getting shorter (DEKKER, 2003). Plants grown in the climate chambers set panicles at the same time as would plants grown under natural conditions (DEKKER, 2003). We observed that the earlier seedlings emerge, the longer they delay development of reproductive parts. Therefore, later emerging arable plants have a shorter vegetative development period (FORCELLA et al., 2000; DEKKER, 2003). Similar behaviour was reported for *A. retroflexus* (COSTEA et al., 2004), but was not confirmed by our experiment for this species.

*Reproduction phase: Amaranthus retroflexus* plants in the climate chambers were creeping near the ground, grew sideward and tillered more, when compared to plants grown in the fields. This growth habit was likely a response on low red and far-red light levels in the climate chamber (COSTEA et al., 2004; GIMPLINGER and KAUL, 2009). Plants grown outside from seeds of the same population did show a normal growth habit (PETERS and GEROWITT, 2014). This could explain why *A. retroflexus* was less competitive in comparison to the other two weed species. Some *A. retroflexus* plants also seemed to lack senescence. Unlike *E. crus-galli* and *S. viridis*, this species did not match its life cycle to the length of the season (SAUER, 1967). Even towards the end, some plants were still green and had not finished ripening. Some plants just grew and grew. As a result, we have not found differences in seed production and we can only partly confirm with HYVÖNEN (2011), who reported that raised temperatures enhance seed output but not overall growth.

*Echinochloa crus-galli* is better suited to the predicted future conditions because plants had more panicles and tillers under these conditions. This resulted in totally more seeds per plant (BARRETT and WILSON, 1981). If arable cropping conditions allow, the species will likely extend its seed bank. This is especially the case under continuous maize cropping (FRIED et al., 2010). Since we have not found any differences in vegetative biomass, we assume that *E. crus-galli* mainly invests the possible benefits of warmer conditions into reproduction.

*Setaria viridis* is well adapted to current and future climatic conditions and can make use of its phenotypic plasticity (DEKKER, 2003). We observed higher variances of plant parameters throughout the replications under the climate change scenario. Since several biotypes are typical for the genus *Setaria*, the high variance reflects genetic plasticity within the used *Setaria* population (DEKKER, 2003). A future climate may select for certain ecotypes that are better suited for future conditions, thus enhancing fitness. Our results are in accordance with SWANTON et al. (1999), who reported less biomass but increased reproductive output under warmer conditions. For *S. viridis*, we determined also a slight increase in seed production per plant and less dry matter content per plant in the chamber with predicted future conditions. However, higher temperature difference between the climate chambers may have been needed for significant results (DOUGLAS et al., 1985; SWANTON et al., 1999).

In summary, although the responses were species-specific, *E. crus-galli* and *S. viridis* had higher reproductive output under the scenario with predicted future conditions. This may lead to better long-term population development, as the weeds are able to build-up their seed banks.

**Development under crop competition**

This series of measurements was performed to study the effect of maize competition on the vegetative development of the weeds under climate change conditions. The broad phenotypic responses of E. *crus-galli* and *S. viridis* when grown with maize suggest that they likely will increase their success in maize when cropped under climate change conditions.

Plants of *A. retroflexus* grew even more deformed as single plants grown in the smaller pots (see above). Contrarily, OTTE et al. (2006) reported that *A. retroflexus* is highly competitive even when shading occurs. It is also possible that temperatures in the climate chambers were still too low for the plants (GIMPLINGER and KAUL, 2009; HYVÖNEN, 2011; OVEISI et al., 2013).

Under the maize competition, *S. viridis* was able to balance growth to match optimally the low light levels. Plants grown in the smaller pots showed no differences in habit and other phenological properties compared to plants grown together with maize. This result confirms studies of DEKKER (2003). However, we cannot confirm the reported result that *S. viridis* responds to increasing shade levels by reducing tiller production (DOUGLAS et al., 1985; DEKKER, 2003). The determined high phenotypic plasticity may enable the weed to adapt to a broad range of changing conditions.

Of the three weed species investigated, *E. crus-galli* was the least affected in growth and development by the shading of maize. Compared to plants grown individually in the smaller pots, the weed balances the low light availability with growing upwards instead of tillering. The species is able to adapt fast to ecological factors such as shading, because of its broad genome, proliferation and crop mimicking. Nevertheless, BARRETT and WILSON (1981) also showed that high phenotypic plasticity may result in differences in tiller production of *E. crus-galli*.

**Implications for crop protection**

From the predicted future conditions *Echinochloa crus-galli* profited most, followed by *Setaria viridis*. *Amaranthus retroflexus* was the least benefiting species of the three tested weeds possibly due to the artificial conditions in the climate chambers. In detail, our study revealed that each weed species responded differently to changes in climate conditions.

Narrow crop rotations and continuous cropping of maize are likely in Central Europe in the future (MEHRTENS et al., 2005; WEBER and GUT, 2005; FRIED et al., 2010). In subsequent years, *S. viridis* and

*E. crus-galli* will likely build up their seed banks due to better emergence and higher seed output (BARRETT and WILSON, 1981; DEKKER, 2003). Better growth and faster vegetative development when grown within maize under climate change conditions will also lead to better long-term population development of the weeds in the future (DOUGLAS et al., 1985).

The results of our study indicate that under future climate conditions various weed management strategies are needed to ensure control of the tested weeds (OLESEN and BINDI, 2002; PETERS et al., 2014). For agricultural purposes, we suggest to integrate management practices such as variations in the sowing date of maize or in the choice of cultivars that result in timely harvesting, and thus reduce the chance for the late emerging weeds to fully develop and produce seeds under climate change conditions. A challenge for maize breeding is to select for fast growing and developing cultivars, since our study revealed a trade-off between the vegetative growth of the weed species and their generative reproduction when cropped together with maize (SARABI et al., 2011). Farmers themselves should avoid short crop rotations with maize alone or other late spring sown crops. Continuous cropping of this type of crop will select for particularly prolific biotypes of *S. viridis* and *E. crus-galli* (BARRETT and WILSON, 1981; DEKKER, 2003). Furthermore, we propose that necessary herbicide treatments should be applied late in the season to cover late emerging weed cohorts with high temperature requirements, especially those of *S. viridis* (DEKKER, 2003; BECKIE and TARDIF, 2012).

## Conclusions

Climate change exerts impacts on weeds during their whole life cycle. In order to get insight into underlying processes, it is necessary to determine biological parameters at the time of emergence, early growth and at the time of reproduction. As a result, climate mediated alterations in the measured biological and demographic attributes allow predictions of long-term population development of the weed species (FRIED et al., 2010; PETERS et al., 2014). Biological properties and demographic data can also be used to predict the population development under future conditions and to improve bioclimatic models (PETERS and GEROWITT, 2014). Furthermore, with future climate change costly crop protection measures at different development stages of the weeds may be needed for successful weed management. In order to continue high production under future conditions, crop protection has to be adapted to the biological responses of weeds to climate change.

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Address of the corresponding author:
Kristian Peters, University of Rostock, Faculty of Agricultural and Environmental Sciences, Crop Health, Satower Straße 48, D-18051 Rostock, Germany.
E-mail: kristian.peters@uni-rostock.de