

Source capacity during flowering affects grain yield of amaranth (*Amaranthus* sp.)

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ABSTRACT

Amaranth is a promising C₄-crop. However, for a wider spread of the crop a better understanding of factors that are influencing yield formation is crucial for optimizing the plant phenotype and enhancing yield. The present study wanted to clarify the effects of assimilate sources and sinks on yield formation by artificially altering source or sink size. Field experiments were conducted in Eastern Austria during three years with three genotypes, applying source-sink manipulation treatments at mid flowering (control, 50% of inflorescence removed, 50% or 100% of leaves removed). At maturity we measured shoot, inflorescence and grain dry matter, thousand kernel mass and number of seeds per plant. An average grain yield level of about 3.5 t/ha dry matter on control plots indicated favorable growth conditions for amaranth in general. The removal of all leaves had a strong detrimental effect on all parameters, but severity of yield reduction due to defoliation differed between genotypes, ranging from –49% to –73%. Contrastingly, 50% flower reduction did not have any significant effects. Also with 50% defoliation no significant yield reduction was observed. We conclude that source strength of amaranth during flowering is more yield limiting than its sink capacity.

Keywords: grain amaranth; source/sink manipulation; defoliation; flower reduction; yield components

Amaranth is a promising C₄-crop that might gain importance particularly with increasing temperatures and drought conditions. Due to the nutritional value of its grain, amaranth is a good supplement for human nutrition and it supplies an alternative food resource in view of increasing cereal food allergies and celiac disease (Berghofer and Schoenlechner 2002, Gimplinger et al. 2007). Germplasm is available with substantial variability in important traits for yield formation (Kaul et al. 1996, 2000). For a wider spread of the crop beyond traditional regions of production high and stable yields are required, but physiological processes and their role in grain production of amaranth are hardly studied. A better understanding of factors that influence yield formation is crucial for optimizing the plant phenotype and enhancing yield (Gimplinger and Kaul 2009).

Although photosynthesis is the main process for growth of a plant, the interaction between assimilate supply (source) and demand (sink) requires

attention. Yield can be limited by source strength, sink capacity or co-limited by both, also depending on the development stages at which limiting factors arise (Hay and Walker 1989, Borrás et al. 2004). Treatments applied for studying source-sink relationship are: reduction or increase of source activity by shading, defoliation or elevating levels of CO₂ or light. Sink capacity is altered by reducing storage organs like flowers, grains, spikes or pods (Evans 1993, Borrás et al. 2004).

Borrás et al. (2004) reviewed source-sink manipulations in maize, soybean and wheat. They concluded that during seed filling the growth of seeds is usually more sink-limited. Maize reacted with decreases in seed dry mass when assimilates were reduced but did not really respond to increases in assimilate availability. Soybean seeds responded very much to manipulations which indicated a large degree of co-limitation by source and sink. Egli and Bruening (2001) suggest source limitation if photosynthesis

is reduced and sink limitation under increased assimilate availability. Seed mass of wheat was only little responsive to changes in assimilate availability (Borras et al. 2004, Cartelle et al. 2006). The removal of spikelets of *Sorghum bicolor* increased the mass per seed, while shading reduced grain yield and seed size (Muchow and Wilson 1976, Gambin and Borras 2007). In sunflower individual seed mass increased with percentage of floret removal but the increase could not compensate the overall yield loss (Charlet and Miller 1993).

No experiments have been published so far, which investigated source-sink relationships in amaranth based on systematic variations of both factors. Due to (i) the specific morphology of amaranth inflorescences; (ii) the comparatively long and undetermined period of seed set that occurs largely in parallel and not clearly preceding to seed fill, and (iii) amaranth's lack of relation with other well-researched crops, results cannot easily be transferred. We hypothesize that changes in sink capacity by removing flowers and young seeds impair seed number and grain yield, but the seed mass might increase. Contrastingly, source reduction by removing leaf area impairs seed number, seed mass and grain yield.

MATERIAL AND METHODS

Field experiments were carried out on a chernozem (silty loam to loamy silt, 2.2% organic

substance, pH 7.6) at the Experimental Farm Groß-Enzersdorf (48°12'N, 16°33'E, 153 m a.s.l.) in Eastern Austria between 2006 and 2008. Mean annual precipitation is 541 mm, mean annual temperature is 10.5°C.

The experiments were designed in split-plots at 2–3 replicates with genotypes on main plots and source-sink manipulation treatments on sub-plots. In 2006 and 2007 only 2 replications could be established due to low plant emergence in parts of the field. The plots were sown with a row distance of 0.375 m. Crop density of 30–35 plants/m² was obtained by hand-thinning. No fertilizer was added due to high soil fertility, especially mineral N supply. Important dates of the experiments are given in Table 1.

Seeds of genotypes adapted to the Pannonian climate were provided by the breeder Dr. Georg Dobos (Zeno Projekte, Vienna). The genotypes belong to different species and differ in plant morphology and time to maturity. Amar is a late maturing, sparsely branching, tall type with dense inflorescences. Neuer Typ is an early maturing, strongly branching, semidwarf type. Anderer Typ is similar to Neuer Typ with respect to grain maturity, but about one week later in flowering. It is hardly branching and shows a rather compact inflorescence. More details are given by Gimplinger et al. (2008) and Gimplinger and Kaul (2009).

At mid anthesis (defined as more than 50% of inflorescence with anthers visible) the following manipulation treatments were applied onetime

Table 1. Important dates within field experiments

		2006	2007	2008
Sowing date		May 10	May 10	May 26
Dates of manipulation treatments (at mid anthesis)	Neuer Typ	July 12	July 03	July 14
	Anderer Typ	July 20	July 16	July 25
	Amar	July 27	July 24	August 11
Harvest dates (at full maturity)	Neuer Typ			
	Defoliated plots	August 16	July 27	August 11
	Other plots	August 16	August 13	September 01
	Anderer Typ			
	Defoliated plots	August 16	August 23	August 21
	Other plots	August 16	August 23	September 18
	Amar			
	Defoliated plots	September 14	September 10	September 09
Other plots	September 14	September 10	October 20	

on 20 plants per plot (10 adjacent plants in each of two neighboring rows):

- Complete defoliation by manual removal of all leaves;
- 50% flower reduction by cutting off segments of 5 cm alternately from all around the inflorescence;
- Untreated control.

In 2007 and 2008 an additional treatment of partly defoliation was introduced with one genotype (Neuer Typ), applying 50% leaf reduction by cutting off every second leaf.

At maturity the treated plants (except the border plants) were hand-harvested by cutting stems at the soil surface. These samples were equivalent to 0.6–0.7 m² per plot. The plants were separated into stems, leaves and inflorescences. The biomass was dried (100°C, up to constant mass) before weighting. The inflorescences were processed by a stationary ear thresher and the grain was cleaned by sieves and a wind separation system. Seed counts (1000 seeds per plot) were made with a Pfeuffer-Contador seed counter, the thousand kernel mass was determined and the number of seeds per plant was calculated. Due to early ripening of the defoliated plants these sub-plots were sometimes harvested earlier.

Data were analyzed using the SAS version 9.1 (Cary, USA) and applying PROC GLM according to the split-plot design across years. For that purpose, the variance of ‘block within year’ was used as error term for testing the years’ main effect. Multiple comparisons of means were performed using the Student-Newman-Keuls test at $P = 0.05$.

The average yield level of our experiments was about 3.5 t/ha of grain dry matter on control plots. A significant year effect was observed. The yield was substantially lower in 2006 compared to the following years. However, no interactions between years and treatments occurred (data not shown).

RESULTS AND DISCUSSION

The removal of all leaves had a strong effect on all analyzed parameters. It reduced grain yield, above-ground biomass and the mass of the inflorescences (Table 2). The lower grain yield resulted from a lower thousand kernel mass and less seeds per plant. We observed that the defoliated plants matured earlier than the other treatments. Contrastingly, flower reduction did not have any significant effects on the parameters under study, which did not differ from the untreated plants.

The severity of yield reduction due to defoliation differed between genotypes, as a significant genotype × treatment interaction could be observed. The yield decrease was for Amar –73%, for Neuer Typ –66% and for Anderer Typ –49% (compared to the control; Table 3). The thousand kernel mass was significantly impaired by defoliation only with Neuer Typ, but the number of seeds per plant was strongly reduced with all genotypes.

Partly defoliation by 50% (only Neuer Typ, 2 years) did not have any influence on the analyzed parameters (Table 4). No significant differences between the manipulated and the untreated plants concerning grain yield and yield components could be observed.

The growth conditions were favorable for amaranth in all experimental years, indicated by an average yield level of about 3.5 t/ha of grain dry matter on control plots. Although the experimental year had an effect on yield, no interactions between years and treatments occurred. Thus we reported consistent effects of our manipulation treatments across different environmental conditions.

Source-sink manipulations were tested at specific development stages of wheat, maize and soybean, and the development stage had a major influence on the obtained yield (Hay and Walker 1989, Egli and Bruening 2001, Borrás et al. 2004). Thus, our

Table 2. Influence of manipulated sources and sinks on yield components of grain amaranth (means across three genotypes and three years)

Treatment	Grain yield	Shoot biomass	Inflorescence biomass	Thousand kernel mass (g DM)	Seeds per plant (calculated)
	(kg DM/ha)				
Control	3489.2 ^a	10 586.7 ^a	6491.3 ^a	0.774 ^a	17 087 ^a
Flower reduction 50%	3215.9 ^a	9920.2 ^a	5845.4 ^a	0.792 ^a	15 672 ^a
Defoliation 100%	1246.3 ^b	6004.7 ^b	3035.3 ^b	0.699 ^b	6197 ^b

Numbers with different letters are significantly different ($P = 0.05$). DM – dry matter

Table 3. Influence of defoliation on yield components of grain amaranth as affected by genotype (means across three years)

Treatment	Genotype	Grain yield	Inflorescence biomass	Thousand kernel mass (g DM)	Seeds per plant (calculated)
		(kg DM/ha)			
Control	Amar	4318.6	7719.0	0.595	27 203
	Neuer Typ	3325.1	6451.3	0.923	12 506
	Anderer Typ	2824.0	5303.5	0.806	11 553
Defoliation 100%	Amar	1178.1	2879.2	0.548	8233
	Neuer Typ	1132.9	2755.8	0.791	4693
	Anderer Typ	1428.0	3470.9	0.758	5665
<i>LSD</i> _{0.05} for interaction treatment × genotype		606.2	1262.7	0.062	3876

DM – dry matter

results are valid for amaranth only if manipulation treatments are applied at the stage when 50% of inflorescences are visibly flowering. At this specific stage we assumed to find most probably the strongest effects on yield and the most important interactions between sources and sinks. The right timing for treatment application in amaranth is complicated by the continuous, overlapping inflorescence growth, flower production and seed development (Aufhammer 2000). Presumably some leaf re-growth may have occurred after the defoliation treatments, but we have no data about new leaf appearance, while the effects of flower re-growth are reflected in our results.

Sink reduction by flower removal. Although 50% of existing flowers and seeds were cut off, this loss of biomass and also photosynthetic area did not influence yield production. The removal of sink tissues at that amount did not have any effect on grain yield and other performance parameters.

In soybean (Liu et al. 2006, Proulx and Naeve 2009), sunflower (Charlet and Miller 1993), and sorghum (Muchow and Wilson 1976), removal of flowers, pods or spikes resulted in increased grain

size but yield reduction. Also in wheat and maize, individual grain mass could partly compensate for reduced grain numbers (Madani et al. 2010, Oveysi 2010) but did not always respond (Borras et al. 2004).

In contrast to these results amaranth showed no increase in seed mass or reduced seed numbers per plant. Compensation between the yield components in reaction to the manipulation did not occur as proposed by Evans (1993). The achieved grain yield could be attributed to both, seed number and seed mass at an equal level as the untreated controls. Obviously the plants were able to compensate the sudden loss of sink capacity completely by subsequently producing new flowers and seeds. Muchow and Wilson (1976) suggested that sorghum spikelets that would abort under normal conditions remain viable when competition is reduced by spikelet removal. This could also apply in the present case of amaranth but was not studied.

Source reduction by defoliation. The complete loss of leaves led to a severe yield reduction due to the loss of the main assimilating tissues. It affected both yield components, seed number per

Table 4. Influence of manipulated sources and sinks on yield components of Neuer Typ (means across two years)

Treatment	Grain yield	Shoot biomass	Inflorescence biomass	Thousand kernel mass (g DM)	Seeds per plant (calculated)
	(kg DM/ha)				
Control	3623.9 ^a	9364.9 ^a	6616.8 ^a	0.941 ^a	12 039 ^a
Leaf removal 50%	3498.5 ^a	8273.1 ^a	5733.7 ^a	0.910 ^a	12 326 ^a
Flower reduction 50%	3417.3 ^a	8501.7 ^a	5899.2 ^a	0.953 ^a	12 662 ^a

Numbers with different letters are significantly different ($P = 0.05$). DM – dry matter

plant and seed mass. Therefore, a strong source limitation can be presumed. This is in accordance with other studies where reduced sources due to shading or defoliation decreased yield and seed mass (Andrade and Ferreiro 1996, Borrás et al. 2004).

Amaranth genotypes, however, showed differences in severity of yield reduction after defoliation. Amar, the genotype with the highest yield under control conditions, showed the largest yield loss (about –70%). The number of seeds per plant was also reduced by 70%, so the yield loss of Amar was mainly due to a lack of individual sinks, as seed mass was not affected. Differences between genotypes might be due to interactions between genotype and environment during the partly divergent periods between defoliation treatment and harvest. Other reasons for the smaller yield reduction observed with Neuer Typ and Anderer Typ might be their smaller growth, comparatively small leaf area and biomass, and earlier ripening compared with Amar. A smaller leaf biomass implies e.g. a smaller reduction of shoot biomass at defoliation.

However, we observed no total breakdown of grain production when all leaves were removed. Thus we assume that some assimilation happened in other plant tissues along with utilization of previously stored assimilates. In a review, Tambussi et al. (2007) concluded that especially under source limitations the photosynthetic activity of ears of C3 cereals contributes substantially to grain yield. Aschan and Pfanz (2003) confirmed the photosynthetic activity of flowers and other green organs for different plants. Costea and Tardif (2003) mentioned that the structure of bracteoles of amaranth suggests photosynthesis as one of their functions.

The partly defoliation at 50% of leaves, however, did not affect any of the yield parameters which indicates that no source limitation occurred at that level of defoliation at least for Neuer Typ. We can hardly estimate from the present data whether the plants with 50% of leaves left were able to provide enough previously stored assimilates for grain filling or they compensated the loss of leaf area by other photosynthetically active tissues, e.g. floral photosynthesis.

To get a detailed picture of production of assimilates in different tissues and their distribution to different sinks, assimilate partitioning could be studied using isotopes to trace the fate of fixed

carbon in the plant. For a first insight into the source-sink relationship in amaranth, we concentrated on the yield effects of source and sink manipulations. Based on these results, we conclude that leaf area of amaranth is more limiting for yield than its sink capacity. This information may help plant breeders in selecting high yielding phenotypes of amaranth. While photosynthetic tissues of amaranth should be well developed for yield securing, inflorescence size can be restricted. This is also compatible with our own findings on crop density effects that indicate agronomic advantages of dense crops of > 50 plants/m² producing comparatively small inflorescences (Gimplinger et al. 2008).

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